An investigation of the effect of lead and zinc upon the production and relative competitive ability of the grasses agrostis stolonifera, festuca ovina and festuca rubra with reference to their distribution in Upper Teesdale

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AN INVESTIGATION OF THE EFFECT OF LEAD AND ZINC UPON THE PRODUCTION AND RELATIVE COMPETITIVE ABILITY OF THE GRASSES AGROSTIS STOLONIFERA, FESTUCA OVINA AND FESTUCA RUBRA WITH REFERENCE TO THEIR DISTRIBUTION IN UPPER TEESDALE

by

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TABLE OF CONTENTS

TABLE OF CONTENTS (Continued)

LIST OF TABLES AND FIGURES

1. INTRODUCTION

1. INTRODUCTION

1.1 The Teesdale rarities

The area of the North Pennines known as Upper Teesdale has long been famous for its rare plants, which include pre-alpine, alpine, arcticalpine and subarctic species. These plants are growing in a climate which is only marginally subarctic (Manley, 1942) and are believed to be relict members of a post glacial flora (Böcher, 1951).

Pigott (1956) gives a full description of the rare communities. The two main types of substrate on which they are found are the outcrops of metamorphosed rock known as "sugar-limestone" and the wet flushes. The communities on the sugar-limestone are notable for the numerous bare patches, the total cover often being 30% (Bellamy and Tickle, 1965). Bellamy et al (1969) have also recognised the existence of distinct boundary communities containing rare species, between areas of wet and dry ground. Here, the oscillation of the water table gives rise to a zone of vegetational instability, which prevents invasion and establishment by the more common species from the adjoining land.

In the same paper, a parallel is drawn between the Teesdale plant communities and true alpine tundra ecosystems. It was demonstrated that, although the production of the Teesdale communities cannot be correlated with climatic or edaphic changes, the net annual aerial production of all the communities containing arcticalpine species was less than 150 grams dry matter per square metre. This limit is not exceeded by most true alpine tundra ecosystems. However, it must be noted that only those communities with 100% cover were taken

into consideration.

The most widely accepted explanation for the persistence of the relict communities is that competitive interaction with typical lowland species is less severe than might be expected.

The fact that lowland grasses are found growing alongside most of the rare species (Pigott, 1956) clearly supports this view. There are two mechanisms by which the competitive interaction may have been reduced:

(i) The Teesdale relict populations may be less sensitive to competition than they are in other regions

(ii) The lowland competitors are less vigorous in this region.

The second explanation is the more feasible and is implicit in the account of Pigott (1956).

1.2 Stress factors

1.2.1 Climate

Perhaps the most obvious stress factor which could depress the performance and competitive ability of the lowland grass species is the almost subarctic climate of Upper Teesdale. However, several of the surrounding areas of the North Pennines have an identical climate so it is unlikely that climatic factors alone could depress performance significantly, although they may reinforce the effect of other factors, such as low nutrient supply. One interesting demonstration should however, be borne in mind. Marshall (1971) showed that a short term amelioration of climate, achieved by the use of a cold frame in the field, significantly increased the prod-

uction of the lowland grass species rather than the rarities.

1.2.2 Grazing

Pigott (1956) suggested that grazing and trampling by sheep in the sugar-limestone areas could maintain an open habitat, so giving a selective advantage to the shade intolerant rare species. However, Marshall (1971) and Jeffrey and Pigott (1973) have demonstrated that short-term removal of this pressure produces only insignificant changes in the structure of the sward. Even so, it is still possible that grazing could exert a long-term effect, by acting selectively on those species which reproduce from seed, as it tends to cause a reduction in the number of inflorescences (Jeffrey, 1970).

1.2.3 Heavy Metal Toxicity

Jeffrey (1970) also mentioned the possibility of the heavy metals in the soil having a selective direct toxicity towards the lowland species. This would seem unlikely as many of the lowland grasses are known to be capable of evolving tolerant races quite rapidly (see e.g. Gregory and Bradshaw, 1965).

1.2.4 Nutrient Deficiency

Deficiency of a major nutrient is yet one more possible stress factor. Jeffrey and Pigott (1973) demonstrated that, although addition of nitrogen alone, did not have any effect upon a community growing upon a flushed sugar-limestone soil, addition of phosphate resulted in a large increase in the total production of the vegetation. This effect was exaggerated by simultaneous addition of nitrogen. Thus, a primary phosphate deficiency is suspected.

It is interesting to see just which species contribute to

the increased standing crop. The frequency of the arctic alpine sedge Kobresia simpliciuscula, which originally dominated the sward, was substantially reduced, whilst the rare Carex species remained unaffected. Three species in fact gained to a far greater extent than any others. These were all lowland grasses. Thus the height of the vegetation was increased, resulting in a critical reduction in the amount of light reaching the Kobresia plants. The most surprising observation was the vast increase of Festuca rubra, a species which had been almost absent from the original turf. Festuca ovina, the most abundant grass originally also showed a great increase, but only just sufficient to retain its supremacy. Agrostis stolonifera made up the remainder of the increase in the standing crop.

It was therefore decided to investigate the competitive interaction of these three species, using the principles of the De Wit school to assess their relative competitive ability.

1.3 The Phosphate Problem

1.3.1 Availability

As well as causing a small standing crop in the vegetation on sugar limestone soils, it is quite possible that a phosphate deficiency could selectively inhibit the growth of the typical lowland species.

The total phosphate content of the soil is, in fact, not abnormally low (Jeffrey and Pigott, 1973) but its availability must have been reduced in some way. The short cool growing season may be reducing the rate of breakdown of organic matter and hence the circulation of phosphate, but it could not have reduced the

availability to the extent that would explain the observations described in the previous section.

1.3.2 Lead

Jeffrey (1970) noted a positive correlation between total inorganic phosphate content and lead concentration in the Teesdale soils. This implies that the lead must be reducing the availability of the phosphate. To test this hypothesis, he grew Festuca ovina at different levels of added lead and phosphate. Growth was indeed elevated by phosphate and depressed by lead. No similar effect could be achieved with barium (the other main metallic component of the mineral veins which dissect the sugar limestone soils (Pigott, 1956)).

1.3.3 Zinc

Marshall (1971) found a relatively high concentration of exchangeable zinc in some Teesdale soils, although there was no correlation with vegetation type. Even though high plant contents were found (>100 ppm), which correlated with low productivity, the plants did not show symptoms of zinc toxicity. It seems likely, therefore, that zinc could be acting in the same way as lead, i.e. decreasing the availability of phosphate.

It was therefore decided to study the effect of a change in the lead and zinc levels of the soil upon the production and the competitive ability of the three grass species (Festuca rubra, Festuca ovina and Agrostis stolonifera) most affected by phosphate addition as described at the end of section 1.2.4.

2. PRINCIPLES OF THE DE WIT SCHOOL ON COMPETITION

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2.1 Development of the theory

To find a basis for mutual interference in pastures De Wit and Ennik (1958) studied competition experiments in annual species. The resulting theories were put forward by De Wit (1960 and 1961) and extended to interpret competition experiments involving perennial species. The problems involved in these new experiments were finally overcome by De Wit and Van den Bergh (1965).

The success of the theories in estimating competitive ability hinges on the fact that fluctuations in growing conditions are taken into account by growing the species concerned in both mixture and monoculture. The basis of the theory is the replacement series. All experiments must be planted in such a way that the sum of the relative planting frequencies (or seed frequencies) always equals one. See example in Table 1.

TABLE 1: A planted replacement series

Pot No.	No. seeds A	seed frequency Z	No. seeds B	seed frequency Z_B
1	0	0	8	1
2	3	.25	6	.75
3	6	.5	4	.5
4	9	.75	2	.25
5	12	1	0	0

N.B. $Z_A + Z_B = 1$ in each pot

2.2 The relative replacement rate

De Wit and Van den Bergh (1965) defined the relative replacement rate of a species A with respect to a species B at the nth harvest with respect to the mth harvest by equation 1.

$$ {}^{nm}\rho_{AB} = \frac{{}^{n}r_A / {}^{m}r_A}{{}^{n}r_B / {}^{m}r_B} \qquad \text{equation 1} $$

where ${}^{n}r_A$ is the relative yield of species A at the nth harvest and the other terms have equivalent meaning. In general, relative yields are defined by equation 2:

$$ r_A = X_A / M_A \qquad \text{equation 2} $$

where X_A is the yield of species A in the mixture and M_A is the yield of species A in the monoculture. It is usual for the mth harvest to be a reference harvest against which all later harvests are compared.

