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EXPERIMENTAL OBSERVATIONS ON COMPETITION IN GRASSES

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## INTRODUCTION

*Agrostis tenuis* and *Festuca ovina* are the dominant components of the *Agrostis-Festuca* grassland which, from an agronomic point of view, is the most important of the natural hill pastures (Rogers & King, 1972). Although the two plants are found together over large tracts of country, very little is known about their interactions. They do not occur exclusively together, but with a number of other minor species, e.g. *Agrostis canina*, *A. stolonifera*, *Festuca rubra*, *Anthoxanthum odoratum*, *Deschampsia flexuosa* and *Thymus drucei*. The species composition of the vegetation varies widely, due mainly to variations in soil moisture and base status, but nevertheless *Agrostis-Festuca* grassland is distinctive and widespread. It is the vegetation occurring on the Brown Earth soils at Moor House in the Northern Pennines. Because most of the Moor House Reserve is covered by blanket peat, dominated by *Calluna vulgaris*, *Eriophorum vaginatum* and *Sphagnum* spp., the areas of grassland that occur are particularly important for sheep grazing. Rawes & Heal (1978) have estimated that between 47 and 110 g m<sup>-2</sup> of the above-ground vegetation is consumed, a mean of 60% of the annual production. The effect of grazing on the composition of these communities is very important. Exclusion of grazing at Moor House resulted not only in increased primary production, which doubled after 15 years, but also in significant changes in species' composition, with an increase in *Agrostis* and in a minor species component, *Deschampsia flexuosa* (Rawes & Heal 1978).

Within the distinctive vegetation type, the proportion of the two species can vary widely, depending, to some degree, on local soil conditions. *Festuca* has a lower nutrient requirement than *Agrostis* and may therefore be more abundant in nutrient poor areas. It is also more drought resistant (Grime & Curtis 1976).

There is conflicting evidence of the effect of sheep grazing on the two species. Some studies have shown that both species increase under grazing (Welch, 1977). Others indicate, however, that *Agrostis* increases in abundance in exclosures, where grazing is prevented and that the sheep will prefer broader leaved grasses such as *Agrostis tenuis* to narrow leaved species such as *Festuca ovina* (Welch & Rawes, 1964; Perkins *et al*, 1978). Some work done in France (Loiseau, 1974) showed that sheep

preferentially graze fine leaved grasses including *Festuca ovina*. The picture appears to be complicated. An unpublished sandwich course student's report on work carried out in Snowdonia (Milner, *pers. comm.*) showed that sheep preferred to eat the species which was present in the smaller amount. Thus, as the percentage of *Agrostis* in the sward increased above 30%, the intensity of grazing of *Agrostis* rapidly fell. The rate of change of grazing intensity for *Festuca* appeared to be constant, but here also grazing intensity increased as the percentage of the species present decreased. Thus in swards of, say, 30% *Agrostis*/70% *Festuca*, sheep would switch to actively grazing the *Agrostis*, while the reverse would be true in swards where *Agrostis* was the more abundant. The same pattern of sheep behaviour was found on 5 different Snowdonia sites. Conversely, work also done in Snowdonia (Perkins *et al.*, 1978) showed that, although *Agrostis* was the more abundant of the two grasses on the site studied, its increase in biomass through the growing season was considerably less than for *Festuca*, due to preferential grazing of the *Agrostis*.

The reasons for the conflicting evidence may be due to the complex interaction between soil and other environmental factors and grazing conditions, so that results of grazing studies could differ from site to site. In a study of the effects of rabbit grazing on the Pembrokeshire Island of Grassholm, Gilham (1955) showed that where rabbit exclosures were built on sheltered *Agrostis* - *Festuca* sites, almost pure *Agrostis* swards developed, while on more exposed sites, *Agrostis* failed to rise to dominance, even though the two species were originally present in approximately equal amounts. Here *Festuca* became the dominant.

