EFFECTS OF NUTRIENT SUPPLY ON THE IMPORTANCE OF ABOVE- AND BELOW-GROUND COMPETITION IN SUCCESSIONAL GRASSLAND SPECIES.

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ABSTRACT. Recent discussions on the importance of above- and below-ground competition along productivity gradients are indicating a need for experiments separating those types of competition. We studied the effects of above- and below-ground competition at different nutrient levels, to evaluate their relative importance on four species from a grassland successional series. The total effect of competition did not change but its quality did change at different nutrient supplies. Most of the reduction of growth at the lowest nutrient level could be ascribed to root competition. At a high nutrient level the relative importance of root and shoot competition was the same or shoot competition was more important. Allocation and architecture measurements indicated that plasticity of architecture (distibution within the shoot) was a better explanation for the successional position of the experimental species than the dry matter allocation to roots, stems and leaves.

INTRODUCTION

Recent debates about the importance of competition along productivity gradients, are indicating a need for experiments separating above- and below-ground competition. The cessation of fertilizer application of formerly agricultural hay-fields in the Netherlands leads to a change from swards which are dominated by only a few species to species-rich communities (Bakker 1987, 1989). This grasslands successional series is probably initiated by a lower nutrient availability and leads to a lower standing crop. This might indicate a shift from light limitation towards nutrient limitation. This pattern of resource availability is reverse as in old field succession as described by Tilman (1985, 1988). However any theory about the mechanism of succession should not depend on the direction of change. Tilman (1988) hypothesised that the species occuring in nutrient poor stages would be charaterized by a higher allocation of available resources to the roots, which should make them better competitors for nutrients. The species of a rich soil would allocate more resources to the stem and leaves which should make them better competitors for light. The mechanism behind the resource ratio hypothesis of succession is therefore that the outcome of competition depends on allocation patterns and resource availabilities.

The competition-concept of Grime (1979) and Thompson (1987) is also concerned with these mechanisms of competition. Their competition-concept considers both a low nutrient and a low light level as stress factors which will select for similar life histories. Grime and Tilman agree that soil nutrient levels, light, disturbance and competition are important factors influencing plant community structure. However, they disagree about the ways in wich these factors interact to structure plant communities. Grime and Thompson assume that competition only occurs at high nutrient levels. Tilman assumes that competition occurs at every nutrient level, but that the quality of competition differs at different nutrient levels. Root competition would be more important at low nutrients while shoot competition would be more important at high nutrients. Berendse (1989) and Olff (1989a) found a higher shoot:root ratio of species from poorer successional stages, which contradicts the asumptions of the resource ratio hypothesis of Tilman.

Succession may be characterized by a change of species composition. New species have to establish themselves in an already excisting plant community. Esthablishment can take place after seedflow or regeneration from the seedbank (Harper 1977). To understand the mechanisms of succession it is therefore necessary to do experiments on the process of esthablishment of invading species in an existing community. Snaydon and Howe (1986) experimented with invading grass seedlings in an established ryegrass sward in relation to gaps and disturbance. However they did not regard the competitive ability of the species as depended on their ecological distribution. We used their technique for separating the effects of above- and below-ground competition on growth and allocation at different nutrient levels, to evaluate their relative importance along a productivity gradient.

MATERIALS & METHODS

Experimental species. Four species with different successional positions were selected for the experiment (Table 1). Lolium perenne L. and Rumex acetosa L. are found in fertilized meadows and pastures. Anthoxanthum odoratum L. and Plantago lanceolata L. are species which increase in abundance after the fertilization of these pastures is stopped.

Experimental design. Seeds of each species were germinated at 15/25°C on wet filter paper. After 7 days the seedlings of Lolium and Anthoxanthum were transferred to pots (ϕ 30 cm), 1 species per pot, each containing 18,000 g of silver sand and 5% (v/v) perlite. The seedlings were planted in three circels with a radius of 1.25, 3.75 and 8.75 cm respectively. Each circel consisted of 8 seedlings which were placed at regular distances of each other. The pots were placed in a greenhouse in april 1989 with an average temperature of 21°C and a relative humidity of ± 50%. Three times a week the pots received 1 liter of nutrient solution. On the other days the plants were superficially watered with demineralized water. After four weeks the invading species were planted in the pots. These seedlings were also germinated for 7 days on wet filter paper at 15/25°C. In each pot 8 seedlings of each species were planted (one species per pot), four between the inner and middle circle and the other four between the middle and outer circle of the sward species (Fig. 1). In this way the invading species experienced sward-densities of respectively 800 and 9000 plants/m^2 . The invading species were also planted in pots without a sward (0 plants/m^2). Half of the pots received a below ground PVC tube around the 8 invading seedlings to prevent root competition. The PVC tubes had a diameter of 4 cm and length of 28 cm and were installed prior to sward planting. In the treatment which involved the exclusion of root competition were the invading species transplanted in these tubes. The nutrient levels were dillutions of the same stock (Table 2).

This revealed a design in which the factors were:

(1) two types of sward (Lolium and Anthoxanthum)

(2) four invading species (Lolium, Anthoxanthum, Rumex and Plantago)

(3) two nutrient levels

(4) three types of competition (none, shoot and full)

(5) two densities (800 plants m^2 , 9000 plants m^2).

Each combination of treatment was replicated in two blocks (pots).

The two grass species were not planted in the pots in which their own sward was growing, because of practical reasons and because we were not interested in interspecific competition.

Measurements. During the course of growth several traits of the invading species were measured (Table 3). Performed measurements were: length and width longest leaf, number of leaves, number of tillers, length of petioles(dicots) or leafsheath(grasses) of the longest leaf and number of spikes. The petiole to leaf ratio was computed by dividing the petiole length by the sum of petiole and leaf length. The dry weight of the plants was estimated as leaf number*leaf length (for Lolium and Anthoxanthum) or leaf number*leaf length*leaf width (for Rumex and Plantago) at four moments during growth. At the same time these measurements were performed on single-grown plants of the same species, which were harvested, dried and weighed afterwards. This allowed the computation of regression equations between estimated and actual dry weights.

All plants were harvested within a week, 32 days after planting the invading species. The leaf area of each shoot was determined using a Li-Cor photo-electric leaf area meter. The specific leaf area was computed as the leaf area divided by the dry weight of the leaf. The shoot and root dry weight were measured after drying at 50°C for 48 hours. The shoot was devided in leaves higher and lower than 4 cm and in petioles higher and lower than 4 cm and in flowers, in order to describe differences in vertical distribution of biomass

Statistical analysis. All weight and size charateristics of the invading species were logarithmic transformed, to reduce inhomogeneity of variances, and subjected to analysis of variance (ANOVA). Contrasts between groups were computed for length of longest leaf using the Student-Newman-Keuls test, or orthogonal contrasts within the ANOVA.

RESULTS

Yield of swards. The yield of both types of swards was increased (Fig. 2) at higher nutrient levels. The differences between the two swards were very small. Lolium had a higher root dry weight, but a lower shoot dry weight than Anthoxanthum.

Total dry weigt of invading species.
The results of the analysis of variance for total dry weight are listed in Table 4. The most important factors explaining the variance in total dry weight were competition, nutrients, density and the interaction competition x density. The competition effect in the Lolium sward explained a much smaller part of the variance than competition in the Anthoxanthum sward.

The yield of the four invading species increased with nutrient supply (Fig. 3). The increasing densities had a decreasing effect on the yield, especially at the highest nutrient level. Plants grown only with shoot competition had a higher yield than plants grown in full competition. The differences between plants grown at 800 or 9000 plants/m² were very small but significant (Table 5). Because of the great difference between 0 and 800 plants/m² the two highest densities were taken together in the rest of the analysis.

The below-ground tubes reduced the growth of the invading seedlings independendly from the competition treatment. To account for this effect the dry weight of plants growing in tubes were multiplied with a correction-factor. This correction-factor was computed as the ratio of total dry weight of plants in tube and without tubes in pots without sward. All other measured traits are submitted to a similar correction computed seperately for each trait (Table 6).

Reduction of growth by competition. It was impossible to separate the roots of the invading species from the sward species at high nutrient conditions in full competition. Therefore were at this treatment combination only the shoot dry weight analyzed. The effect of competition was defined as percentage the reduction in shoot dry weight of plants grown in a sward compared to plants grown without a sward. This reduction can be partitioned in a part that is caused by root competition and a part that is caused by shoot competition. The reduction caused by shoot competition is the difference between invading species shoot dry weight grown without a sward and grown in a sward with tubes. The reduction caused by root competition was defined as the difference in shoot dry weight of invading species grown in a sward with tubes and without tubes. The total effect of competition (Fig. 4) was in both high and low levels of nutrient supplies of the same magnitude, but the relative importance of root and shoot competition was very different. Most of the reduction of growth at the lowest nutrient level could be ascribed to root competition. At a high nutrient level the importance of root and shoot competition was the same or shoot competition was more important. When the two types of sward are compared in their ability te reduce the growth of invading species the only clear differences were found at low nutrients. Lolium had a greater influence on shoot competition compared to the Anthoxanthum sward. Both Lolium and Anthoxanthum were more influenced by shoot competition in low nutrients than Rumex and Plantago.

Allocation. The effects of the treatments on root dry weight were small compared with the effects on shoot dry weight. The comparision of allocation of dry weight to roots, leaves, petioles and flowers shows that all species had a lower root weight ratio (RWR) at high nutrient conditions (Fig. 5). With an increase of competition (contr => shoot => full) root dry weight fraction increased suggesting an increase in nutrient or light limitation. The reproductive effort of Plantago decreased with increasing competition.

The allocation within the shoot shows that none of the species altered their vertical dry weight distribution at low nutrients with increasing competition (Fig 6). However, at high nutrients with increasing competition their was a greater allocation to the highest leaves. Only Rumex in full competition with Anthoxanthum showed a different pattern, with a lower allocation to the highest leaves.

Length longest leaf. The length of the longest leaf was greater at higher nutrient level (Fig 7). Shoot competition had little effect at low nutrients but at high nutrients Plantago, Lolium and Anthoxanthum had longer leaves than the control. However this longer leaf was not maintained at full competition. Rumex did not increase its leaf length under shoot competition. The decrease at full competition was the similar as in the other three species.

In the analysis of variance (Table 7) competition, nutrients and species were the major factors explaining the variance in leaf length. All possible interactions between these three factors were significant.

Length of Petioles to leaf ratio. The petiole to leaf ratio was only affected by competition in Rumex (Fig 8). At high nutrients the length of the petioles was greater than at low nutrients. This ratio increased with shoot competition and this increase was maintained at full competition.

Length:Width ratio. The length:width ratio of the longest leaf shows that in Rumex in full competition this ratio was decreased at both nutrient levels and in both swards (Fig 9). Plantago further increased this ratio at full competition.

Specific leaf area. The specific leaf area (Fig. 10) was greater for all species at the high nutrients level, Full competition decreased the specific leaf area and shoot competition increased the specific leaf area at both nutrient levels and in both swards.

Growth. The growth of the invading species during the experiment was calculated (Table 8) from estimated shoot dry weight at different times. The results (Fig. 11) show that differences between control, shoot and root competition occured after 20 days. And were in most cases constantly increasing with time.

DISCUSSION

It is clear from our results that it is not possible to find a single factor which can explain the successional position of the four species. Snaydon and Howe (1986) found with an increasing ryegrass density from 40 to 160 plants/m^2 little effect on the dry weight of invading seedlings. The densities used in this study, 800 and 9000 plants/m^2 are compared with their study very high, but the time before harvesting the seedlings was in our study 32 days and Snaydon and Howe harvested the plants after one year. Furthermore, the experiment was performed in a greenhouse which resulted in higher growth rates. However, the differences between 800 and 9000 plants/m^2 were very small and therefore were taken together.