In the same paper, the authors introduced the relative yield total which in many cases is about equal to one (equation 3).

$$ R\,Y\,T = r_A + r_B = 1 \qquad \text{equation 3} $$

Combining this with equation 1 gives:

$$ \text{(a)}\ {}^{n}r_A = \frac{{}^{nm}\rho_{AB} \cdot {}^{m}r_A}{{}^{nm}\rho_{AB} \cdot {}^{m}r_A + {}^{m}r_B} \quad \text{and (b)}\ {}^{n}r_B = \frac{{}^{m}r_B}{{}^{nm}\rho_{AB} \cdot {}^{m}r_a + {}^{m}r_B} $$

equation 4

Van den Bergh (1968) gave perhaps the best description of the relative replacement rate. He stated that it characterizes the competitive interference, irrespective of the variable effects of changing growing conditions on the yield of the species in monoculture. The resultant of the competitive abilities of the two species can be shown as a series of graphs of yield versus relative yield or reference harvest (replacement diagrams) but it is best illustrated by presenting the $\int$ values as a course line, by plotting them on a logarithmic scale against time.

The yields used in calculating $\int$ values may be measured as any convenient parameter such as dry weight, leaf area or tiller production, as De Wit and Van den Bergh (1965) have demonstrated that the magnitude of $\int$ is independent of the method of yield determination.

2.3 Exclusive species

When RYT = 1 the species are said to be exclusive (De Wit and Van den Bergh, 1965). This means that the relative replacement rate is independent of the species composition, i.e. if a species gains at one frequency, it will gain to the same extent as another. An estimate of the confidence limits is impossible, at no two sets of yield data are independent, owing to the results being obtained as pairs from each pot (Van den Bergh, 1968).

If $\int_{AB}$ in equation 4(a) and $\int_{AB}^{-1}$ in equation 4(b) are replaced by k_{AB} and k_{BA} respectively, then deviation of RYT from one is reflected in the product $k_{AB} \cdot k_{BA}$. These k factors are called relative crowding

coefficients (De Wit, 1960). When the two species are exclusive then k_{AB} is the reciprocal of k_{BA} and $k_{AB} \equiv \rho_{AB}$.

If, however, the product deviates systematically from one, then the species are not exclusive and are influencing each other in some way other than simply competing for the same space. Space, in this context, refers to the factors essential to the growth of both species and available as a finite supply, such as light and nutrients. The term was introduced by De Wit (1960).

When $k_{AB} \cdot k_{BA} > 1$, then the species are mutually stimulating (De Wit, 1960; Bakhuis and Kleter, 1965; De Wit, Tow and Ennik, 1966). Conversely, when $k_{AB} \cdot k_{BA} < 1$ the species are mutually suppressing (De Wit, 1960; Van den Bergh and Elberse, 1962).

3. MATERIALS AND METHODS

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3.1 Competition experiments

3.1.1 Soils

Two peaty soils were used, one taken from Upper Teesdale (OS ref. NY 816295) and the other from the Sunbiggin Tarn region of the North Pennines (OS ref. NY 675075).

To confirm that the Teesdale soil did have the higher heavy metal content, a preliminary analysis was carried out to determine the concentrations of the most important cations. Details of the technique are given in 3.1.3. It can be seen from the results in Table 2 that only in the levels of lead, zinc and cadmium does the Teesdale soil exceed twice that of the Sunbiggin.

TABLE 2: Levels (ppm) of ammonium acetate - extractable cations in the soils

Metal	Ca	Mg	Na	K	Mn	Fe
Teesdale	6150	75	70	55	12	1.5
Sunbiggin	3900	77	47	45	13	1.3

Metal	Cu	Al	Cd	Pb	Zn
Teesdale	1.0	1.5	1.1	9.5	12.0
Sunbiggin	0.6	1.3	0.5	3.1	4.9

So that any effect due to the levels of lead or zinc in the soil, could be isolated, it was decided to grow the plants under the four soil conditions shown in Table 3.

TABLE 3: Experimental soil conditions

Source of soil	Added metal	Treatment Notation
Teesdale	None	TO
Teesdale	Lead	TL
Sunbiggin	None	SO
Sunbiggin	Zinc	SZ

3.1.2 Soil treatments

Lead was supplied as a freshly prepared solution of lead acetate, and zinc, as a solution of zinc sulphate. These salts were chosen for their high solubility and so that any secondary

effect on plant growth, due to the anion, such as would have been observed with nitrates, could be avoided.

Four-inch plastic plant pots, filled to within one inch of the rim, were treated with 10 ml of these solutions at the concentrations shown in Table 4. The corresponding resultant levels in the surface of the soil several days after treatment are shown alongside.

TABLE 4: Preliminary soil treatments

Soil	Solution added	Resultant level in soil
Teesdale	6.6×10^{-3}M	14
	$Pb(MeCO_2)_2$	ppm Pb
	1.9×10^{-3}M	25
Sunbiggin	5.7×10^{-3}M	27
	$ZnSO_4$	ppm Zn
	17.0×10^{-3}M	55

These results determined the initial treatment of the pots in the main experiment, as given in Table 5. Soil analyses on control pots, 1, 2, 3 and 6 weeks after planting determined the subsequent additions which were necessary to maintain a level of about 30ppm lead and 50ppm zinc in the TL and SZ treatments respectively. These analyses also confirmed that the Teesdale zinc and Sunbiggin lead levels remained unchanged throughout.

TABLE 5: The solutions added to treatments TL and SZ throughout the experiment

	1 week before planting	1, 3,5 and 7 weeks after planting
TL	10 ml 2.9×10^{-3}M Pb $(MeCO_2)_2$	10 ml 2.9×10^{-3}M Pb $(MeCO_2)_2$
SZ	10 ml 17.0×10^{-3}M $ZnSO_4$	10 ml 8.5×10^{-3}M $ZnSO_4$

Every addition was followed by 5 ml distilled water which, whilst facilitating even distribution of the metals throughout the soil, was not so great a volume as to cause direct loss of solution through the base of the pot. At the same time, all SO and TO pots were given 15 ml distilled water, so that their moisture content would not fall below that of the SZ and TL treatments.

3.1.3 Soil analysis

The extraction procedure was based upon that of MacLean et al (1969). Every result was obtained by taking the mean of the analyses on three pots.

Approximately 10g of soil was abstracted from the surface region (0.3 cm depth) of each pot. This was oven dried and ground to a fine powder using a mortar and pestle. 1.00g was then shaken for about three hours with 25 ml N ammonium acetate. After standing for a further two hours the suspension was filtered overnight using "Whatman 42", quantitative grade filter paper. The

clear solution was then remade with distilled water to 25 ml in a volumetric flask.

The concentrations of the relevant cations in this solution were then measured using a Perkin Elmer 403 Atomic Absorbtion Spectrophotometer, and the values obtained, converted to the weight of metal in unit weight of soil.

3.1.4 Cultivation of the grasses

(i) Planting

The seeds were germinated in covered Petri dishes on moist Whatman no. 1 filter paper at laboratory temperature. The dishes were replenished with distilled water every two days. Before planting each seedling was cut down, if necessary, to 0.5-1 cm shoot length. Although each seed was pressed gently into the moist prepared soil individually, the arrangement of individuals of the same and of different species in each pot was random.

(ii) Replacement series

For each soil treatment sets of five pots were used. These were planted with the numbers of seedlings given in Table 6. Use of seedlings rather than seeds ensured a much greater probability of each set remaining a replacement series.

TABLE 6: Planted replacement series

a) Agrostis stolonifera (A) series

	Pot No.				
	1	2	3	4	5
No. of A.stolonifera plants	16	12	8	4	0
No. of Festuca rubra plants	0	4	8	12	16

TABLE 6 (Continued)

b) *Festuca ovina* (O) Series

	Pot No.				
	1	2	3	4	5
No. of *F. ovina* plants	16	12	8	4	0
No. of *F. rubra* plants	0	4	8	12	16

(iii) First seed batch

The first batch of seeds were from the end of a merchant's stock and only had 30% germination success. Whilst a second supply was being ordered two replicates of the O series were planted for each treatment. Throughout these pots there was poor seedling establishment by both species. The *F. ovina* plants also exhibited low growth rate, all being <4 cms high after three weeks growth. Any further measurements were therefore abandoned but pots containing a reasonable number of growing plants were used as control pots and sacrificed at intervals for soil analysis, to give advance information on the levels of the added metals in the different treatments.