There is also the question of intensity of grazing, which may be an important factor. In studies carried out near Aberystwyth, Jones & Iorweth (1967) reported that after two years at a high sheep stocking rate, *Agrostis* had increased significantly, though it did not do so when sheep stocking density was lower. On the other hand, *Festuca* had increased most markedly in the treatment involving low sheep numbers, and had declined at the highest stocking rate, but it also declined where no sheep were present. In the same experiment, some parts of the plot were left ungrazed, and here there was considerably more *Agrostis* present when mowing was applied once or twice a season, than where mowing was not carried out. Again, the

converse was true for *Festuca*. The conflicting results from different experiments and different sites tends to emphasise the complexity of the situation, and also the highly dynamic nature of the *Agrostis/Festuca* sward.

While clipping and grazing are clearly not interchangeable treatments, in this project I have been growing the two species together in pot experiments, and applying various clipping treatments. Measurements have been made on tiller numbers, and above- and below-ground dry weights, to determine the effects of the treatments on the two species' interactions. There are clear limitations to the extent of this approach - that only one soil type has been used, that only one planting density, and, in particular, that the mixtures have all been of an initial 1:1 composition, i.e. 50% *Agrostis* and 50% *Festuca*.

The experiments have been of the substitutive rather than the additive form. That is, the overall planting density has been kept constant, so that the pots have contained either a monoculture or a 1:1 mixed culture, with the second species substituting for half of the plants in the monoculture pots.

The arrangements are shown below.

A A A A	F F F F	A F A F
A A A A	F F F F	F A F A
A A A A	F F F F	A F A F
<i>Agrostis</i>	<i>Festuca</i>	<i>Mixed</i>
<i>monoculture</i>	<i>monoculture</i>	<i>culture</i>

Competition experiments can also be of the additive type, in which one species' density is kept constant, and the second species added to it. The problem with this approach is that both density and proportion are varied, and it is virtually impossible to separate the two. It is, however, not infrequently used in studies of competition in plants, because of its particular relevance to field situations, as, for example, when one species invades an area occupied by another.

## METHODS

Both species are highly variable, and produce many ecotypes. It was felt, therefore that it was particularly important to use material that was as near as possible genetically identical. Tillers were therefore extracted from a small turf removed from the *Agrostis/Festuca* grassland at Moor House, and subsequently grown and subdivided in trays in the glass house.

Experimental work was confined to the glass house, except where one treatment was returned to a Moor House sheep enclosure to compare growth in a Merlewood glass house with that at the original site.

The pots each contained 3-4kg of John Innes No. 2 compost, which is a relatively rich medium for these grasses, but no further nutrients were added during the course of the experiments. Twelve tillers were planted in each pot in the arrangements shown on page 3 to give an initial planting density of 800 tillers  $m^{-2}$ . The pots were stood in shallow trays, containing gravel, which were kept topped up with water.

In a preliminary trial to test the importance of possible ecotypic variation, *Agrostis* tillers were also removed from a site near Windermere. The growth of the two sources of *Agrostis* under the same experimental conditions was quite different. After 40 weeks, the pots were harvested. In the monoculture the *Agrostis* plants from Windermere produced greater dry weight, but fewer tillers than those from Moor House, and in mixed cultures with *Festuca*, they were more vigorous than the Moor House plants in suppressing *Festuca*. Fine leaved *Festuca* plants generally produced considerably less dry weight than *Agrostis* but also tillered more abundantly. Thus individual tiller weight was lower. Because of the marked difference shown by the two *Agrostis* populations in the preliminary trial, subsequent work was carried out using only the clonal material from Moor House.

## RESULTS AND DISCUSSION

## Experiment 1.

This was planted in February 1976, and extended over two growing seasons. After an initial 3 month establishment period, half the pots were clipped at 2 week intervals to 2cm height. The remaining pots were left unclipped. Harvests were taken six times over the two seasons, and one set of pots was returned to an enclosure at Moor House to compare the unclipped glass house growth at the final harvest with growth made at Moor House over the same period.

Experimental lay-out in the glass house was in a randomised block of 3 blocks x 2 treatments x 6 harvests x 3 spp. combinations.