The used technique of below-ground tubes to prevent root competition worked very good, only when plants grew bigger they found a negative effect of the tubes. Using below ground-tubes restricts the duration of the experiments unless bigger tubes are used. However, this limits the density at which plants can be grown. It appeared to be necessary to run a control without a sward with and without tubes, so tube effects can be measured. Snaydon & Howe found also a lower seedling yield in the presence of below-ground tubes. They appointed this to the restriction of nutrient uptake. But probably this lower yield was caused by the negative effect on growth by the tubes.

It is stricking that an Anthoxanthum sward has less roots than a Lolium sward but the reduction in growth of the invading species, at low nutrients, is almost completely caused through root competition (Fig 2, Fig 4). It is shown that competition is of equal importance under low and high nutrient levels, but shifts from root to shoot competition by increasing nutrient availability. This is in agreement with the resource-ratio hypothesis of Tilman(1988), but the expected differences in allocation patterns were not found. The allocation proces seems to be an allocation within the root, Anthoxanthum reduces its rooting depth (Olff 1989b) but seems to be a better competitor for nutrients. At high nutrients there were no differences in the importance of shoot competition between the two swards. The allocation within the shoot shows that Plantago could in lengthen its leaves and make them smaller under increasing competition for light. An adaptive plastic reaction of Rumex might be found in its petioles, the response to competition is to make them longer. This adaptation of Rumex is usefull in a dense vegetation, by lengthening its petioles it is possible to overgrow other plants and escape from light limitation. An other adaptation to light limitation seems to be the plasticity in specific leaf area. Rumex and Lolium are showing a greater plasticity in changing specific leaf area compared to Anthoxanthum and Plantago. These two species can enhance their specific leaf area under lower light conditions, as was also found by Olff(1989b). This might be an advantage for these two species since they are found under light limiting conditions, in the earlier successional stages. The range in which Plantago and Anthoxanthum can change their specific leaf area is much smaller than in Rumex and Lolium. It is for Plantago and Anthoxanthum not necessary to be able to adjust their specific leaf area because they occur in a successional stage where light is not limiting. Lolium and Rumex occur in a successional stage where they are exposed to various light conditions, dark in the sward but light when the plants have overgrown their neighbours.

The interspecific differences in plasticity of traits seem therefore to be the important factors in the mechanism behind succession. The allocation within the root and within the shoot seems to be of more importance than allocation between root and shoot. Plasticity of some traits are different for species from different successional stages. The four species in the present study show still an overlap in their response to nutrient and competition. It might be interesting to see how species react from the very poor successional stages, and to examine the importance of root and shoot competition under field conditions (see Wilson&Tilman 1989).

Bakker, J.P. (1987) Restoration of species-rich grassland after a period of fertilizer application. In Disturbance in Grasslands (ed. J. van Andel, J.P. Bakker & R.W. Snaydon), pp 51-66. Junk, Dordrecht.

Bakker, J.P. (1989) Nature management by cutting and grazing. Kluwer Academic Publishers, Dordrecht.

Berendse, F. (1989) Competition and nutrient losses from the plant. In Variation in growth rate and productivity. Physiological, biochemical and morphological background; ecological and agronomic consequences (ed. J.T. Lambers), (in press) SPb Academic Publishers, The Hague.

Grime, J.P. (1979) Plant strategies & vegetation processes, Wiley & Sons, Chichester.

Harper, J.L. (1977) The population biology of plants, Academic Press, London.

Olff, H., van Andel, J. & Bakker, J.P. (1989) Biomass and shoot: root allocation of five species from a grassland succession series at different combinations of light intensity and nutrient availabiliy. Functional ecology (in press).

Olff, H. (1989b) Separation of level and ratio effects of light and nutrients on growth, allocation and architecture of successional grassland species. (in prep.).

Snaydon, R.W. & Howe, C.D. (1986) Root and shoot competition between established ryegrass and invading grass seedlings. Journal of Applied Ecology 23, 667-674.

Thompson, K. (1987) The resource ratio hypothesis and the meaning of competition. Functional Ecology 1, 297-315.

Thompson, K. & Grime, J.P. (1988) Competition reconsidered, a reply to Tilman. Functional Ecology 2, 114-116.

Tilman, D. (1980) Resources: A graphical mechanistic approach to competition and predation. American Naturalist. 166, 362-393.

Tilman, D. (1985) The resource-ratio hypothesis of plant succession. American Naturalist. 125, 827-852.

Tilman, D. (1987) On the meaning of competition and the mechanisms of competitive superiority. Functional Ecology 1, 304-316.

Tilman, D. (1988) Plant strategies and the dynamics and structure of plant communities. Monographs in population biology 26. Princeton University Press, New Jersey.

Table 1. Seed sources of the experimental species.

Species	Abrev.	Population	Location
Lolium perenne	LP	Trade seed	
Anthoxanthum odoratum	AO	Oude Molen	
Plantago lanceolata	PL	Burgvallen	53°N 6°40'E
Rumex acetosa	RA	Burgvallen	53°N 6°40'E

Table 2. Levels of nutrients in solutions (mmol/l). Levels of micronutrients are the same for both solutions.

Nutrient	Low	High
K^+	0.58	4.67
Ca^{2+}	0.38	3.00
Mg^{2+}	0.17	1.33
NO_3^-	1.00	8.00
$H_2PO_4^-$	0.08	0.67
SO_4^{2-}	0.29	2.33

Table 3. Time (days after transplanting) the of measurements on the invading species.

Trait	Lolium	Anthoxanthum	Rumex	Plantago
Number of leaves	1-16-23-32	1-16-23-32	1-16-23-32	1-16-23-32
Length longest leaf	1-16-23-32	1-16-23-32	1-16-23-32	1-16-23-32
Width longest leaf			1-16-23-32	1-16-23-32
Length petiole			1-16-23-32	
Length sheat	1-16-23-32	1-16-23-32		
Number of tillers	1-16-23-32	1-16-23-32		
Number of flowers				32
Leaf dry weight	32	32	32	32
Petiole dry weight			32	32
Sheat dry weight	32	32		
Root dry weight	32	32	32	32
Flower dry weight				32
Leaf area	32	32	32	32

Table 4. Analysis of variance of the effect of the type of competition, level of nutrients and density of the sward on the total dry weight of invading species in two types of sward.
F-values are given with their level of significance (*-p<0.05; **-p<0.01; ***-p<0.001; ns-not significant).
The total dry weight was log transformed prior to the analyses.

Effect	df	F(Lolium sward)	F(Anthoxanthum sward)
Competition	1	186.37***	1072.28***
Nutrients	1	681.86***	835.62***
Species	2	46.32***	44.26***
Density	2	698.25***	1651.10***
Com x Nut	1	0.54 ns	6.82***
Com x Spe	2	1.31 ns	8.45***
Com x Den	2	280.58***	806.33***
Nut x Spe	2	10.32***	21.69***
Nut x Den	2	24.46***	76.57***
Spe x Den	4	2.42*	14.14***
Com x Nut x Spe	2	3.53*	3.02*
Com x Nut x Den	2	0.36 ns	1.89 ns
Com x Spe x Den	4	2.68*	0.83 ns
Nut x Spe x Den	4	3.39**	6.46***
C x N x S x D	4	2.89*	0.48 ns

Table 5. Contrasts for the factor density for the ANOVA given in table 4.

	Lolium sward			Anthoxanthum sward		
Density	parameter estimates	t-value	p	parameter estimates	t-value	p
0-800	0.6699	28.37	<0.001	0.9035	44.28	<0.001
0-9000	0.7649	32.39	<0.001	1.0023	49.13	<0.001
800-9000	0,0950	3.48	0.001	0.0987	4.18	<0.001

Table 6. Correction factors for the different traits, neccesary because the tubes had a negative influence on the growth.

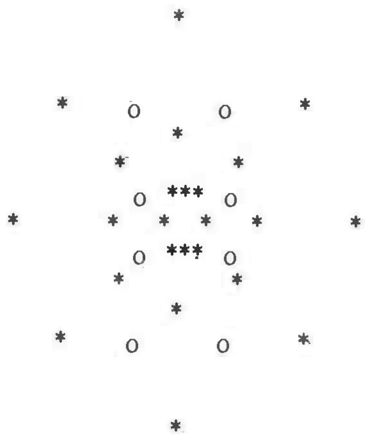
Low nutrients	Species			
Trait	LP	AO	RA	PL
Total dry weight	2.1103	1.9329	2.1456	1.9181
Leaf length	1.1100	1.3002	1.7156	1.3570
Leaf width			1.4051	1.6122
Petiole length			1.8557	
Sheat length	1.8644	2.1607		
Leaf dry weight	2.7329	2.2500	2.7761	1.9527
Leaf area	2.8435	3.4139	2.8844	2.4000
High nutrients				
Total dry weight	1.6785	2.0942	2.7846	2.0860
Leaf length	1.4439	1.7167	2.2339	1.7937
Leaf width			1.5947	1.6223
Petiole length			2.0472	
Sheat length	1.8503	1.8105		
Leaf dry weight	1.9066	2.1641	3.4725	2.3975
Leaf area	3.0705	3.3933	4.6183	3.2734

Table 7. Analysis of variance of the effect of type of competition and nutrients on the length of the longest leaf of the invading species in two types of swards.
F-values are given with their level of significance
(*-p<0.05; **-p<0.01; ***-p<0.001: ns-not significant).
The leaf length was log transformed prior to the analyses.

Effect	df	F(Lolium sward)	F(Anthoxanthum sward)
Competition	3	245.03***	503.18***
Nutrients	1	1985.80***	2236.84***
Species	2	947.85***	1110.73***
Com x nut	3	20.73***	41.74***
Com x Spe	6	47.32***	65.86***
Nut x Spe	2	24.53***	33.54***
Com x Nut x Spe	6	3.33*	4.17***

Table 8. Correlations between estimated and actual above-ground biomass. LL=length of longest leaf, NL=number of leaves, WL=width of longest leaf.

Low nutrients		
Lolium	Biomass= 0.00134+0.0000333(LL*NL)	r^2 =0.80***
Anthoxanthum	Biomass=-0.00166+0.0000754(LL*NL)	r^2 =0.92***
Rumex	Biomass= 0.00170+0.0000294(LL*NL*WL)	r^2 =0.92***
Plantago	Biomass= 0.00287+0.0000324(LL*NL*WL)	r^2 =0.84***
High nutrients		
Lolium	Biomass=-0.00234+0.0000801(LL*NL)	r^2 =0.91***
Anthoxanthum	Biomass=-0.02 +0.0000999(LL*NL)	r^2 =0.96***
Rumex	Biomass= 0.02 +0.0000178(LL*NL*WL)	r^2 =0.94***
PLantago	Biomass= 0.00098+0.0000283(LL*NL*WL)	r^2 =0.83***



* Sward species

o Invading species with or without below-ground tubes

Fig 1: Planting design in the pots.