(iv) Second seed batch

Eighty per cent of the seeds taken from the second batch had germinated within a week, so confirming that the failure of the first plants had been due to poor quality seed. Three replicates of the A series were then planted, followed by two replicates of the O series one week later, so that the times of harvesting would be staggered.

(v) Maintenance

The pots were kept in a greenhouse with whitewashed glass panels. Replicates of each treatment and series were placed in different areas of the greenhouse to allow for any variation in light regime. Watering was carried out almost every day using the minimum amount which would keep the soil surface moist, so that significant leaching of metal ions through the base of the pots was avoided. Any possible transfer of metal ions between pots via the bases was prevented by standing the pots on corrugated asbestos boards.

3.1.5 Harvesting

The plants in each pot were cut at 4 cm above the soil surface at 3, 6 and 9 weeks after planting. The plant material of each species in each pot was dried in small paper bags in an oven at 105-110^{o}C for about 40 hours. Each sample was then weighed on an analytical grade balance, accurate to 10^{-5} grams.

3.2 Chemical analysis of plant tissue

3.2.1 Digestion

(i) Tissue Samples

To give a reasonable amount of tissue for digestion, all *F. ovina* material yielded from each soil treatment was bulked as one sample. *A. stolonifera* was bulked in the same way. As *F. rubra* had yielded a great deal more tissue than the other two species it was decided to compare the tissue from plants grown in monoculture with that of plants grown in competition with (a)

A. stolonifera and (b) F. ovina. Thus, the 20 samples shown in Table 7 were digested at the same time as a blank containing no plant tissue.

TABLE 7: Approximate weights (mg) of tissue for digestion

	TO	TL	SO	SZ
A. Stolonifera	15	15	25	25
F. ovina		40		
F. rubra - monoculture		130		
" " - mixture with A. stolonifera		130		
" " - mixture with F. ovina		65		

(ii) Experimental procedure

Each sample was chopped and weighed to 10^{-4} g in a wide necked 150 ml conical flask. Approximately 10 ml analytical grade concentrated nitric acid was added and the mixture left overnight at room temperature. 2-3 ml of analytical grade perchloric acid was then added, and the mixture heated on a sand bath. After about one hour white fumes were observed, indicating that ignition had taken place. As soon as the solution had become colourless, distilled water was added to prevent evaporation to dryness with the subsequent explosion. After removal from the heat it was diluted to 25 ml in a volumetric flask, filtration being unnecessary owing to the presence of only minute quantities of silica.

3.2.2 Lead and zinc analysis

The concentrations of lead and zinc in the digest solutions

were measured using a Perkin Elmer 403 Atomic Absorbtion Spectrophotometer, with standard operating procedure. The levels of calcium, magnesium, sodium and potassium were also checked in this way but all proved to be too low to be able to give any significant Broad Band Interference. Conversion of the measured concentration to actual levels in the tissue was carried out by multiplying by the appropriate dilution factor for each sample.

3.2.3 Phosphate analysis

The method was based on that of Kitson and Mellor (1944) for determining orthophosphate as a molybdivanadate complex.

(i) Phosphate standards

These were all made by dilution of a 50µg/ml solution which was made up as follows:

0.2195g KH_2PO_4 in 500 ml distilled water + 25 ml 3.5M H_2SO_4 made up to one litre.

(ii) Reagent

This was made by mixing the two solutions (a) and (b) and making up to 250 ml.

(a) 0.3125g ammonium metavanadate in 100 ml 8M HNO_3

(b) 12.5g ammonium molybdate in 100 ml distilled water

(iii) Method

1 ml of the above reagent was added to exactly 2 ml of the digest or standard solution and the mixture made up to exactly 4 ml. It was allowed to stand for 20-30 minutes to allow the yellow colour of the complex to develop.

(iv) Spectrophotometry

The absorbance of the mixtures was measured using a Unicam SP600 UV spectrophotometer. The phosphate concentrations of the digests were in the range 2-7 µg/ml. Apha (1971) recommends a wavelength of 440 mµ for such measurements but at this wavelength the slight yellowish tinge of some of the digests gave a small but significant absorbance. However, use of a 470 mµ wavelength for all measurements eliminated this problem, whilst retaining linearity in the desired concentration range.

3.3 Germination experiments

3.3.1 Lead and zinc levels

As germination in the various soil treatments had been avoided, the percentage germination of each species was determined, at levels of lead and zinc in the same range as those experienced by seedlings in the main experiment. Swaine et al (1960) have shown that ammonium acetate extracts of soils contain approximately 25% of the lead and zinc removed by hydrochloric acid extraction. It has also been shown that the zinc removed by the acid extraction is equal to (Nelson et al, 1959; and Martens, 1968) or even slightly greater than (Keefer et al, 1971) that which is available to the plant. Accordingly, the highest levels of lead and zinc used were approximately four times the amounts extracted by ammonium acetate, in the TL and SZ treatments respectively.

3.3.2 Method

The solutions used are shown in Table 8. Unlike the main

experiment, lead acetate could not be used, owing to the precipitation of basic lead carbonate when solutions are allowed to stand in air (Ephraim,1948).

Ten seeds of a single species were placed on Whatman No. 1 filter paper in Petri dishes, which were replenished with the appropriate solution whenever necessary so that the substrate was always moist. Twenty dishes for each solution were used for each species. The number of seeds germinated in each of these replicates was counted after two weeks.

TABLE 8: Germination solutions

Condition	Solution	Metal concentration ug/ml
Control	distilled water	0
Low lead	0.19×10^{-3} M Pb $(NO_3)_2$	40 Pb
High lead	0.58×10^{-3} M Pb $(NO_3)_2$	120 Pb
Low zinc	1.22×10^{-3} M Zn SO_4	80 Zn
High zinc	3.68×10^{-3} M Zn SO_4	240 Zn

4. RESULTS

4. RESULTS

4.1 Germination Experiments

TABLE 9: Percentage germination expressed as mean ± 95% confidence limits

	F. rubra	A. solonifera	F. ovina
Control	87.5 ± 5.3	64.0 ± 7.3	86.5 ± 5.8
Low lead	85.5 ± 5.3	49.5 ± 7.3	76.5 ± 6.2
High lead	84.0 ± 5.0	40.5 ± 8.4	76.0 ± 6.3
Low zinc	84.5 ± 4.3	38.5 ± 7.6	80.5 ± 5.4
High zinc	79.0 ± 5.9	31.0 ± 5.9	78.0 ± 6.4

It can be seen from Table 9 that for every species with each metal, the percentage germination is always greatest in the control and lowest under high metal conditions. However, the difference between the high and low conditions in every case never achieves the level of 5% significance. Certain of the differences between the control and other conditions also fail to reach this level. These will be considered for each species separately.

(i) Festuca rubra

Lead never appears to affect germination. Zinc only causes a significant reduction at the high concentration.

(ii) Agrostis stolonifera

Both levels of lead and zinc used gave a highly significant reduction in germination, ranging from one-third to one-half of the control. This was the only species which showed a particularly noticeable (though still not significant) difference between the results for the two concentrations of each metal.

(iii) Festuca ovina

The reduction due to the presence of lead in the germination solution was clearly significant but, in the case of zinc, the high level was needed before any significant change in the percentage germination took place.

4.2 Growth of monocultures

The total yield throughout the nine week period of growth was calculated for each pot containing a monoculture, by summing the dry matter yields of its three harvests. The

mean values for each treatment are presented in Table 10.

TABLE 10: Total yield (mg dry matter) of monocultures expressed as mean ± 90% confidence limits

	F. rubra	A. stolonifera	F. ovina
TO	35.1 ± 6.4	3.8 ± 1.2	12.5 ± 5.8
TL	34.6 ± 3.6	3.3 ± 0.9	10.5 ± 6.2
SO	32.6 ± 4.5	12.5*	11.4 ± 0.7
SZ	33.6 ± 6.2	9.8*	9.0 ± 3.1

N.B. F. rubra values are means of 5 pots

A. stolonifera values are means of 3 pots

F. ovina values are means of 2 pots

For the values marked *, inconsistent results combined with the small sample size prevented confidence limits of any reasonable magnitude being given.

The production of F. rubra is unaffected by either change of soil or addition of lead or zinc. A. stolonifera cannot be proven to behave any differently owing to the unreliability of two of the results. However, F. ovina, whilst remaining unaffected by change of soil and addition of lead, does suffer a 20% decrease in growth (significant at the 5% level) when zinc is added to the soil.