Figure 1 shows the number of tillers produced per original tiller in the first four harvests (it was not possible to separate the tillers from the original tussocks to count them in the second season, when the final two harvests were made). Maximum tiller number peaked at mid-season in the unclipped pots, although the *Agrostis* monoculture treatment could not be counted after the third harvest, as the plants had become too intergrown. In the clipped pots, there was little, if any, increase in tiller numbers after the first harvest, which was carried out 3 weeks after the first clip was made. It seems likely, therefore, that the additional tillers produced in these pots had appeared before the clipping treatment was applied. Figure 2 shows the above-ground weight per pot, in the unclipped treatment. There was a gradual increase in biomass during the first year, so that in the later part of the season, weight increase must have been due to tiller weight increasing, since tillers numbers had started to decline. In the second season, *Festuca* monoculture continued to increase, and in the mixed pots, the proportion of this species (which was small) appeared to increase too. The pattern was similar in below-ground weights, though with a more marked decline in *Agrostis* monoculture by the sixth harvest.

Unfortunately the very hot dry summer of 1976 proved too extreme for many of the plants clipped to 2cm to survive, and many died in late June/July. Thus the results obtained were really only sufficient to analyse in the unclipped treatment. However, it was apparent that clipping had a dramatic effect on the production of both species. Because of the high death rate, there was little increase in the cumulative weight (i.e. including the weight of clippings removed every 2 weeks) over the harvests, but it did not exceed 3.0g above-ground in either species, compared with the final harvest weight

of 115g in unclipped *Agrostis* and 63g in *Festuca* monocultures.

Figure 2 showed that the yield of *Agrostis* and *Festuca* in the unclipped mixed pots was lower than the *Agrostis* monoculture, but higher than *Festuca* monoculture. This can be examined straightforwardly by plotting monoculture yields on the two axes of a graph, and joining the two points. If neither species has a directly detrimental effect on the other (such as might happen if a toxin were produced by the roots), and if there is no direct benefit (as might happen in a grass/legume mixture due to nitrogen fixation) then the mixture yield should lie at some point along the line joining the two points (van den Bergh, 1968). It was found that in every case there was no significant departure from this observation.

The proportion of *Festuca* in the mixture fell to between 5 and 10% of the total above-ground biomass in the first season. There was, however, no indication that the *Agrostis* was suppressing it entirely (Figure 3), and at the final harvest, the proportion of *Festuca* in the mixtures had increased slightly. The below-ground weights showed the same pattern, with *Festuca* contributing less than 10% of the total root mass until the final harvest when it increased to 13%.

In the clipped treatment, *Festuca* was a much more important component of the mixture pots increasing from 20% to more than 50% between the first and the final harvests, but this was partly due to its greater ability to survive the rigours of the 1976 summer.

The yields for the pots returned to Moor House were far lower than those obtained in the unclipped glass house pots at the final harvest. The effect was particularly dramatic in above-ground weights, though a similar less marked effect was shown in the roots (Table 1).

Above-ground live to dead weight ratios were compared between the final glass house harvest and the Moor House pots. The proportion of live green leaves in the Moor House pots was considerably higher (contributing 50% or more, compared with about 35% in the glass house pots). There was also evidence of rabbit grazing in the Moor House pots, which must have occurred fairly continuously over the experimental period to allow for the higher green: dead ratio. It would also, presumably, exaggerate the difference between the yields of the glass house and the Moor House pots and account for a much lower above : below-ground ratio (less than 1 in the Moor House treatment,



and more than 5 in the glass house).

#### Experiment II.

Analysis of the results from this experiment is not yet completed, but for the purpose of discussion I have included some preliminary results in this paper. The experiment was begun in 1979 and the final harvest taken in April 1980. Monocultures were not included, and the 1:1 mixed cultures were subjected to a range of clipping treatments, which were carried out on all the plants in the pot, or on only one of the two species. The plants were either left unclipped, or clipped to 5cm or 10 cm at 2 week intervals. The higher clipping levels were chosen because of the effect of the 2cm clip in Experiment 1. There were therefore 9 different combinations:-

UFUA UF10A UF5A 10FUA 10F10A 10F5A 5FUA 5F10A 5F5A (where U is unclipped, 10 is 10cm and 5 is 5cm clip, F, *Festuca*, A, *Agrostis*) and the experimental design was a randomised block of 3 blocks x 9 treatments x 3 harvests.