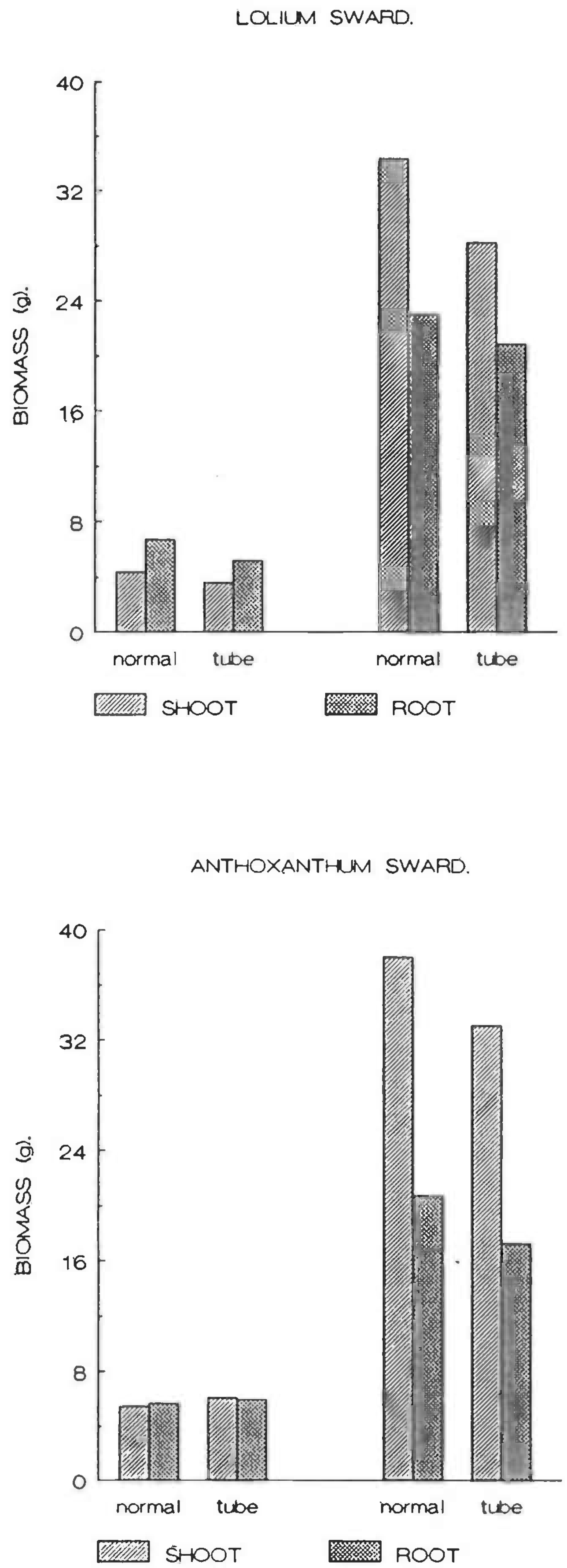


Fig 2: The yield of the two swards at two nutrient levels and with or without tubes.

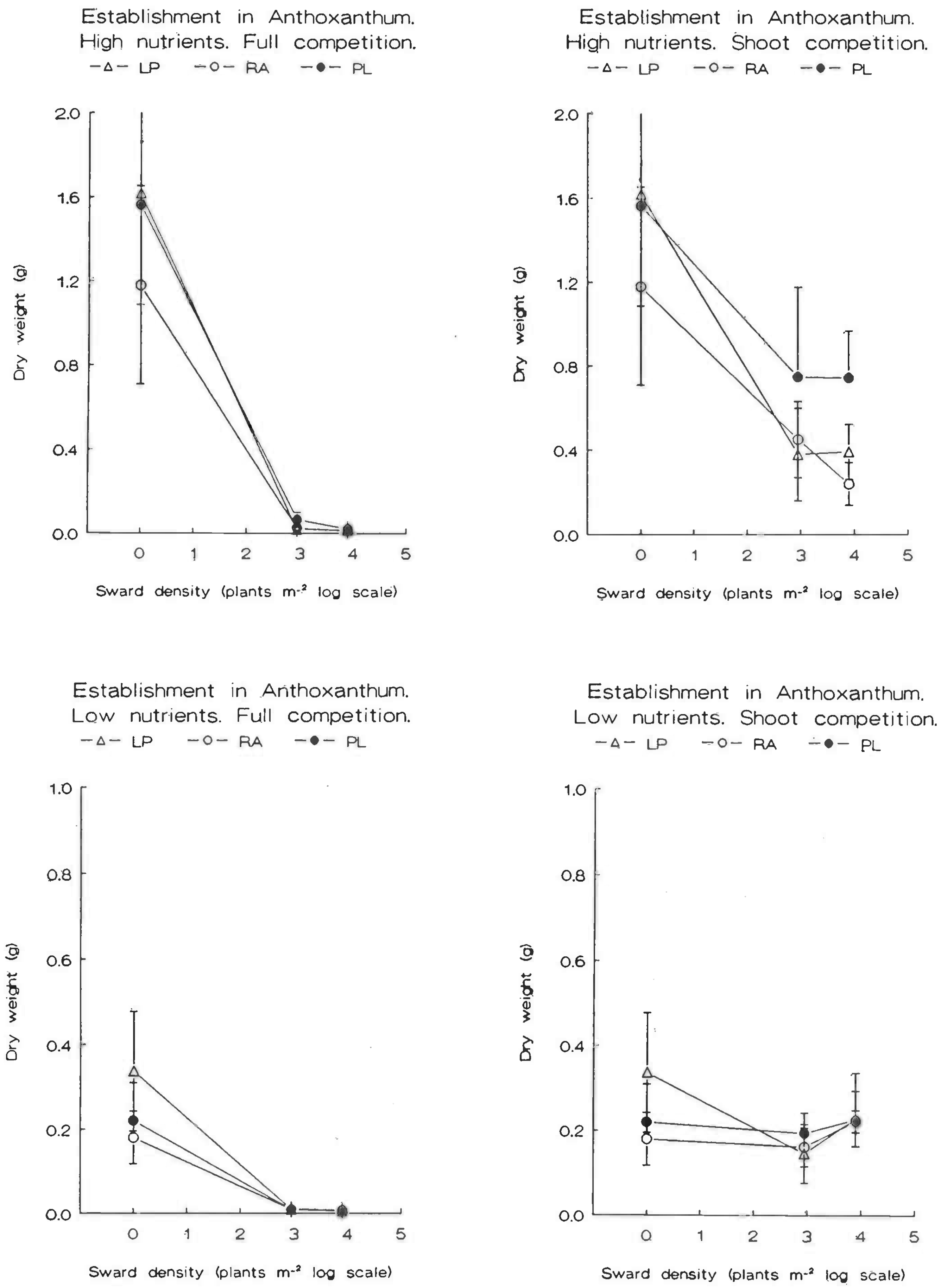
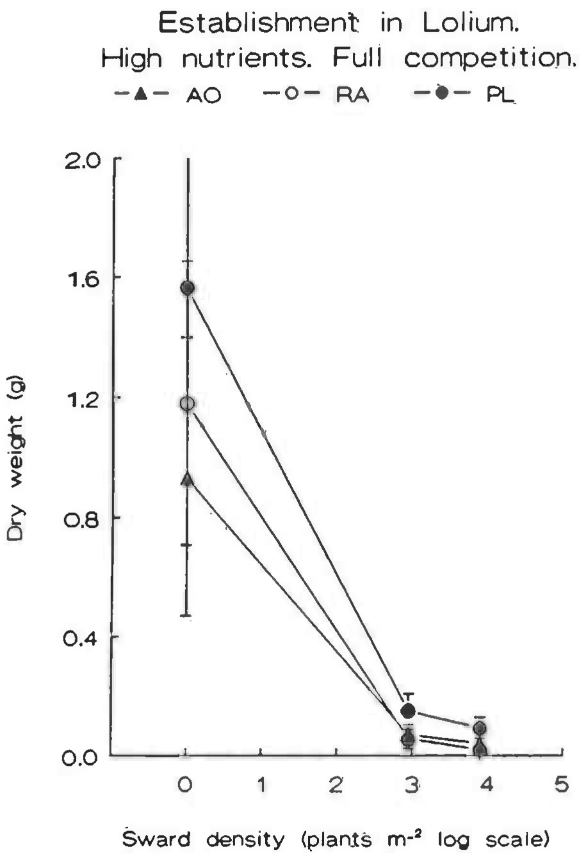
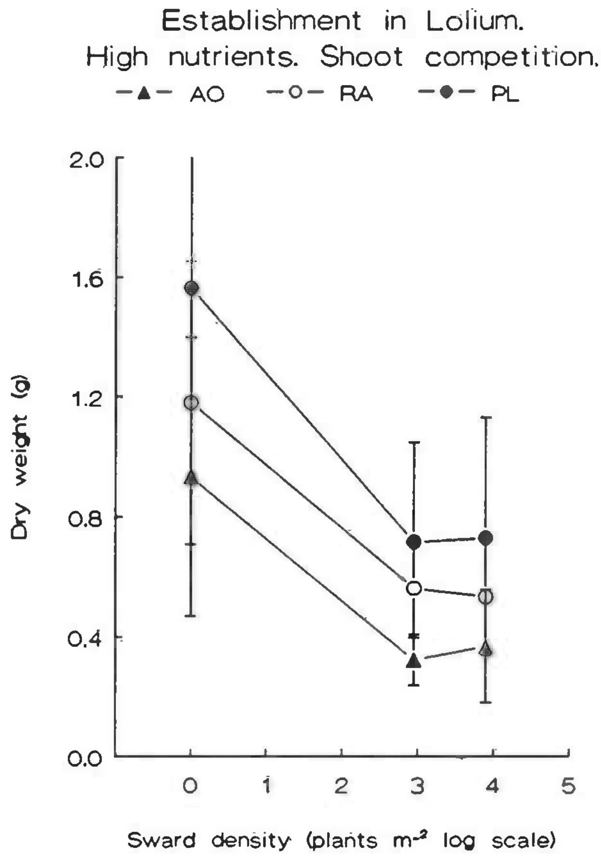


Fig 3: The yield of the four invading species, in two sward types, at two nutrient levels, and three types of competition. Total dry weight is given except at high nutrients in full competition than shoot dry weight is used.


Establishment in Lolium.
High nutrients. Full competition.
AO
RA
PL
Dry weight (g)
2.0
1.6
1.2
0.8
0.4
0.0
0
1
2
3
4
5
Sward density (plants m-2 log scale)


Establishment in Lolium.
High nutrients. Shoot competition.
AO
RA
PL
Dry weight (g)
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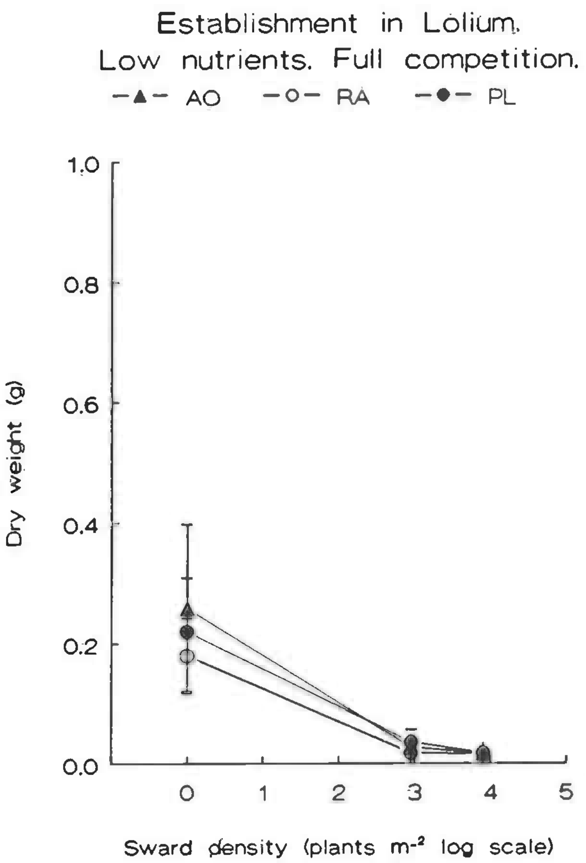
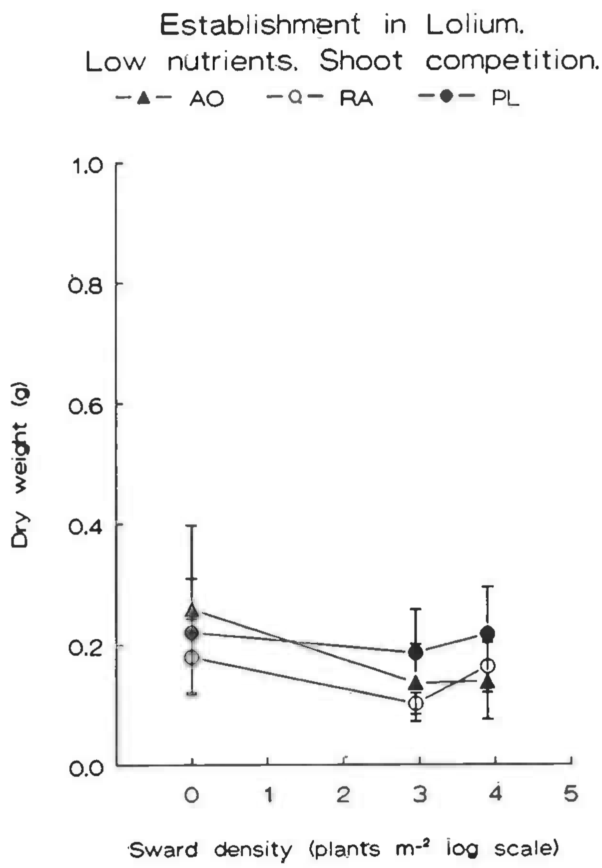
1.2
0.8
0.4
0.0
0
1
2
3
4
5
Sward density (plants m-2 log scale)