4.3 Analysis of the competition experiments

4.311 Verification of RYT = 1

In this and following sections general principles of

calculation will be illustrated by reference to the Agrostis series, but they apply equally to the data of the Ovina series.

The mean yields of each species in monoculture (M_A and M_R) and in each mixture (X_A and X_R) were calculated and are shown in Appendix 1. Shown alongside are the relative yield values (r_A and r_R) which follow from these by equation 2:

$$r_A = X_A/M_A$$

The RYT value for each pair of r values was then calculated by equation 3:

$$RYT = r_A + r_R$$

and the mean value of the three harvests found for each Z_A of every treatment. The magnitude of these means is shown in Figure 1. They demonstrate quite well that the RYT does not deviate significantly from 1 in any treatment. Thus both pairs of species appear to be mutually exclusive.

4.3.2 Estimation of ρ

The most explicit explanation of this process is given by De Wit (1960).

The r_A and r_R values obtained in 4.3.1 are used to give the ρ values shown in Table 11 by using the equation 1.

$$^{no}\rho_{AR} = \frac{^{n}r_A / {}^{n}r_R}{Z_A / Z_R}$$

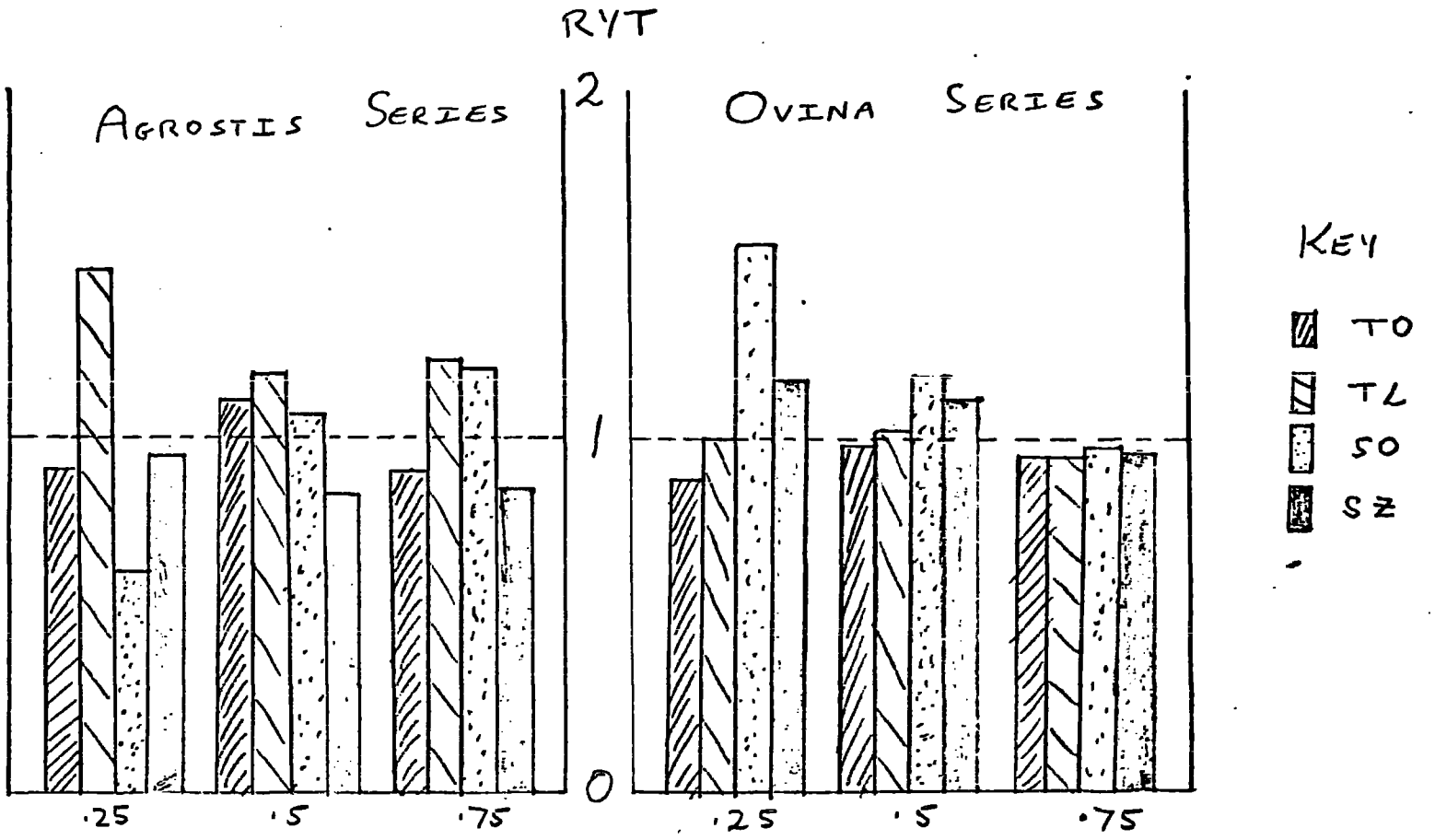


FIG. 1. MEAN RYT VALUES

(ZR VALUES ARE GIVEN BELOW EACH SET OF HISTOGRAMS)

"Harvest 0" is used as reference harvest so that the effect of the treatments on seedling establishment will be shown. An unreliable and inefficient estimate of ρ is obtained for each harvest of each treatment by simply taking the mean of values obtained from each of the three mixtures. This estimate can now be improved as follows. It is first used to predict a relative yield value for each seed frequency of the experiment by employing the equation 4, where the q values are the predicted relative yields.

$$n_{q_A} = \frac{no_{AR} \cdot Z_A}{no_{AR} \cdot Z_A + Z_R} \quad \text{and} \quad n_{q_R} = \frac{Z_R}{no_{AR} \cdot Z_A + Z_R}$$

The actual experimental yields at each seed frequency are then plotted against the corresponding ρ values. If a good straight line can be drawn for both species, then the ρ estimate is satisfactory. If not, then slightly different values of ρ are tried until the best straight lines for each species are obtained. This process is illustrated in Figure 2 by one of the twenty-four estimates carried out. Where the two straight lines cannot be drawn, the value of ρ must depend upon the composition of the mixture.

4.3.3 Construction of replacement diagrams

For each harvest of each treatment, the yield of each species was plotted against seed frequency in replacement diagrams (Figure 3). The smooth curves were drawn using the values of X_A and X_R given in Appendix 2. These were obtained by substituting the final ρ estimate along with the M_A and M_R values from its "

estimation lines" (see example of Figure 2) into equation 4.

This $\int$ value is given above each replacement diagram. It can be seen that the diagrams for the SO treatment of A series harvest 2 and 3 and O series harvest 3 lack these values. This is because no straight lines were possible in their graphs of O_A and O_R against q_A and q_R. The points on these replacement diagrams obviously do not conform to the smooth curves of the adjacent diagrams and hence cannot be described by equation 4. Thus, the species concerned have not been proved to be exclusive under these soil conditions and at these stages of development. It is noteworthy that the RYT values for the SO treatment did, in fact, tend to deviate to the greatest extent from 1 (see Figure 1).

4.3.4 Course Lines

The curvature of the lines of the replacement diagrams is only slight and hence does not give a very clear picture of the progress of the competition experiments. The course lines shown in Figure 4 are much more valuable for any deductions regarding the outcome of competition.