The clipping treatments were intended to represent extreme examples of species selection in grazing.

In pots where one species was clipped and the other left unclipped, there was a dramatic decline in the amount of the clipped species, particularly if the clipping level was 5cm. This was the case for both *Agrostis* and *Festuca*, although in the first year, when 2 harvests were taken, neither species was entirely suppressed by this treatment. In the final harvest, it was apparent that many 5cm clipped plants had died when they were grown in combination with unclipped plants.

The results appear to confirm the slim evidence of Experiment I, that when the mixture is clipped, *Festuca* can compete much more successfully with *Agrostis* than when the mixture is unclipped (Table 2). Results were almost identical for above and below-ground weights. There was also greater production of the low clipped plants of one species when they were grown with low clipped plants of the other than when grown with medium clipped plants, and similarly medium clipped plants grew better with other medium clipped than with unclipped plants. Tables 3 and 4 illustrate this. Table 3 shows the cumulative weight of clippings removed every two weeks (as a mean of 3 blocks) until the final clip made in mid-October 1979.

The plants clipped to 10cm appeared to be considerably more productive than those clipped to 5cm for both species. Although the 5cm clipped plants survived in the main in the first season, the amount of leaf material produced in 2 weeks over 5cm declined progressively. By contrast, 10cm clipped plants continued to grow vigorously. In Table 4, tiller numbers are shown that were counted at the second harvest, made in September 1979. It is apparent that both the degree of clipping of the species concerned, and the condition of the other species are important in determining the number of tillers produced, although to a greater extent in *Festuca*.

#### Note

This report is intended to be a progress report to stimulate discussion, and is not a report of a completed piece of research.

#### ACKNOWLEDGMENTS

I should like to thank the many people under the Job Creation Schemes who helped with the experimental work.

TABLE 1. Yield (g) in the final harvest for unclipped pots in the glass house and at Moor House (Standard deviations are given in brackets)

Treatment	Glass house		Moor House	
	Above-ground	Below-ground	Above-ground	Below-ground
<i>Agrostis</i> mono	115.4 (35.6)	16.7 (23.4)	10.3 (3.2)	12.1 (1.3)
<i>Festuca</i> mono	62.6 (26.6)	17.9 (3.0)	8.6 (0.6)	9.7 (0.7)
<i>Agrostis</i> mixed	96.7 (34.8)	14.5 (10.6)	7.1 (0.6)	8.7 (1.5)
<i>Festuca</i> mixed	9.7 (9.1)	2.1 (2.7)	2.4 (0.5)	2.6 (0.7)

TABLE 2. % *Festuca* in above-ground weights of pots where *Agrostis* and *Festuca* were clipped to the same height. Standard deviations are given in brackets.

	5cm clip	10cm clip	Unclipped
Harvest 1	47.7 (10.0)	46.7 (8.2)	9.1 (3.6)
Harvest 2	42.2 (12.9)	39.6 (10.8)	18.6 (6.5)
Harvest 3	52.1 (3.0)	51.7 (11.7)	22.1 (11.9)

TABLE 3. Cumulative weight (g) of clippings removed from the clipped treatments between May and October 1979.

Treatment	<i>Festuca</i>	Treatment	<i>Agrostis</i>
5F5A	2.7	5A5F	5.3
5F10A	2.0	5A10F	4.1
5FUA	1.0	5AUF	3.1
10F5A	9.1	10A5F	13.4
10F10A	5.7	10A10F	9.0
10FUA	3.2	10AUF	6.2

TABLE 4 Mean no. of tillers per plant counted at harvest 2  
(September, 1979). Standard deviations are given  
in brackets.

*Festuca*

5F with			10F with			UF with		
5A	10A	UA	5A	10A	UA	5A	10A	UA
31 (13)	11 (1)	9 (2)	58 (16)	45 (10)	22 (7)	82 (11)	109 (18)	42 (9)

*Agrostis*

5A with			10A with			UA with		
5F	10F	UF	5F	10F	UF	5F	10F	UF
26 (18)	8 (1)	6 (2)	28 (14)	30 (7)	22 (7)	37 (11)	30 (9)	28 (6)

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FIGURE LEGENDS

Figure 1. Mean number of tillers produced per original tiller in the first four harvests of Experiment I.