Establishment in Lolium.
Low nutrients. Full competition.
AO
RA
PL
Dry weight (g)
1.0
0.8
0.6
0.4
0.2
0.0
0
1
2
3
4
5
Sward density (plants m-2 log scale)


Establishment in Lolium.
Low nutrients. Shoot competition.
AO
RA
PL
Dry weight (g)
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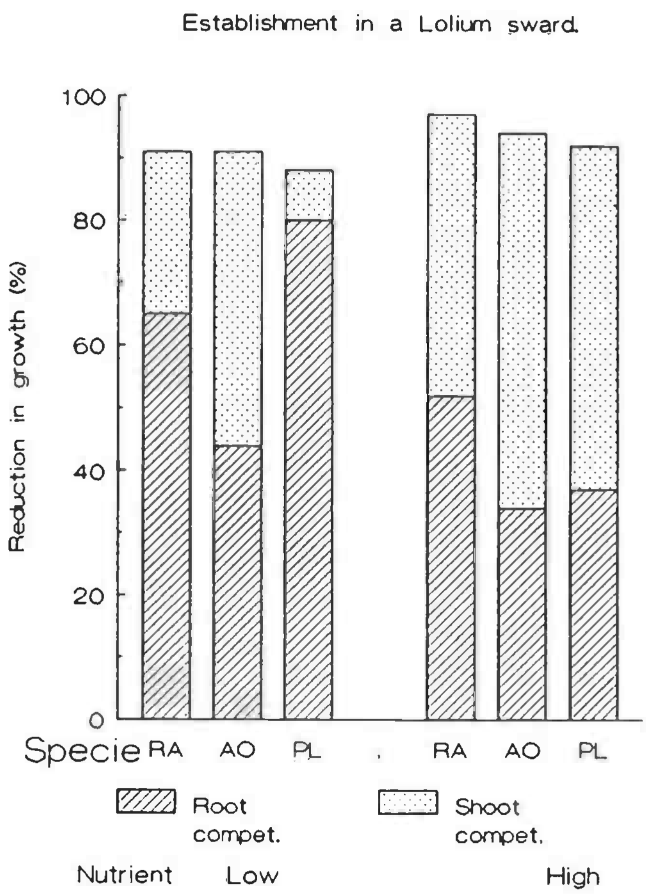
Sward density (plants m-2 log scale)



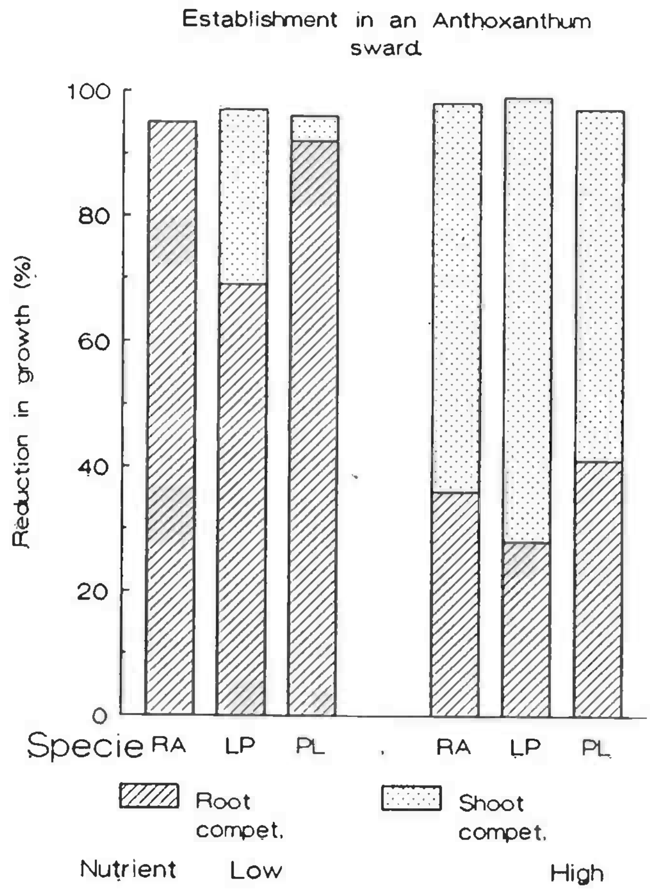


Fig 4: Reduction in growth of the four invading species by root or shoot competition. At two nutrient levels and two types of sward.

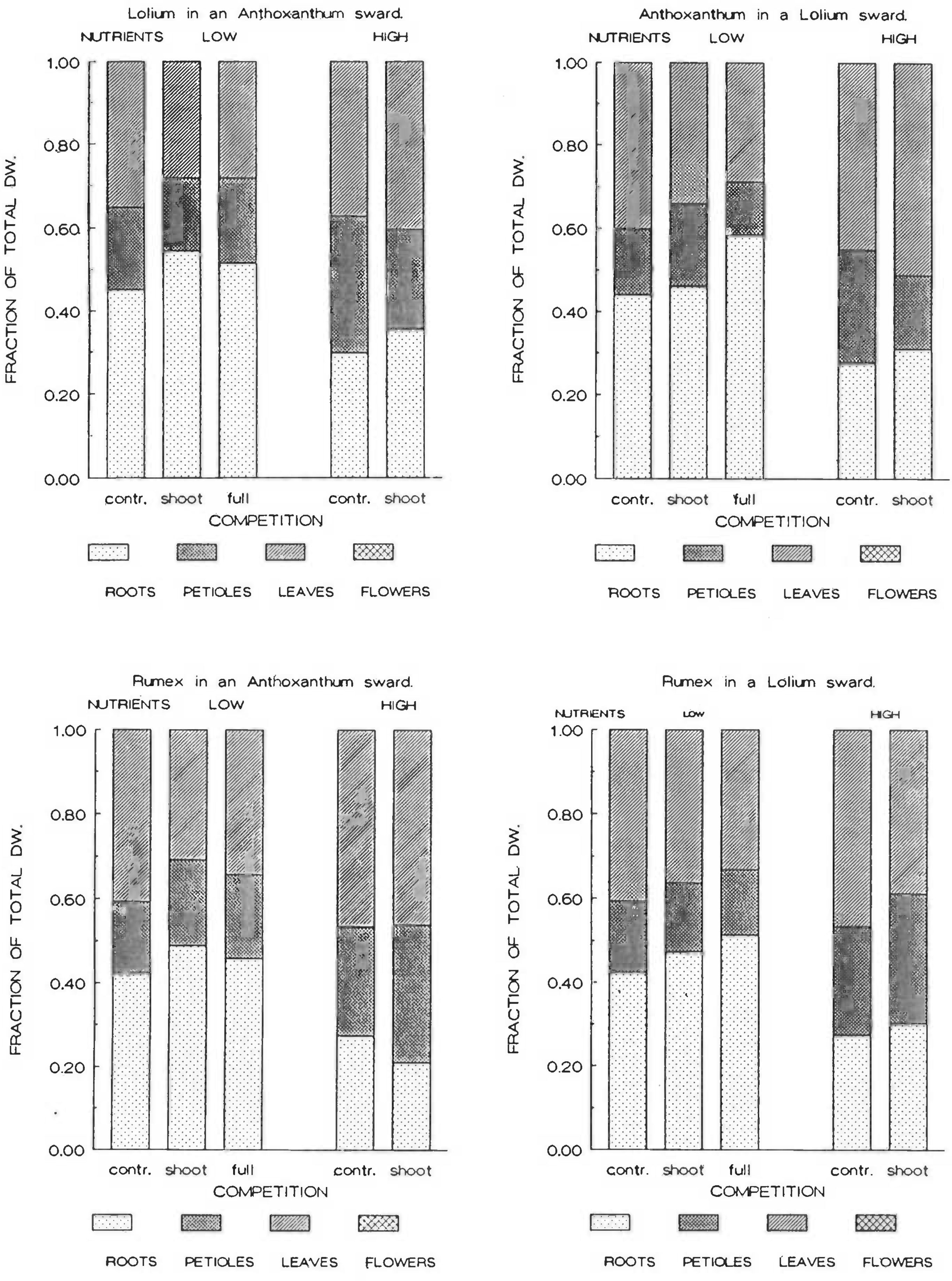
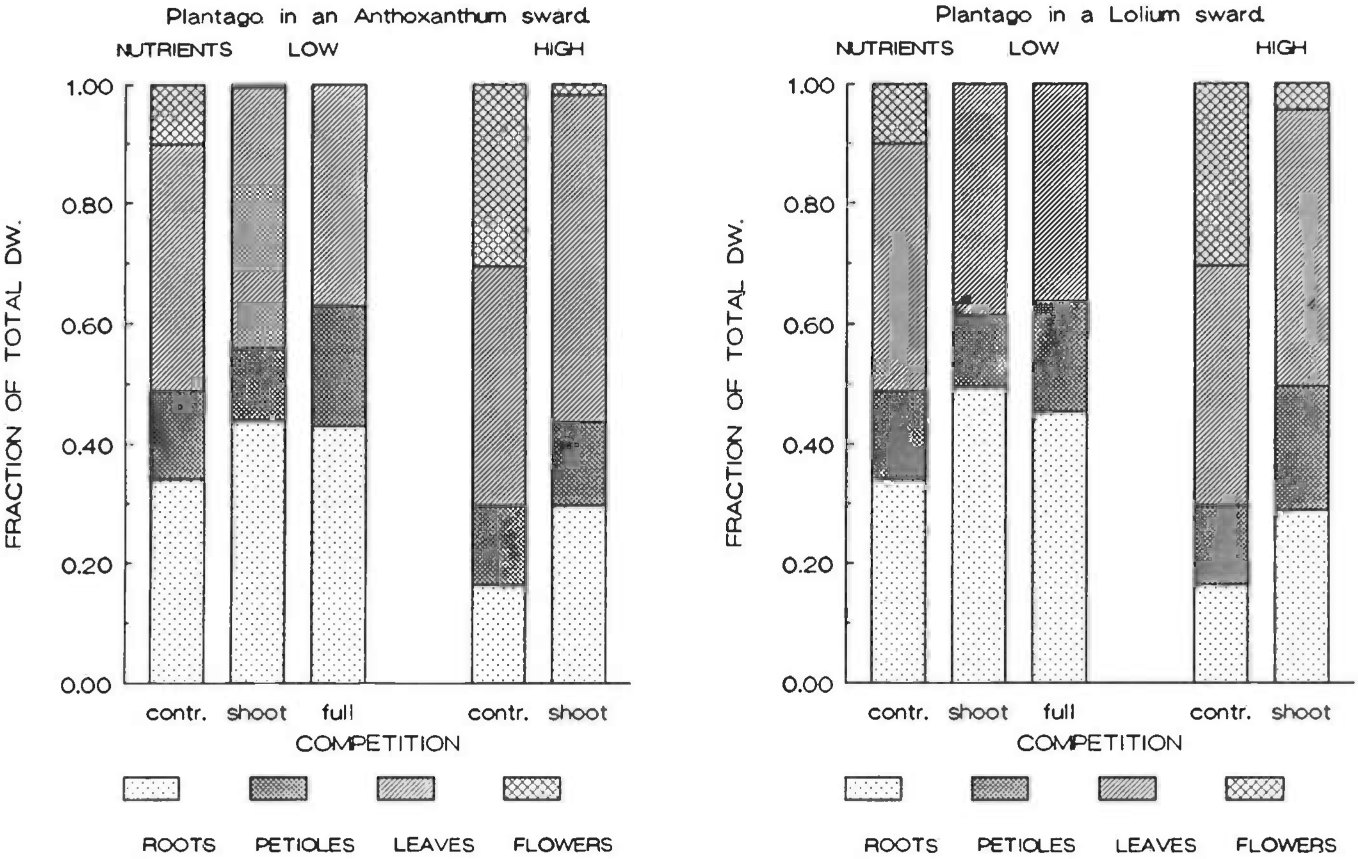