The $^{no}\int_{OA}$ values which make up the third set of course lines in Figure 4 were calculated by the equation:

$$\int_{OA} = \int_{OR} / \int_{AR} \qquad \text{Equation 5}$$

The only line to show a steady progressive change is that for the SZ treatment on the $\int_{OA}$ diagram. This continuous positive slope could imply that Festuca ovina will replace Agrostis stolonifera

TABLE 11: $^{no}\rho_{AR}$ and $^{no}\rho_{QR}$ values

Soil Treatment	Z_R	Agrostis series			Ovina series		
		n=1	n=2	n=3	n=1	n=2	n=3
TO	.75	1.5	1.1	1.4	0.9	2.2	0.5
	.5	1.5	0.6	1.5	0.8	2.4	0.8
	.25	1.3	0.5	1.2	0.6	1.5	0.6
	mean	1.4	0.7	1.4	0.8	2.0	0.6
	corrected mean	1.4	0.7	1.4	0.7	2.0	0.8
TL	.75	0.7	0.6	0.8	0.8	1.3	1.4
	.5	1.6	0.75	1.1	0.9	0.6	1.1
	.25	1.4	0.9	1.5	0.8	0.6	1.6
	mean	1.2	0.75	1.1	0.8	0.8	1.4
	corrected mean	1.0	0.75	1.0	1.0	1.0	1.1
SO	.75	1.2	0.7	0.07	0.8	1.2	1.7
	.5	1.0	1.3	0.18	0.9	0.7	0.9
	.25	0.7	0.6	0.11	0.6	1.6	1.8
	mean	1.0	0.9	0.12	0.8	1.2	1.5
	corrected mean	0.8	-	-	0.8	1.2	-
SZ	.75	0.7	0.2	0.15	0.9	0.8	1.6
	.5	1.4	0.3	0.4	1.4	1.0	2.9
	.25	1.2	0.4	0.4	1.0	0.9	1.6
	mean	1.1	0.3	0.3	1.1	0.9	2.0
	corrected mean	1.0	0.5	0.5	1.0	0.9	2.0

KEY

⊙ F. RUBRA } WITH ORIGINAL ESTIMATE
⊡ F. OVINA } OF $\rho = 0.6$

× F. RUBRA } WITH CORRECTED ESTIMATE
⊠ F. OVINA } OF $\rho = 0.8$

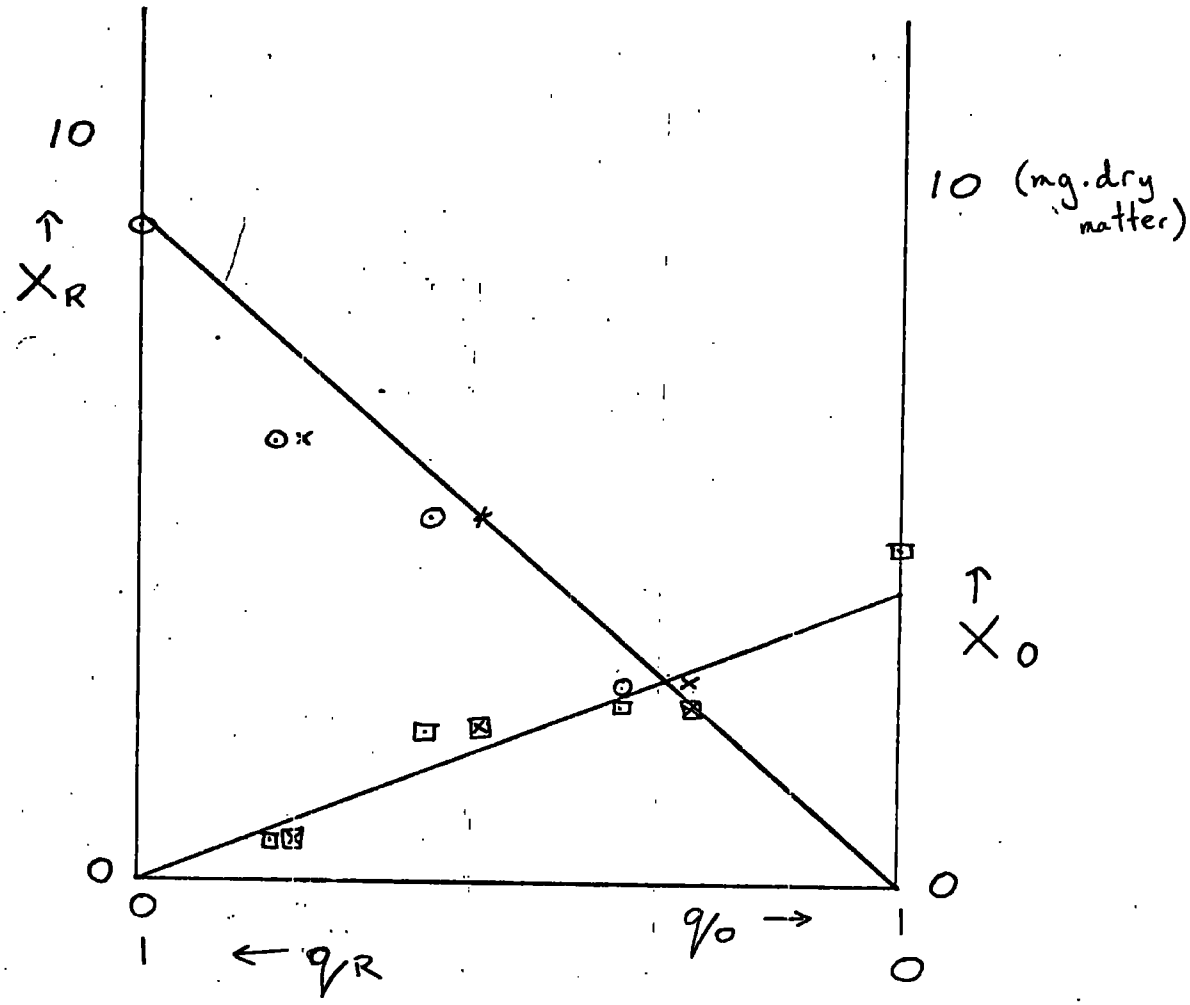


FIG. 2. EXAMPLE OF THE CORRECTION OF A ρ ESTIMATE (OVINA SERIES - TO - HARVEST 3)

FIG. 3. REPLACENT DIAGRAMS - AGROSTIS SERIES

ORDINATE - mg. dry matter of F. rubra (x) and A. stolonifera (o)

ABSCISSA - z_R (1 → 0) and z_A (0 → 1)