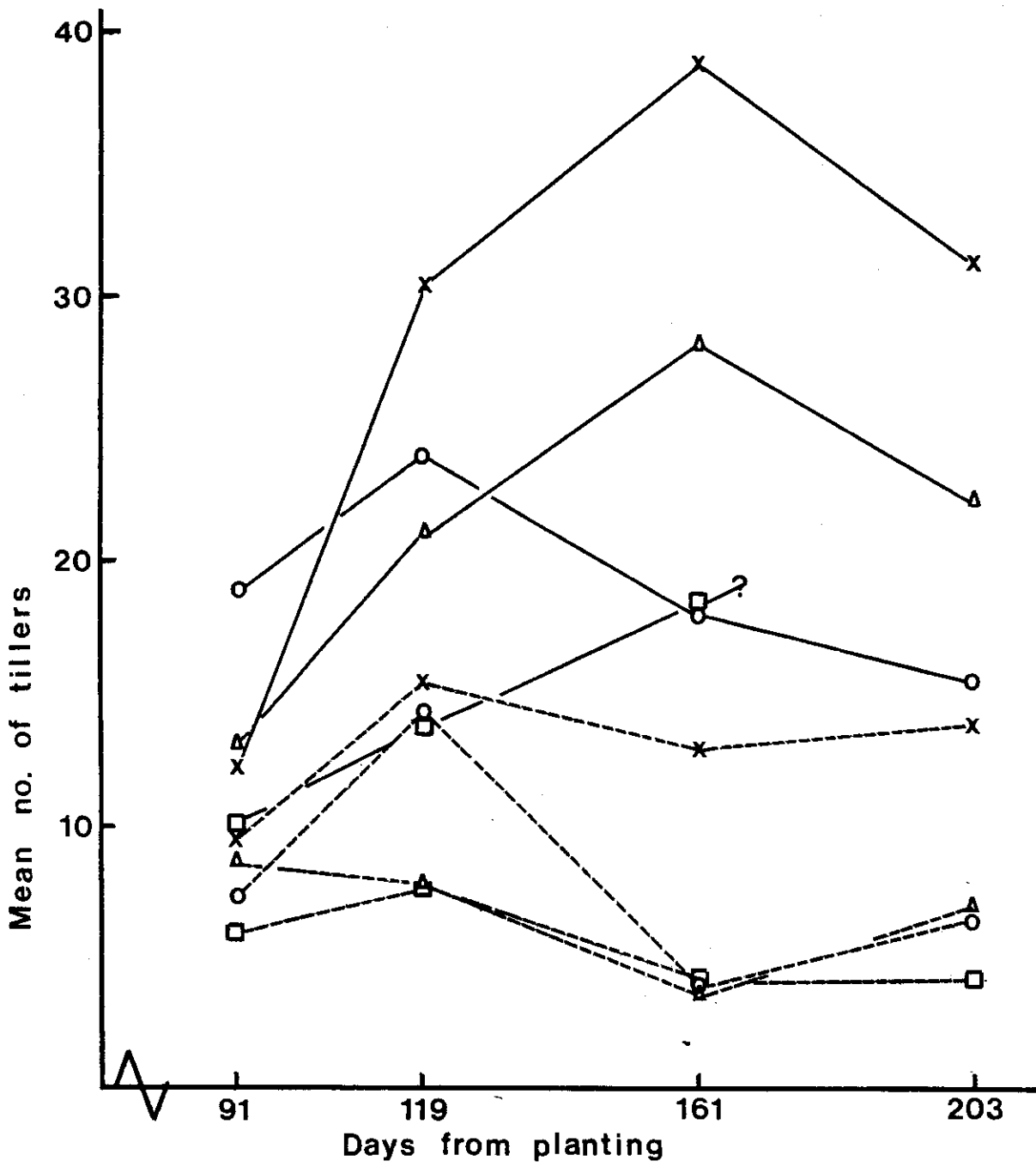
- X *Festuca* monoculture
  - *Agrostis* monoculture
  - *Festuca* in mixed pots
  - △ *Agrostis* in mixed pots
- \_\_\_\_\_ Unclipped treatment  
----- Clipped treatment