Fig 5: Allocation of dry weight of roots, leaves, petioles and flowers.



Plantago in an Anthoxanthum sward
NUTRIENTS LOW HIGH
1.00
0.80
0.60
0.40
0.20
0.00
FRACTION OF TOTAL DW.
contr. shoot full contr. shoot
COMPETITION
ROOTS PETIOLES LEAVES FLOWERS
Plantago in a Lolium sward
NUTRIENTS LOW HIGH
1.00
0.80
0.60
0.40
0.20
0.00
FRACTION OF TOTAL DW.
contr. shoot full contr. shoot
COMPETITION
ROOTS PETIOLES LEAVES FLOWERS

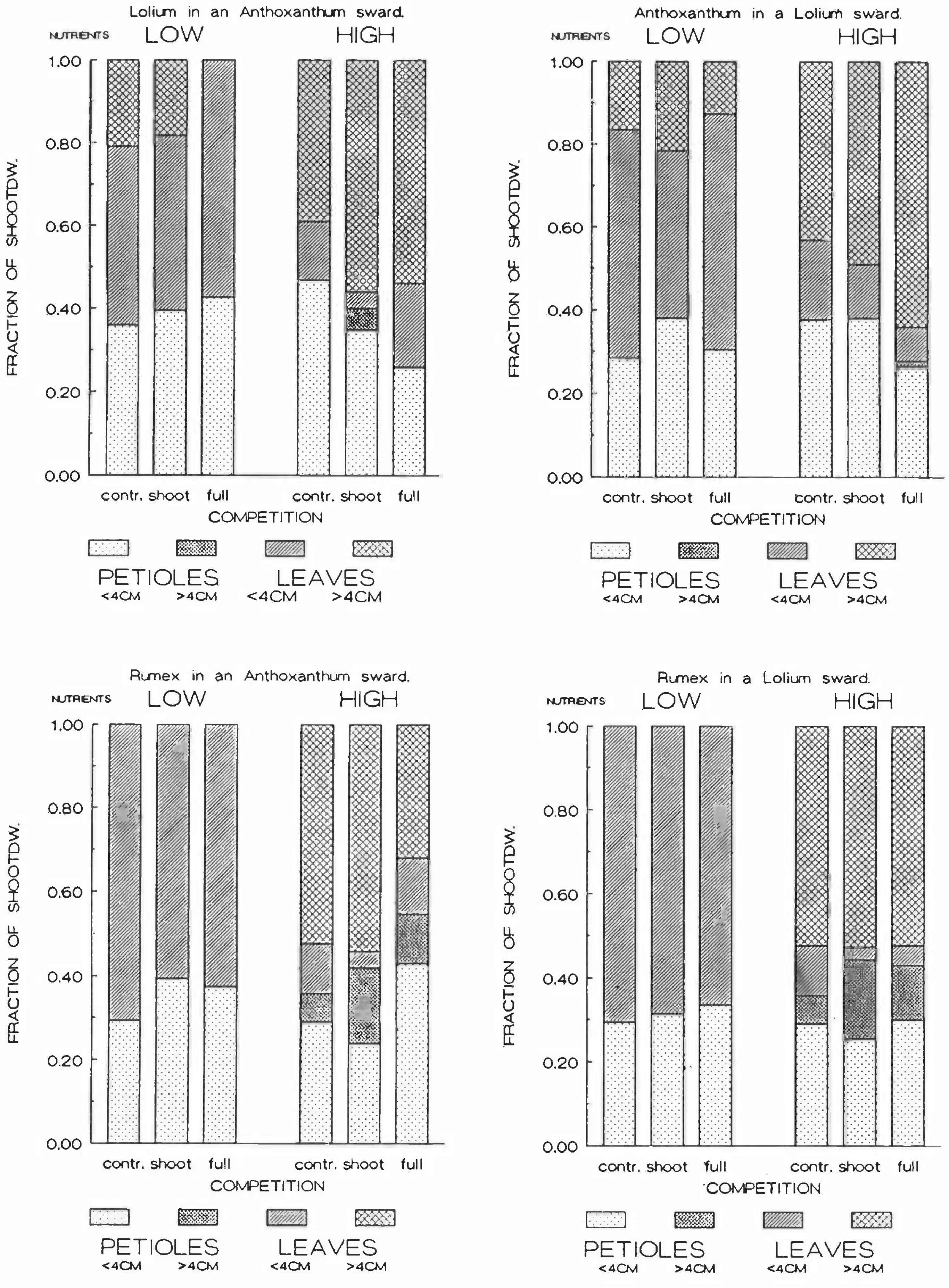
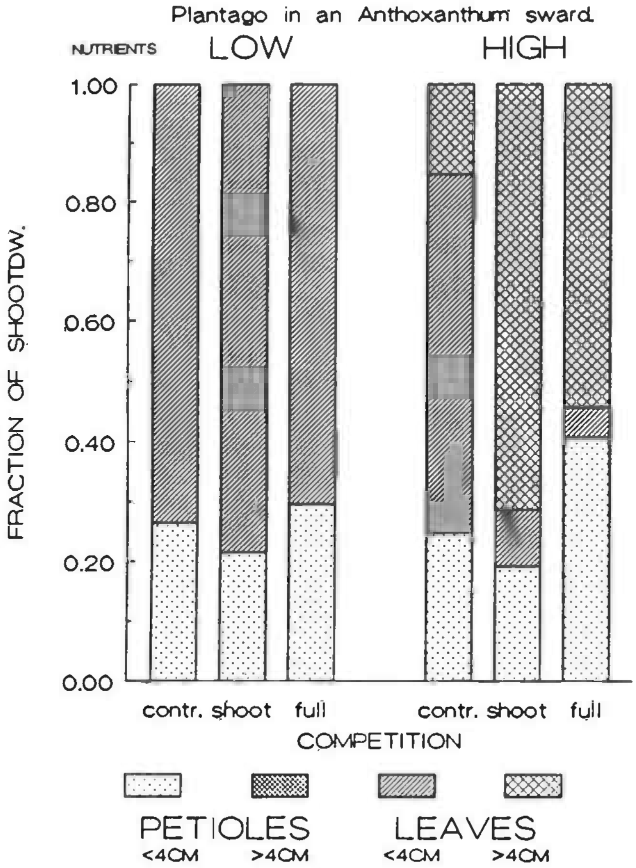
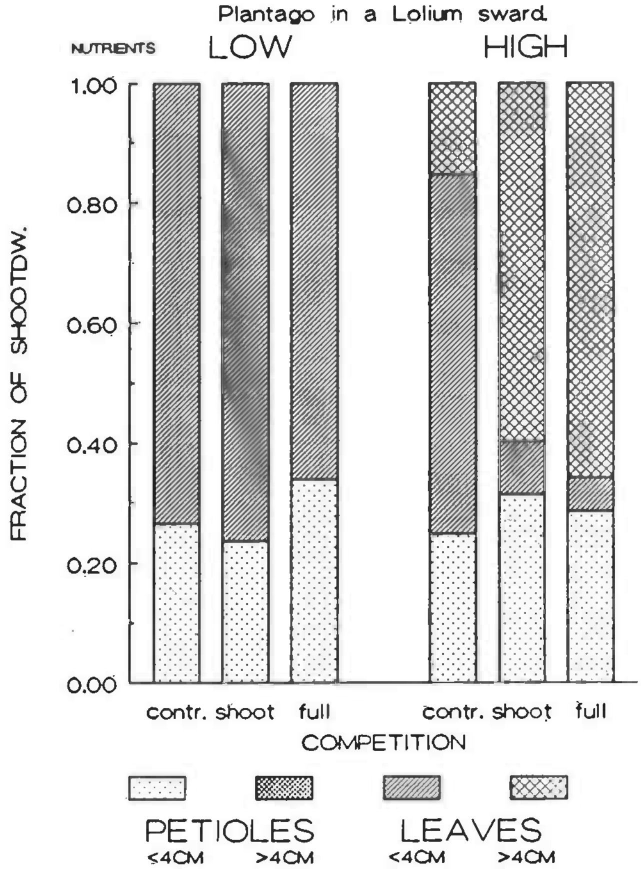


Fig 6: Allocation within the shoot, dry weigt fraction of low leaves <4cm, high leaves >4 cm, low petioles <4cm, high petioles >4cm and flowers is given.