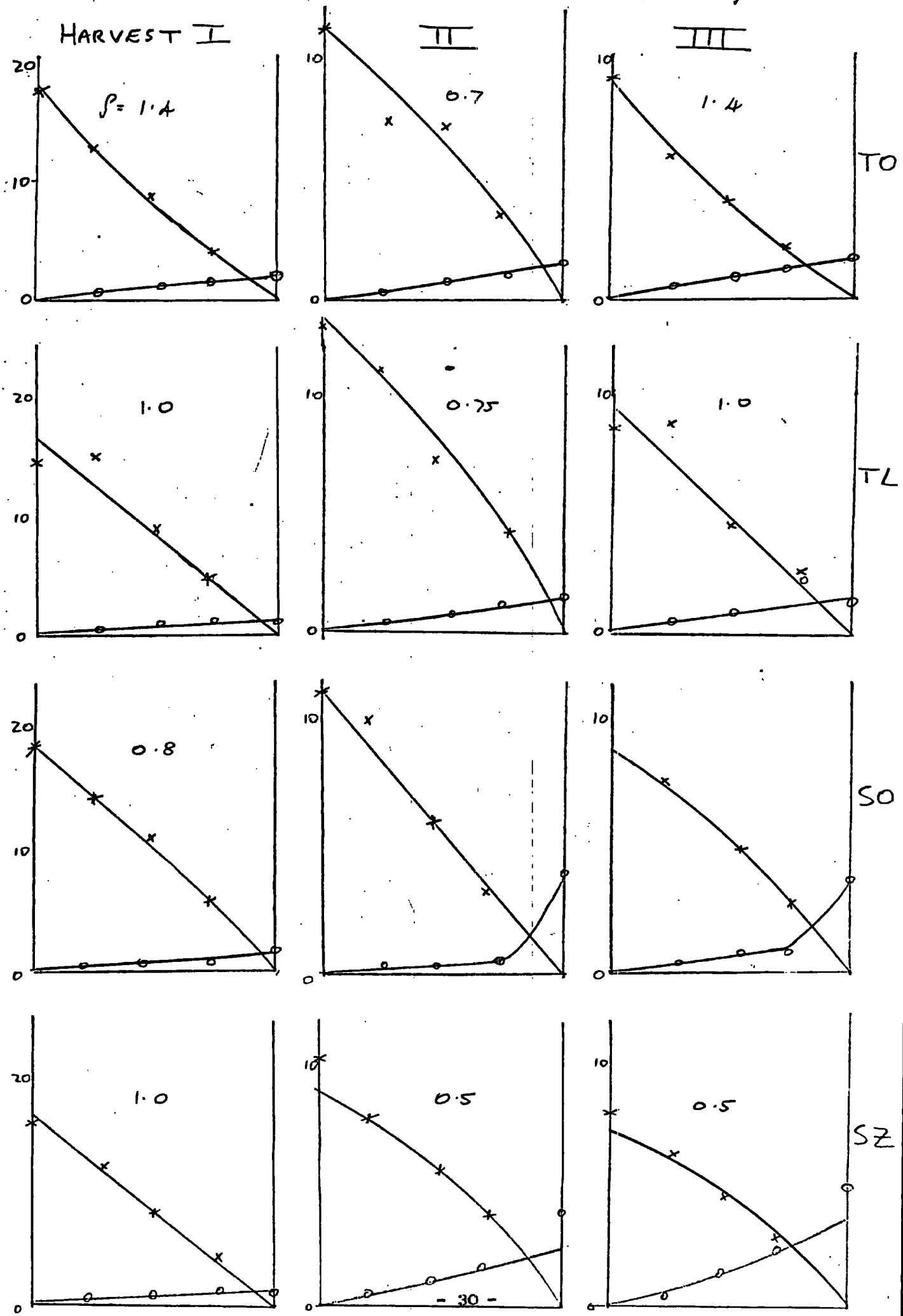
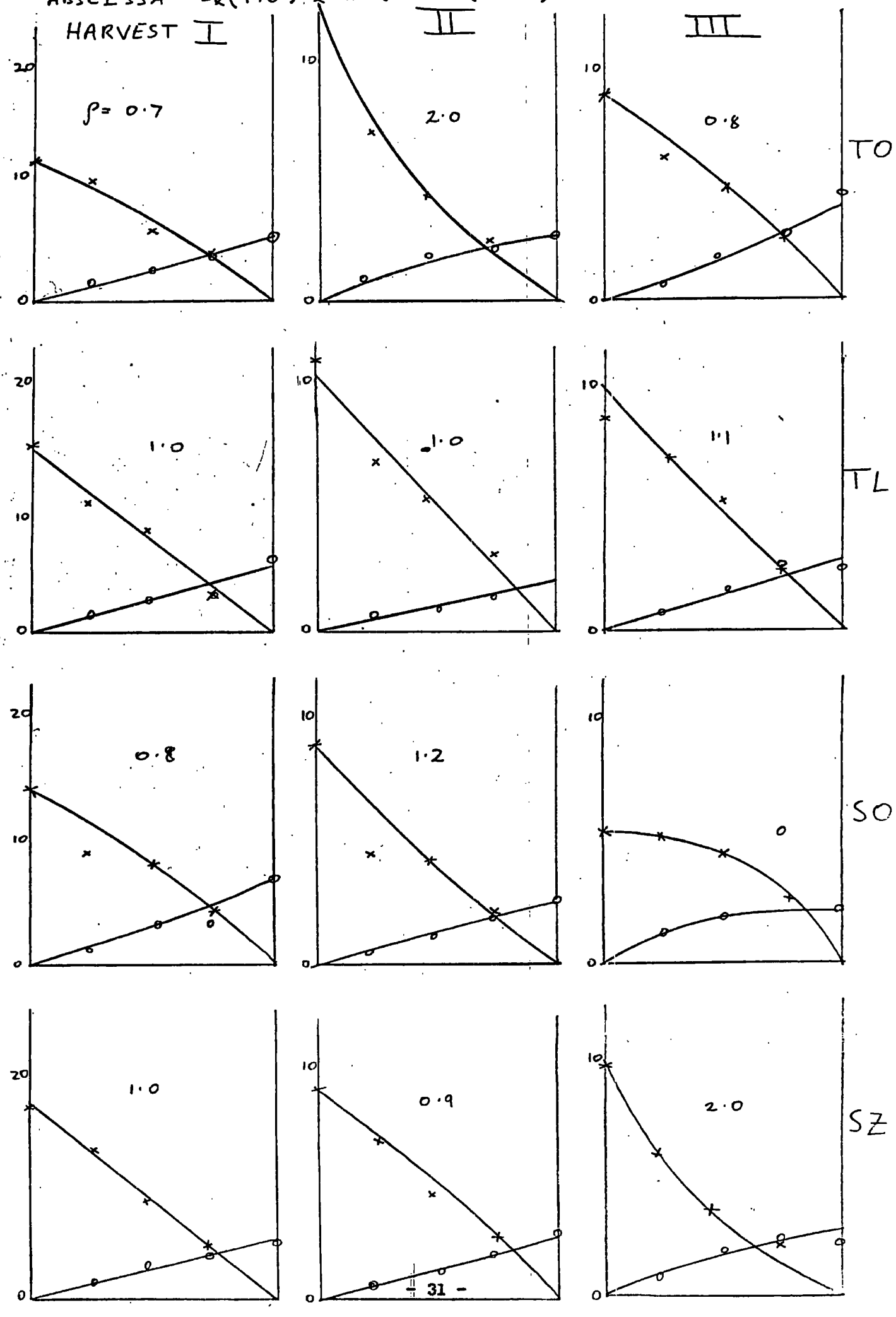


FIG. 3. REPLACEMENT DIAGRAMS - OVINA SERIES

ORDINATE - mg. dry matter of F. rubra (×) and F. ovina (o)
ABSCISSA - z_R (1→0) × and z_o (0→1)



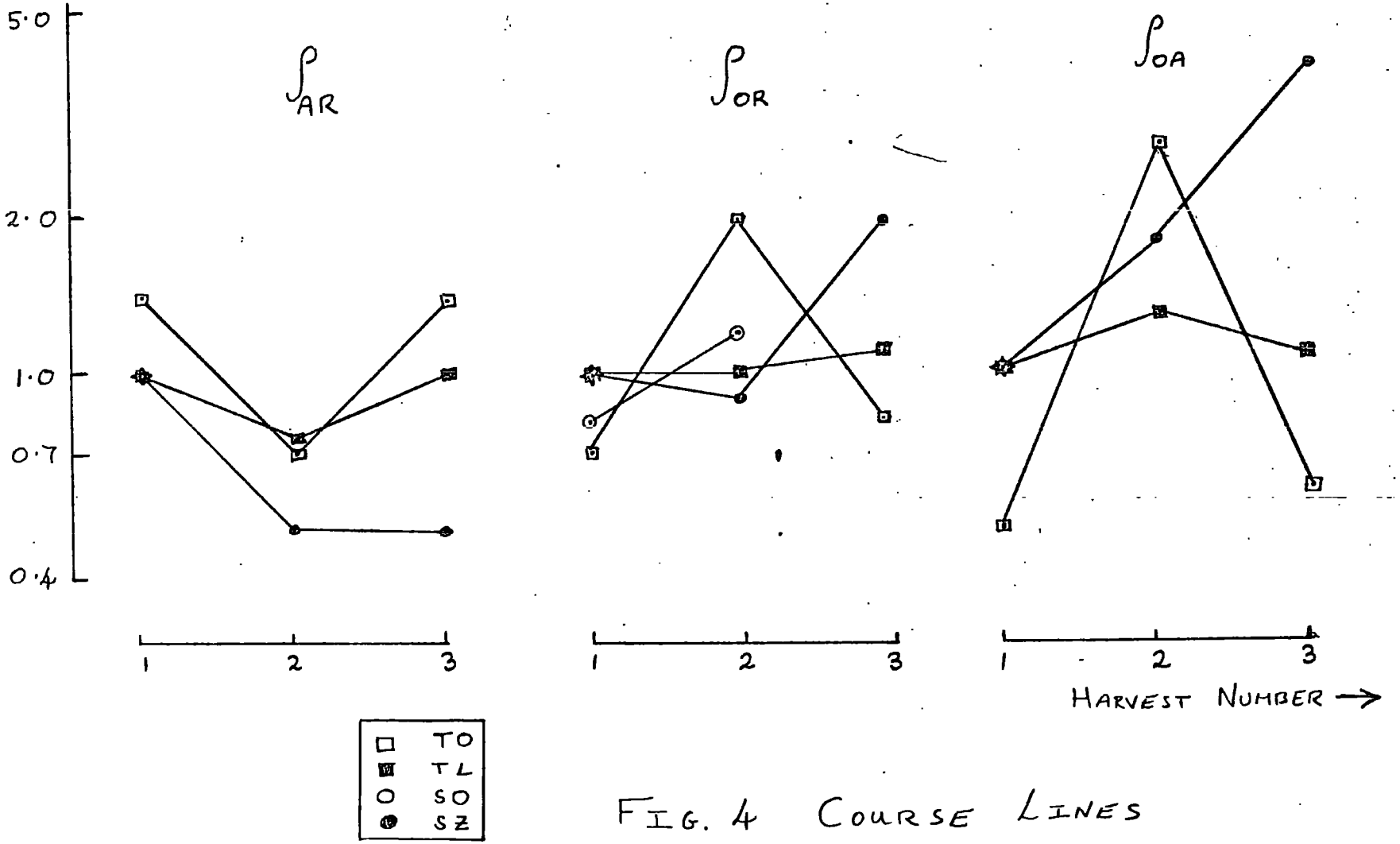


FIG. 4 COURSE LINES

in time.