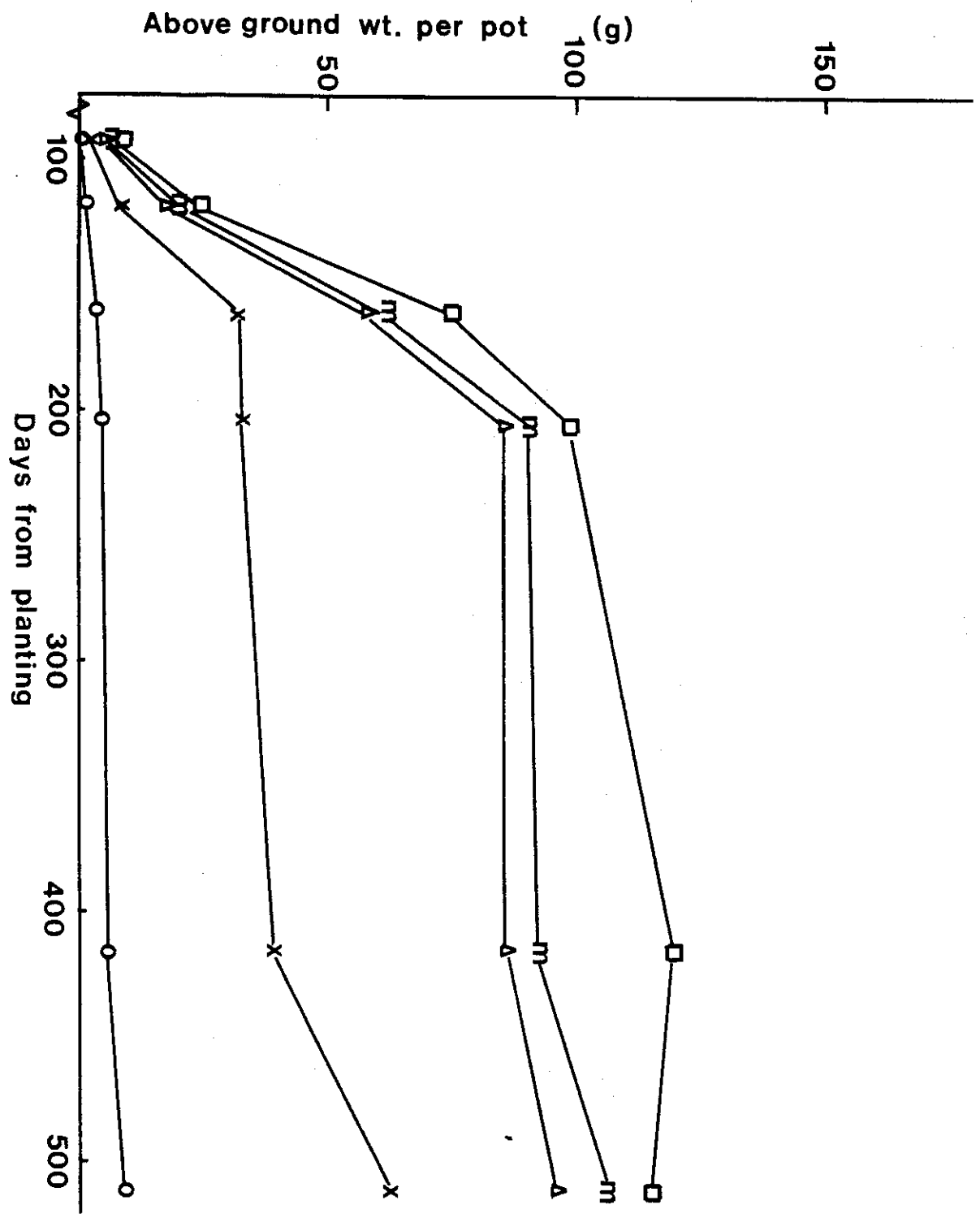
Figure 2. Mean above-ground dry weight (g) per pot in the unclipped treatment.