Plantago in an Anthoxanthum sward
NUTRIENTS LOW HIGH
1.00
0.80
0.60
0.40
0.20
0.00
FRACTION OF SHOOTDW.
contr. shoot full contr. shoot full
COMPETITION
PETIOLES
<4CM >4CM
LEAVES
<4CM >4CM



Plantago in a Lolium sward
NUTRIENTS LOW HIGH
1.00
0.80
0.60
0.40
0.20
0.00
FRACTION OF SHOOTDW.
contr. shoot full contr. shoot full
COMPETITION
PETIOLES
<4CM >4CM
LEAVES
<4CM >4CM

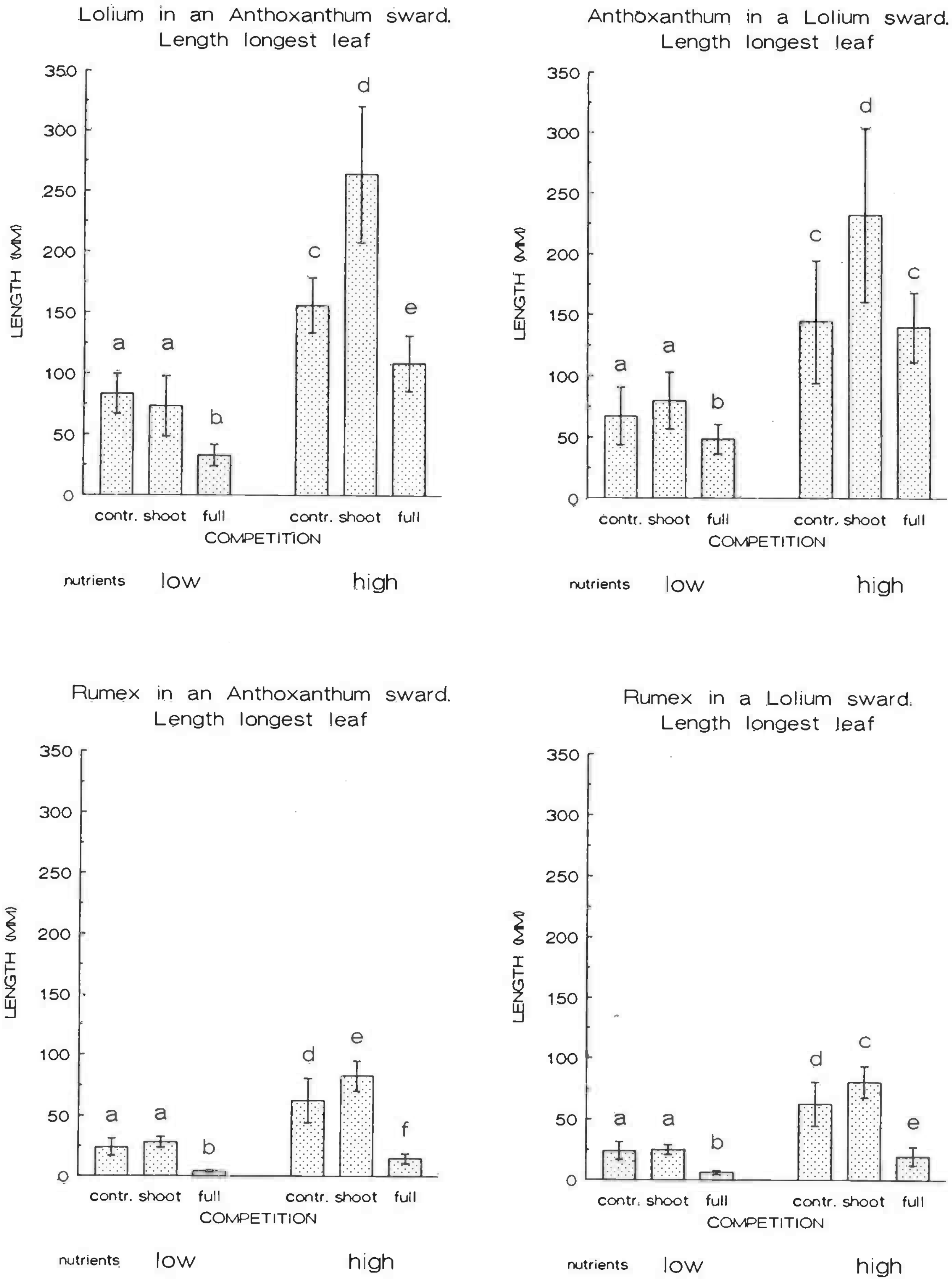
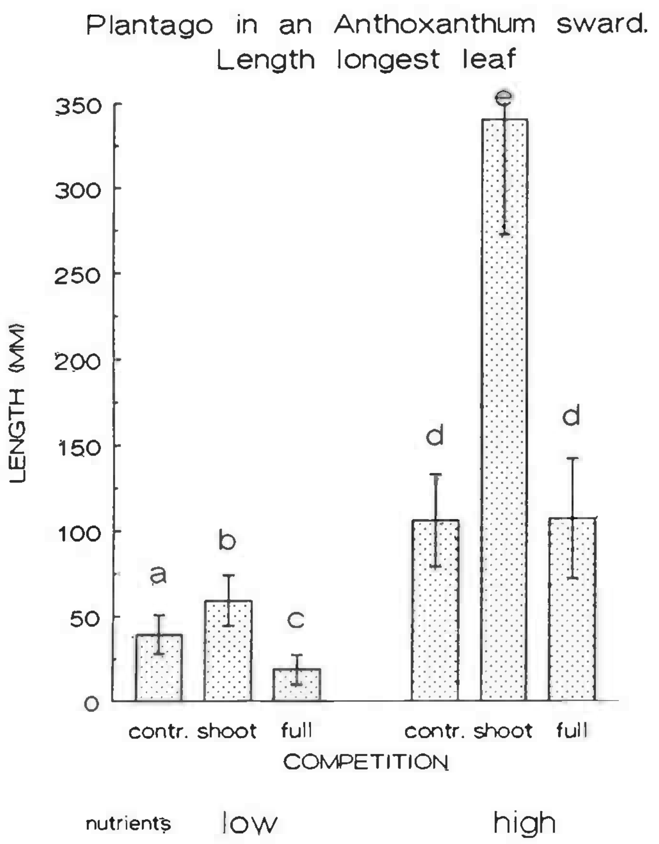
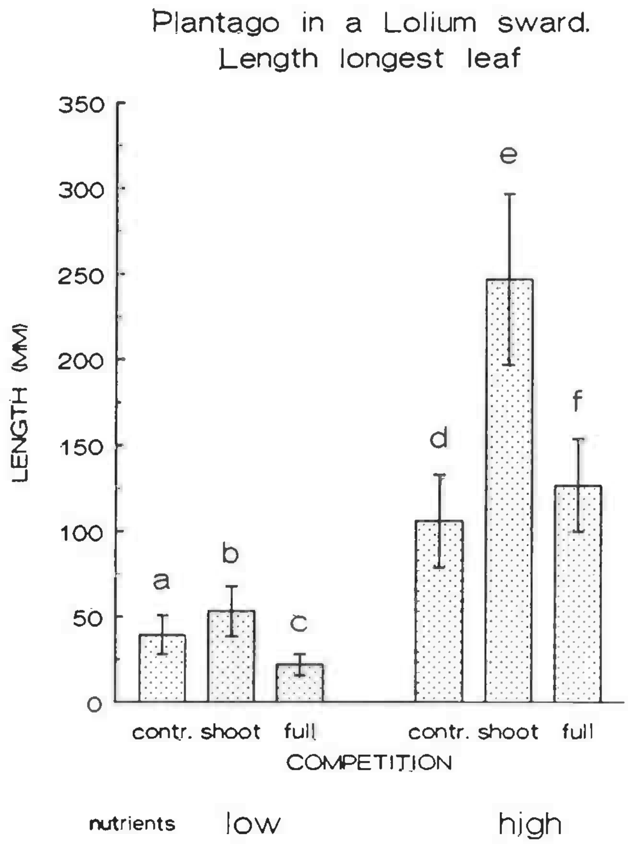


Fig 7: Length longest leaf by two nutrient levels, two types of sward and types of competition.



Plantago in an Anthoxanthum sward.
Length longest leaf
LENGTH (MM)
350
300
250
200
150
100
50
0
a
b
c
d
e
d
contr. shoot full contr. shoot full
COMPETITION
nutrients low high



Plantago in a Lolium sward.
Length longest leaf
LENGTH (MM)
350
300
250
200
150
100
50
0
a
b
c
d
e
f
contr. shoot full contr. shoot full
COMPETITION
nutrients low high

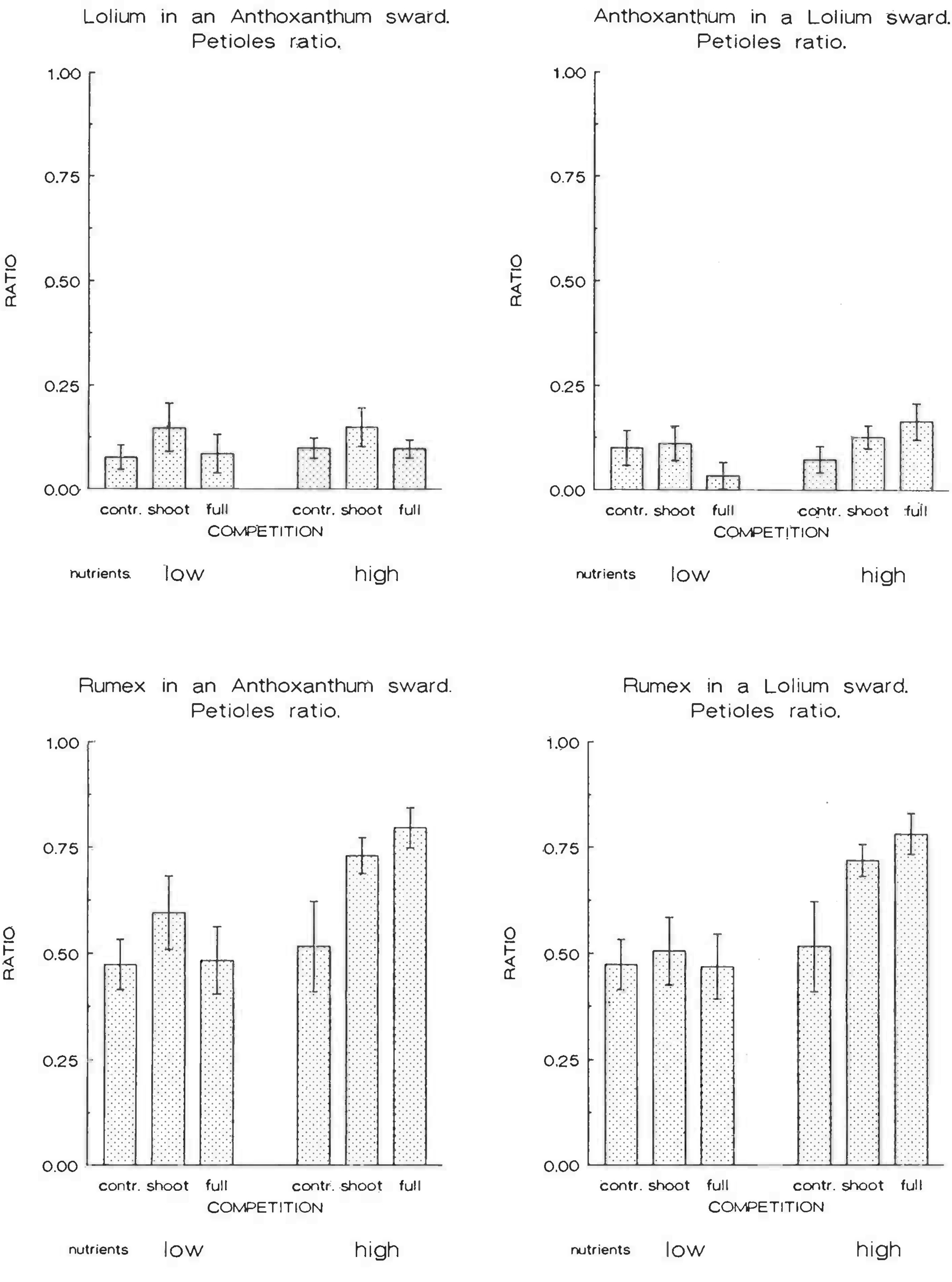


Fig 8: Petioles ratio by two nutrient levels, two types of sward and types of competition.