The only other line worthy of comment is that of the SZ treatment on the ρ_{AR} diagram where the ρ value remains well below one, implying that Festuca rubra is gaining on Agrostis stolonifera.

On all the other lines, either the slope is minimal or the direction of the line is not consistent, so that neither species can definitely be shown to be replacing the other. It follows therefore, that it is impossible to deduce any differences due to change of soil or addition of lead or zinc, in the result of competition.

4.4 Chemical analyses

All results in Table 12.

4.4.1 Zinc

The tissue content of all species when grown on the SZ treatment is about 2½ times that from the SO treatment. For each species, tissue from Teesdale soil has an intermediate content. There are no startling differences between the contents of different species.

4.4.2 Lead

The reaction of each species to the addition of lead to the soil is very different. Whereas F. ovina shows no change, the tissue content of A. stolonifera grown on the TL treatment is twice that when grown on the TO treatment. Similarly, the content of F. rubra is five times as great. However, it should also be noted that the TO levels of A. stolonifera and F. ovina are, in fact, as great as the TL levels of F. rubra (80 ppm).

In contrast to this, all species, when grown on Sunbiggin soil contain about 20 ppm.

4.4.3 Phosphate

The soil treatment does not effect the phosphate content of the tissue. The levels in A. stolonifera seem to be greater than in the other two species. This could have been caused by a combination of the particularly high dilution factor for the A. stolonifera samples and the inaccuracy of the phosphate analytical method at low concentration.

In these, as in the zinc and lead results, the tissue content of F. rubra does not appear to change whether it was grown in monoculture or mixture.

TABLE 12: Chemical analyses of the plant tissue

All results are expressed as ppm

	Soil Treatment	Zinc	Lead	Phosphate
Agrostis stolonifera	TO	200	70	3400
	TL	250	150	5400
	SO	80	15	2000
	SZ	220	18	4100
Festuca ovina	TO	140	80	1800
	TL	170	80	1800
	SO	100	50	1800
	SZ	220	21	2000
F. rubra monoculture	TO	100	16	1100
	TL	80	80	900
	SO	60	16	1000
	SZ	130	13	900
F. rubra in mixture with A. stolonifera	TO	90	15	1200
	TL	90	80	1000
	SO	60	12	1100
	SZ	150	16	1000
F. rubra in mixture with F. ovina	TO	140	20	1500
	TL	160	90	1600
	SO	70	16	1200
	SZ	170	28	1600

5. DISCUSSION

5. DISCUSSION

The germination experiments provided the most statistically reliable results of the whole project. They can be used as a guide as to which species will have the best chance of establishing seedlings. Assuming each species population produces the same number of seeds, then, if the lead content of the soil is increased, Festuca rubra will be by far the most successful. As the zinc content of the soil increases, then F. rubra will again suffer least, but simultaneously, F. ovina will be increasing its lead over Agrostis stolonifera. Of course, there is also the probability that one or all of these species will evolve a tolerant race. See,for example, the work of Wilkins (1960 a and b) on F. ovina.

When discussing the results of the competition experiments, it must be remembered that even if a species can be shown to have a relatively good competitive ability, this does not necessarily imply a high yield (Donald, 1963). The Montgomery effect is often exhibited viz. under sub-optimal conditions, a species normally having low productivity may have a selective advantage (Montgomery, 1912). This is partly due to the fact that innate properties of the plant, such as root growth and uptake activity, may not always be employed to the fullest extent when growing in monoculture(Bradshaw, 1969).

In these experiments, A. stolonifera was always the least productive of the three species and F. rubra by far the most vigorous. The relatively large seed size of F. rubra automatically gives the

seedlings a better chance of establishment under conditions where a major nutrient is deficient (Lloyd and Pigott, 1967). The poor performance of A. stolonifera is consistent with the finding of Bradshaw et al (1960) that it is a species which has a relatively high phosphate requirement for vigorous growth. Indeed, it does appear to take up more phosphate than the other two species.

Neither the lead level, zinc level or change of soil could be shown to influence the phosphate content of any of the three species studied. However, it is possible that a more accurate analytical technique or use of more concentrated digestion solutions would enable the phosphate content to be correlated with metal levels.

The lead content of the plant tissue was certainly affected by the amount of lead in the soil. It is surprising that neither Agrostis stolonifera or Festuca rubra suffered a significant reduction in production when the soil was treated with lead, even though they both increased their lead content by approximately 70 ppm, which, in the case of F. rubra was a fivefold increase.

Festuca ovina did not appear to take up any of the added lead but it must be remembered that analyses were carried out only on leaf tissue. It is therefore possible that lead was indeed taken up but that translocation from the roots to the leaves was in some way prevented. Here in the roots, it could immobilise phosphate. This should then reduce production but no such decrease was observed. However, this species, unlike F. rubra and A. stolonifera, did suffer a statistically significant 20% loss in production when zinc was added to the soil. Exactly the same mechanism can be postulated for this metal. Jeffrey (1970) did in fact achieve a significant reduction

in the growth of F. ovina by adding lead but he was (i) working with sand culture rather than soil and (ii) comparing a culture medium of total lead content 1000 mg/dm^3 with one containing no lead at all. These present experiments, however, have not been able to show that it is the level of lead and zinc in the soil which is the cause of the unexpectedly poor performance of these grasses in Upper Teesdale.

The other main object of the project was to determine the relative competitive ability of the three species. Several changes would have led to improved results. For instance, the amount of time available prevented the use of longer intervals between harvests. This would have eased the problem of the decreasing production in all species, which had been caused by too frequent cutting. Jeffrey (1970) found that a population of Festuca ovina derived from Teesdale was ten times more productive per unit amount of phosphate added than a population of the same species, grown from commercial seed. Use of Teesdale material in this project would almost certainly therefore have resulted in more vigorous growth and hence a much more reliable analysis of the competitive interaction. Unfortunately, collection of seed from the field was impossible owing to the time of year when the work was carried out.

From the results obtained, it is impossible to deduce with any reasonable degree of certainty, the effects of lead or zinc on the outcome of competition. The competition experiments should be continued for longer periods of time to demonstrate any clear trends. It is also possible that during the nine weeks of the experiment,

the individual plants had not developed sufficiently rapidly to interact significantly through space, although Van den Bergh (1968) showed that the total density of seedlings in the pot could be varied considerably without affecting the outcome of the experiment.

It is true that these experiments have been carried out under greenhouse conditions and without the use of a closed sward, so extrapolation to the field situation must be rather less than straightforward. Field investigations on causal ecological relations however, are very difficult due to the continuously changing environment (Van den Bergh, 1968), so experiments such as these, under controlled conditions, are essential.

6. SUMMARY

6. SUMMARY

The percentage germination of the three grass species Agrostis stolonifera, Festuca rubra and F. ovina was determined at different concentrations of lead and zinc. Both metals reduced germination to some extent in all species. In general, A. stolonifera was the most adversely affected and F. rubra was the most tolerant.

The same species were grown in mixture and monoculture in soils of different lead and zinc content, in such a way that a mathematical analysis of the competitive interference could be carried out, using the principles of the De Wit school. The results regarding the influence of lead and zinc upon relative competitive abilities were inconclusive.

Production of the monocultures was unaffected by the metals in all cases except F. ovina, which suffered a small decrease on zinc-treated soil. Phosphate immobilization in the roots was suggested as a possible explanation. It could not be demonstrated that the level of lead and zinc in the soil is the reason for the reduced vigour of these grasses in Upper Teesdale.