- X *Festuca* monoculture
- *Agrostis* monoculture
- *Festuca* in mixed pots
- △ *Agrostis* in mixed pots
- ∩ Total in mixed pots

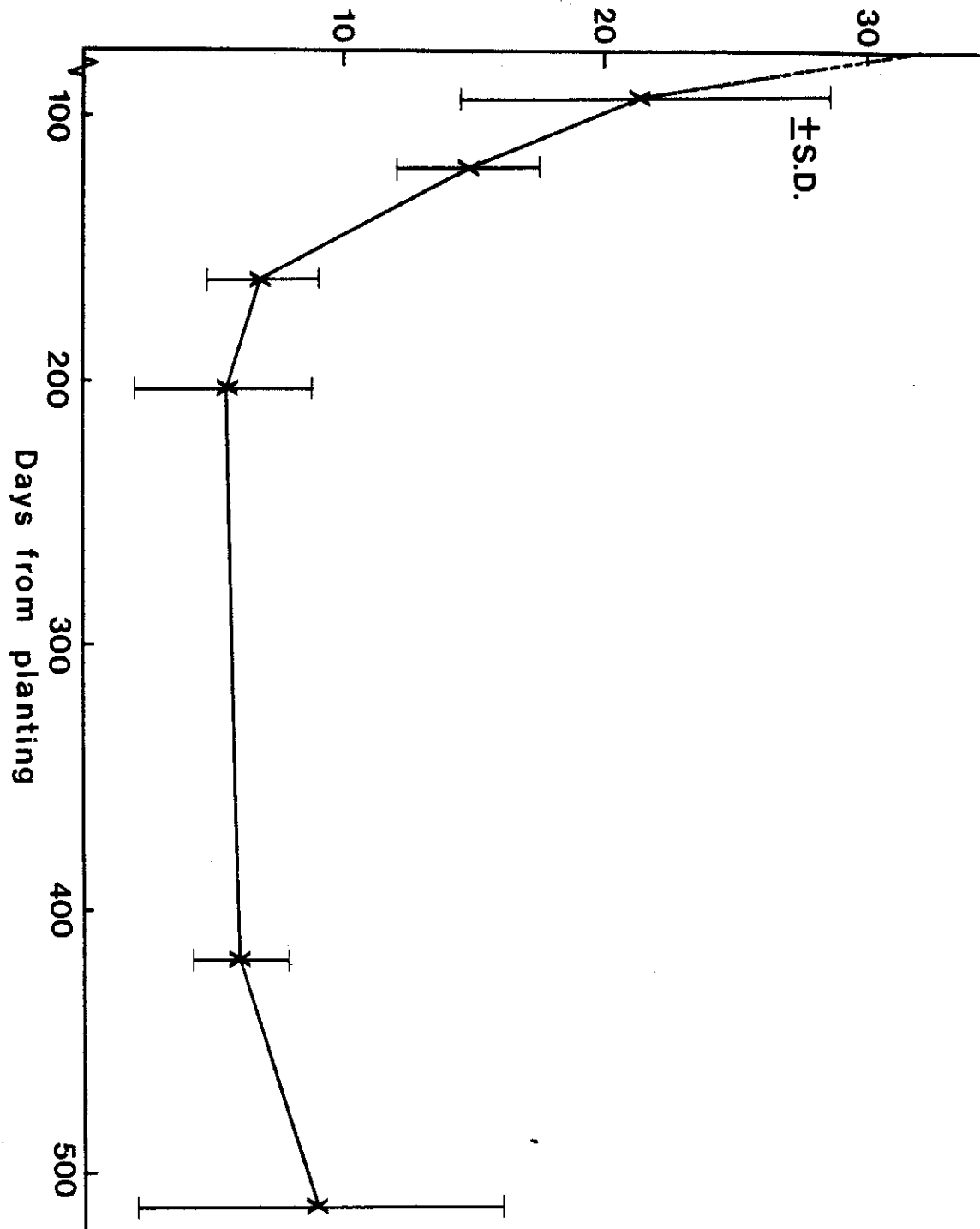
Figure 3. *Festuca* as a percentage of the total above-ground weight, in the unclipped mixed pots.







Festuca, as a percentage of the total  
above-ground dry wt.



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