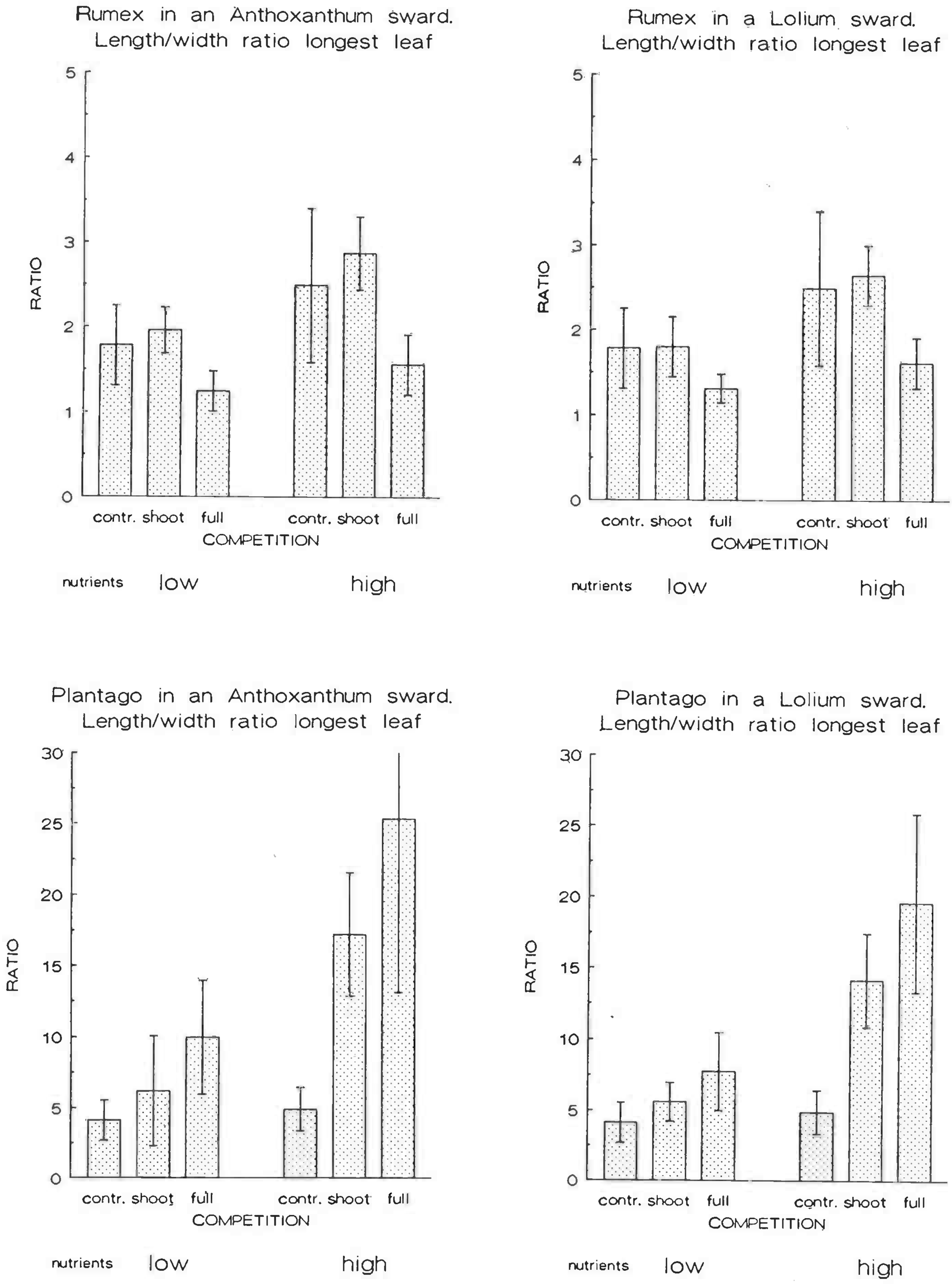


Fig 9: Length:Width ratio of the longest leaf, by two nutrient levels, two types of sward and types of competition.

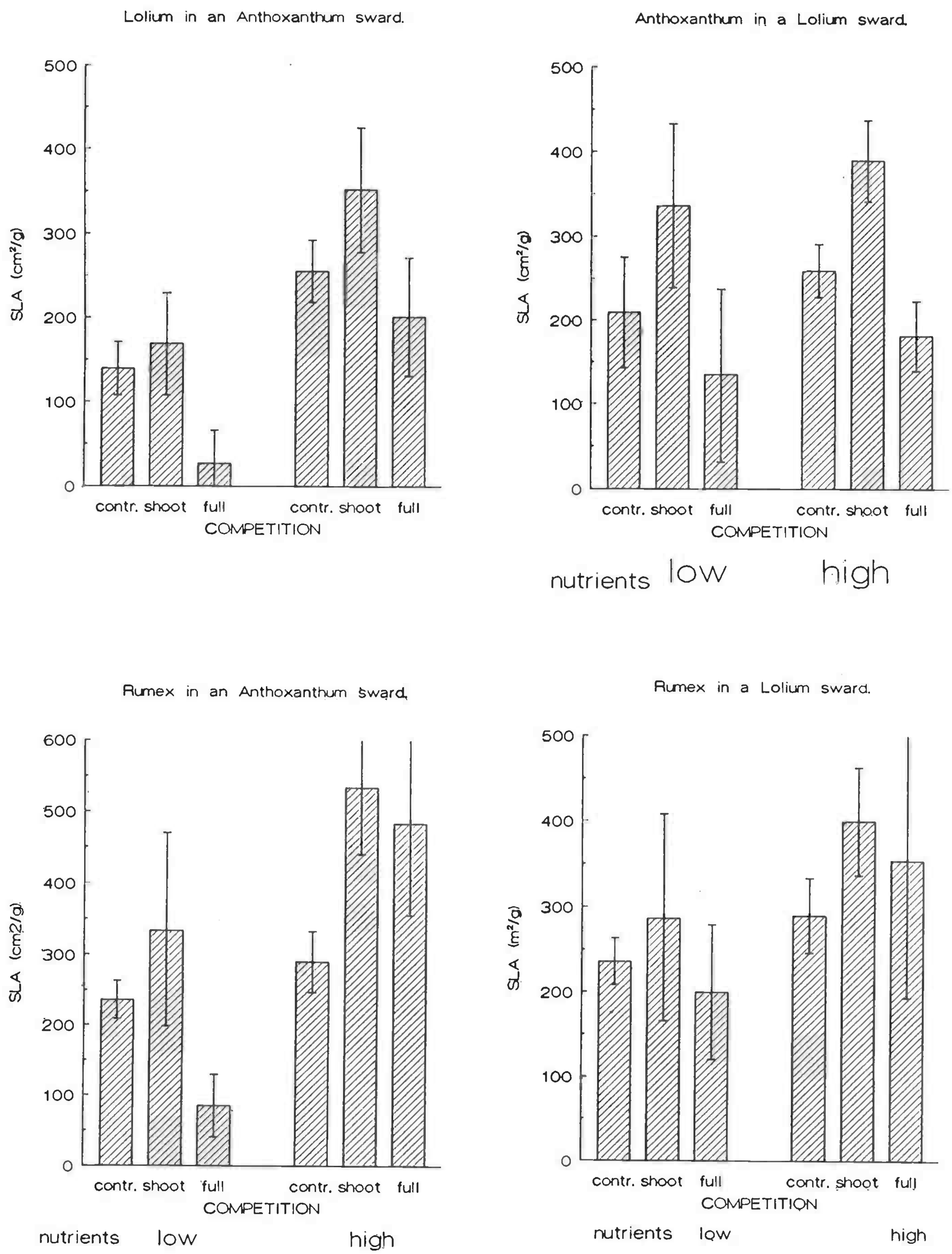
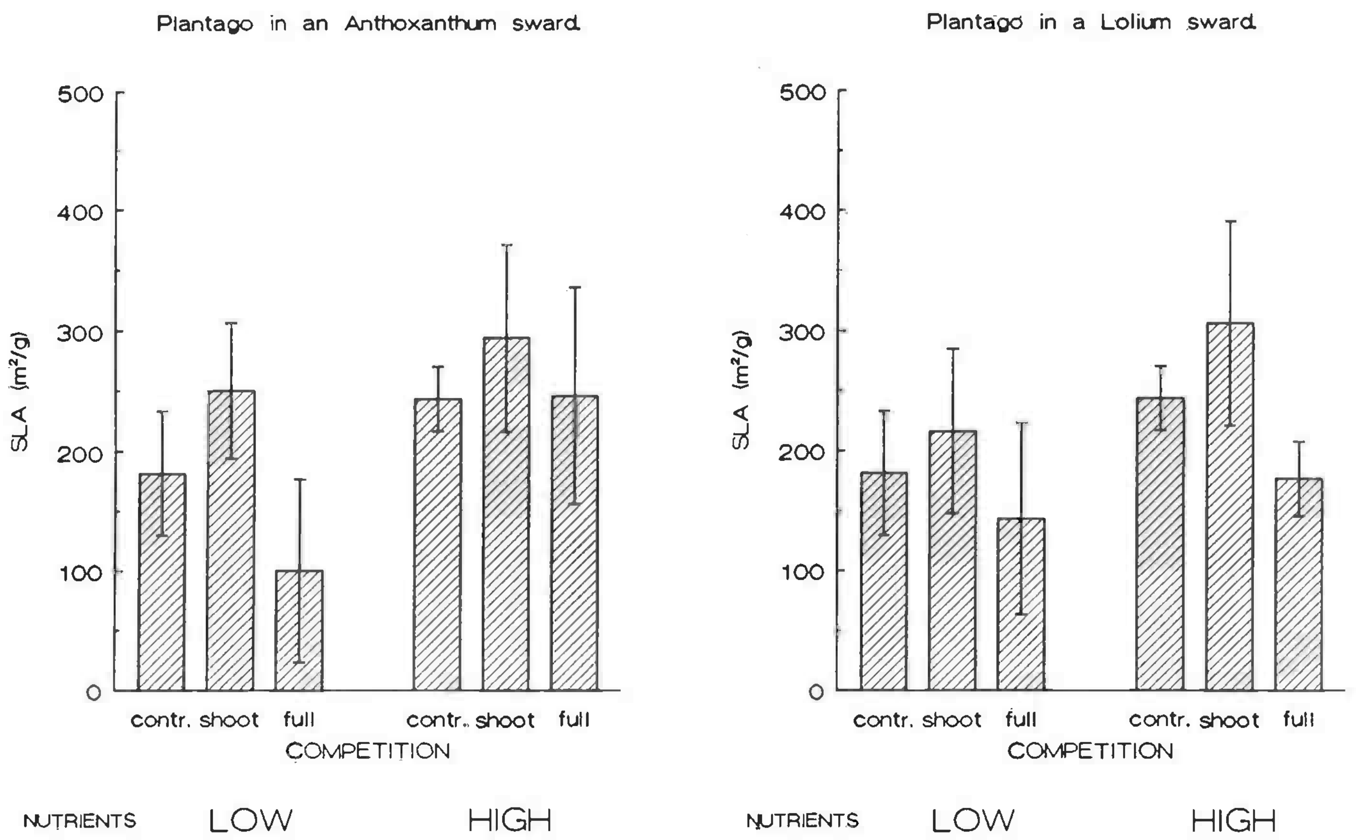
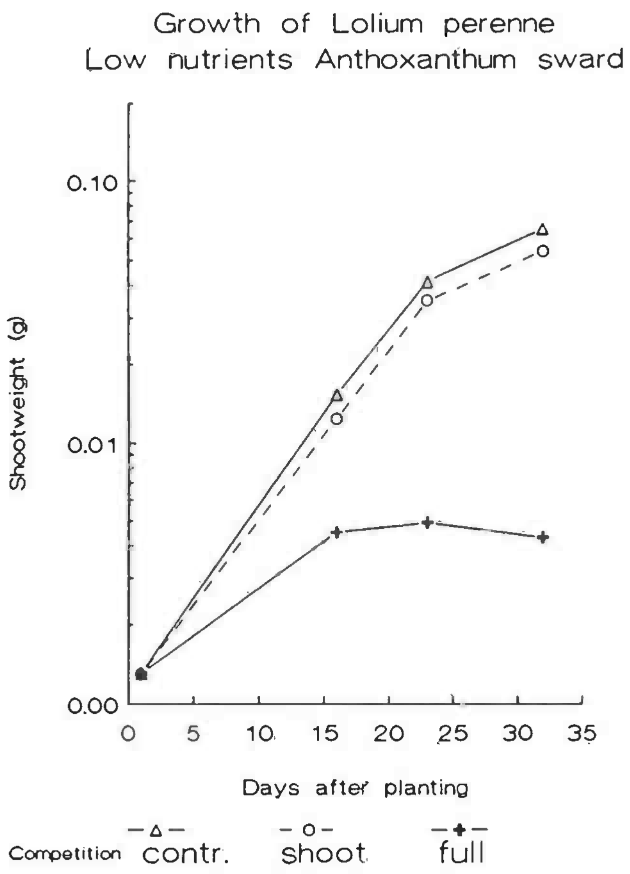
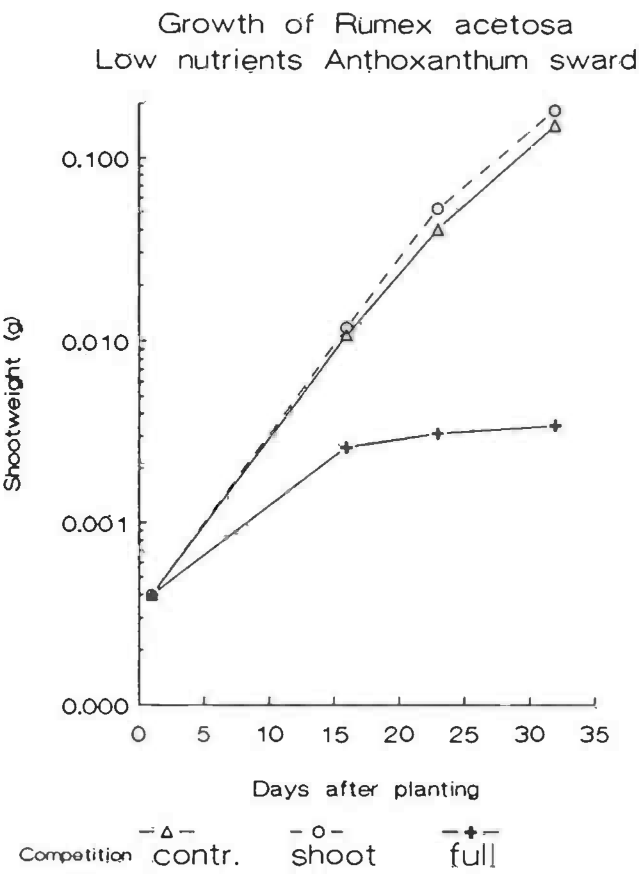