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APPENDIX 1. YIELDS AND (RELATIVE YIELDS)

(M and X are mg. dry matter)

ZR	SOIL TREATMENT	TO			TL			SO			SZ		
	HARVEST NUMBER	1	2	3	1	2	3	1	2	3	1	2	3
		A	G	R O	S	T	I	S		S	E	R	I E S
0	M_A	1·2	1·2	1·5	0·8	1·1	1·4	1·2	4·8	6·6	1·0	3·8	5·0
·25	X_A	1·0	0·5	1·2	1·0	0·9	2·0	0·7	0·2	0·7	1·2	1·4	1·9
	X_R	3·7	3·0	2·1	4·0	4·1	2·5	4·7	2·6	1·8	4·9	3·3	2·4
	$\pm_A$	·83	·42	·80	1·25	·82	1·43	·58	·42	·11	1·2	·37	·38
	$\pm_R$	·21	·27	·23	·30	·32	·31	·26	·23	·30	·32	·31	·31
·5	X_A	0·9	0·5	0·9	0·8	0·4	0·8	0·7	0·3	0·9	0·7	0·5	1·0
	X_R	8·9	7·7	3·6	8·6	6·2	4·2	10·3	5·7	4·9	7·7	4·9	4·3
	$\pm_A$	·75	·42	·60	1·0	·36	·57	·58	·63	·14	·70	·13	·20
	$\pm_R$	·51	·69	·40	·64	·48	·53	·57	·50	·80	·51	·45	·55
·75	X_A	0·4	0·3	0·4	0·2	0·2	0·4	0·4	0·1	0·2	0·2	0·2	0·2
	X_R	12·0	7·3	5·3	14·6	10·9	8·2	14·6	10·4	8·0	12·8	7·1	6·3
	$\pm_A$	·33	·25	·27	·25	·18	·29	·33	·21	·03	·20	·05	·04
	$\pm_R$	·68	·66	·58	1·09	·84	1·03	·81	·92	1·31	·86	·66	·81
1	M_R	17·6	11·1	9·0	13·4	12·9	8·0	18·0	11·3	6·1	15·2	10·8	7·8
	O	V		I	N	A				S	E	R	I E S
0	M_O	5·7	2·4	4·5	6·0	2·6	2·0	7·0	2·4	2·0	4·4	2·5	2·1
·25	X_O	3·3	1·8	2·4	3·2	1·2	2·5	3·3	2·7	5·4	3·7	1·8	2·5
	X_R	3·4	2·2	2·5	3·2	3·0	2·3	4·0	2·1	2·1	4·0	2·4	2·4
	$\pm_O$	·58	·75	·54	·53	·46	1·26	·47	1·12	2·18	·84	·72	1·17
	$\pm_R$	·30	·17	·29	·21	·27	·27	·28	·24	·40	·27	·27	·24
·5	X_O	2·2	1·8	2·0	2·8	0·7	1·5	3·3	0·7	1·7	3·1	1·0	2·1
	X_R	5·6	3·9	4·8	8·3	4·9	5·4	7·9	3·9	4·9	7·5	3·5	3·3
	$\pm_O$	·39	·25	·45	·47	·27	·74	·47	·29	·83	·70	·40	·98
	$\pm_R$	·49	·31	·56	·54	·43	·65	·55	·44	·92	·50	·40	·34
·75	X_O	1·4	0·9	0·6	1·1	0·6	0·7	1·1	0·4	1·1	1·1	0·5	0·6
	X_R	9·9	6·5	5·8	10·2	6·0	7·2	9·1	3·8	5·3	12·2	6·7	5·4
	$\pm_O$	·25	·38	·12	·18	·23	·40	·16	·17	·55	·25	·20	·29
	$\pm_R$	·87	·51	·68	·66	·53	·86	·63	·43	·99	·81	·76	·56
1	M_R	11·4	12·7	8·6	15·4	11·3	8·4	14·4	8·8	5·3	15·0	8·8	9·6

APPENDIX 2. OBSERVED AND CORRECTED YIELDS

AGROSTIS SERIES (all in mg. dry matter)

SOIL TREATMENT	Z_A	HARVEST I				HARVEST II				HARVEST III			
		Observed		Corrected		Observed		Corrected		Observed		Corrected	
		A	R	A	R	A	R	A	R	A	R	A	R
TO	0	–	17.6	–	18.4	–	11.1	–	11.0	–	9.0	–	8.7
	.25	0.4	12.0	0.4	12.5	0.3	7.3	0.2	8.9	0.4	5.3	0.5	5.9
	.5	0.9	8.9	0.7	7.7	0.5	7.7	0.5	6.4	0.9	3.6	0.9	3.6
	.75	1.0	3.7	1.0	3.5	0.5	3.0	0.8	3.4	1.2	2.1	1.2	1.7
	1	1.2	–	1.2	–	1.2	–	1.2	–	1.5	–	1.5	–
TL	0	–	13.4	–	16.0	–	12.9	–	13.1	–	8.0	–	9.0
	.25	0.2	14.6	0.2	11.9	0.2	10.9	0.2	10.5	0.4	8.2	0.4	6.7
	.5	0.8	8.6	0.5	7.9	0.4	6.2	0.5	7.4	0.8	4.2	0.8	4.4
	.75	1.0	4.0	0.8	3.9	0.9	4.1	0.8	4.0	2.0	2.5	1.2	2.1
	1	0.8	–	1.0	–	1.1	–	1.1	–	1.4	–	1.6	–
SO	0	–	18.0	–	18.2	–	11.3			–	6.1		
	.25	0.4	14.6	0.3	14.3	0.1	10.4			0.2	8.0		
	.5	0.7	10.3	0.6	10.0	0.3	5.7			0.9	4.9		
	.75	0.7	4.7	1.0	5.2	0.2	2.6			0.7	1.8		
	1	1.2	–	1.3	–	4.8	–			6.6	–		
SZ	0	–	15.2	–	16.4	–	10.8	–	8.3	–	7.8	–	7.0
	.25	0.2	12.8	0.3	12.3	0.2	7.1	0.3	7.1	0.2	6.3	0.4	6.0
	.5	0.7	7.7	0.7	8.2	0.5	4.9	0.7	5.5	1.0	4.3	1.0	4.7
	.75	1.2	4.9	1.1	4.1	1.4	3.3	1.2	3.3	1.9	2.4	1.9	2.8
	1	1.0	–	1.4	–	3.8	–	2.1	–	5.0	–	3.5	–

APPENDIX 2. OBSERVED AND CORRECTED YIELDS

OVINA SERIES (all in mg. dry matter)

SOIL TREATMENT	z_0	HARVEST I				HARVEST II				HARVEST III			
		Observed		Corrected		Observed		Corrected		Observed		Corrected	
		X_0	X_R	X_0	X_R	X_0	X_R	X_0	X_R	X_0	X_R	X_0	X_R
TO	0	-	11·4	-	11·2	-	12·7	-	12·2	-	8·6	-	
	·25	1·4	9·9	1·0	9·1	0·6	6·5	1·0	7·3	0·6	5·8		
	·5	2·2	5·6	2·2	6·6	0·7	3·9	1·6	4·0	2·0	4·8		
	·75	3·3	3·4	3·7	3·6	1·2	2·2	2·1	1·7	2·4	2·5		
	1	5·7	-	5·4	-	2·6	-	2·4	-	4·5	-		-
TL	0	-	15·4	-	15·1	-	11·3	-	10·3	-	8·4	-	
	·25	1·1	10·2	1·2	11·3	0·6	6·0	0·5	7·7	0·7	7·2		
	·5	2·8	8·3	2·5	7·5	0·7	4·9	1·0	5·1	1·5	5·4		
	·75	3·2	3·2	3·8	3·8	1·2	3·0	1·5	2·6	2·5	2·3		
	1	6·0	-	5·1	-	2·6	-	2·0	-	2·0	-		-
SO	0	-	14·4	-	14·2	-	8·8	-	8·8	-	5·3		
	·25	1·1	9·1	1·4	11·2	0·4	3·8	0·6	6·2	1·1	5·3		
	·5	3·3	7·9	3·0	7·8	0·7	3·9	1·2	3·9	1·7	4·9		
	·75	3·3	4·0	4·8	4·1	2·7	2·1	1·7	1·9	5·4	2·1		
	1	7·0	-	6·8	-	2·4	-	2·2	-	2·0	-		
SZ	0	-	15·4	-	15·6	-	8·8	-	8·8	-	9·6	-	9·8
	·25	1·1	12·2	1·2	11·7	0·5	6·7	0·5	6·8	0·6	5·4	1·0	5·9
	·5	3·1	7·5	2·3	7·7	1·0	3·5	1·1	4·7	2·1	3·3	1·7	3·2
	·75	3·7	4·0	3·5	3·8	1·8	2·4	1·7	2·4	2·5	2·4	2·1	1·4
	1	4·4	-	4·7	-	2·5	-	2·4	-	2·1	-	2·5	-