Fig 10: Specific leaf area, by two nutrient levels, two types of sward and types of competition.


Plantago in an Anthoxanthum sward
500
400
300
200
100
0
SLA (m²/g)
contr. shoot full contr. shoot full
COMPETITION
NUTRIENTS LOW HIGH
Plantago in a Lolium sward
500
400
300
200
100
0
SLA (m²/g)
contr. shoot full contr. shoot full
COMPETITION
NUTRIENTS LOW HIGH





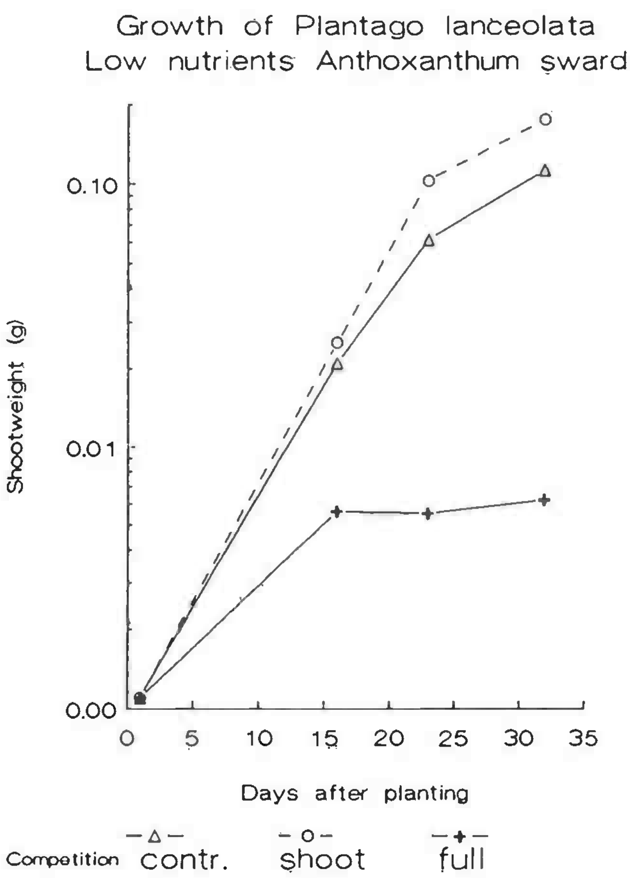
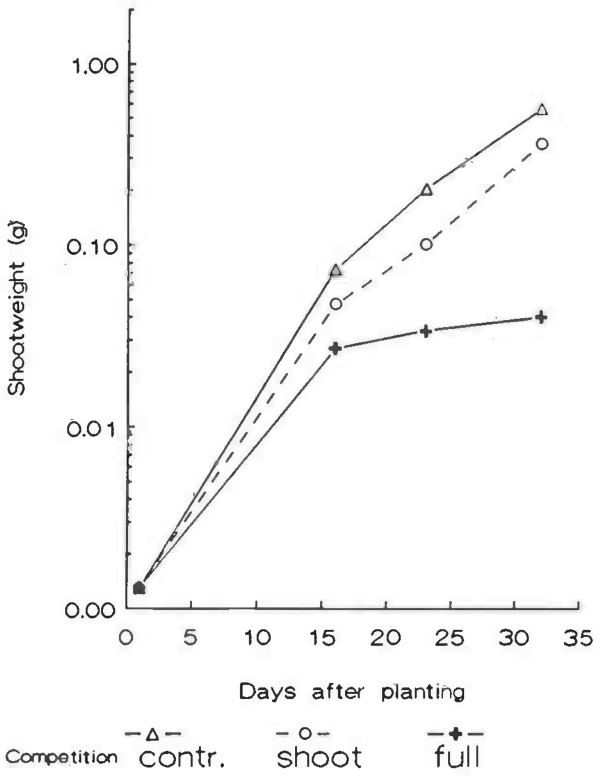
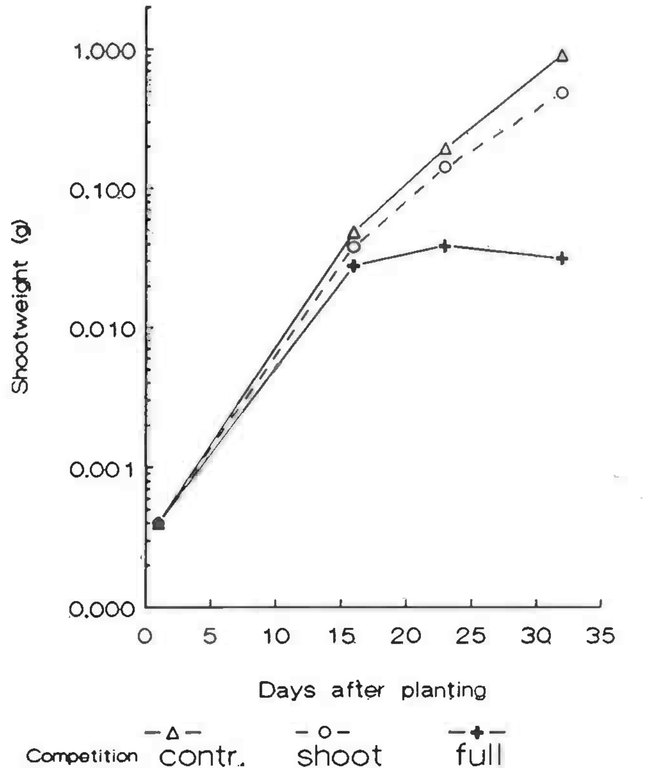


Fig 11: Growth of the invading species during the experiment, the shoot dry weight is given.

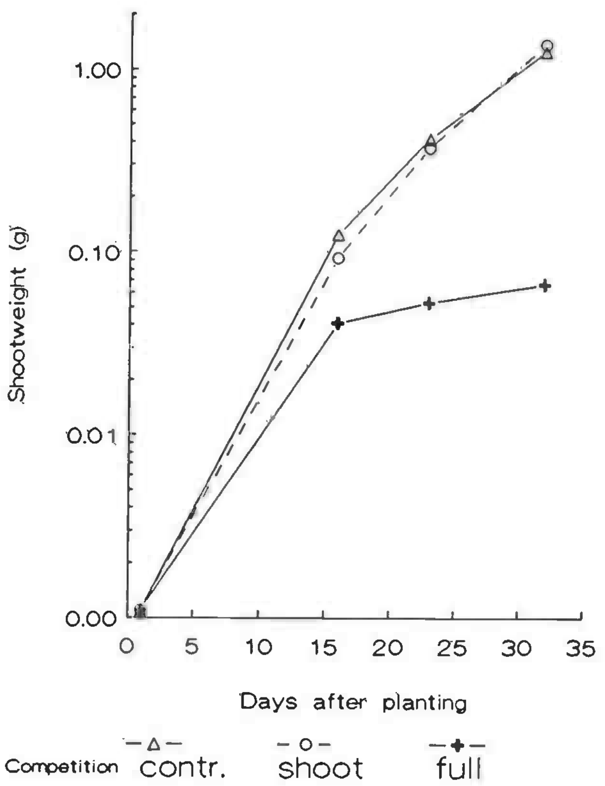
Growth of Lolium perenne
High nutrients Anthoxanthum sward

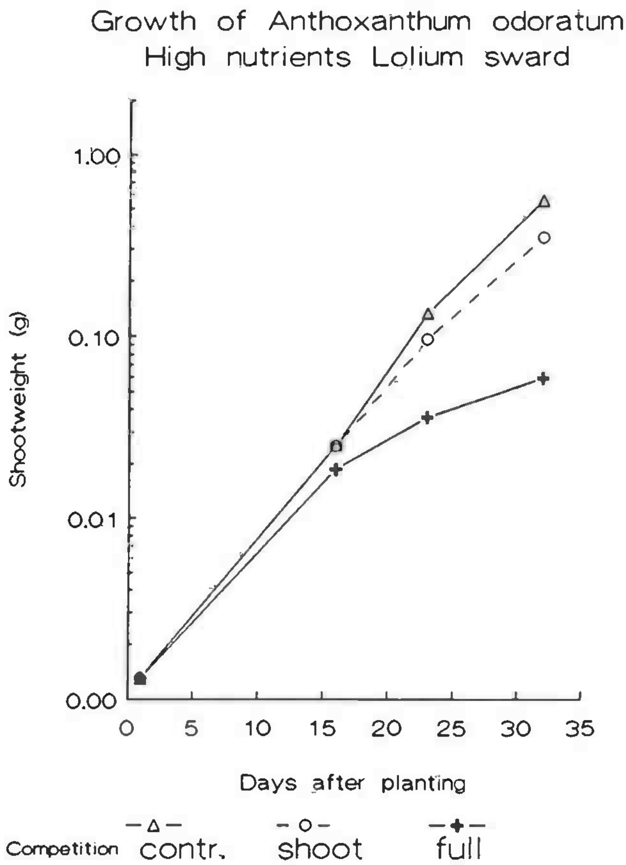


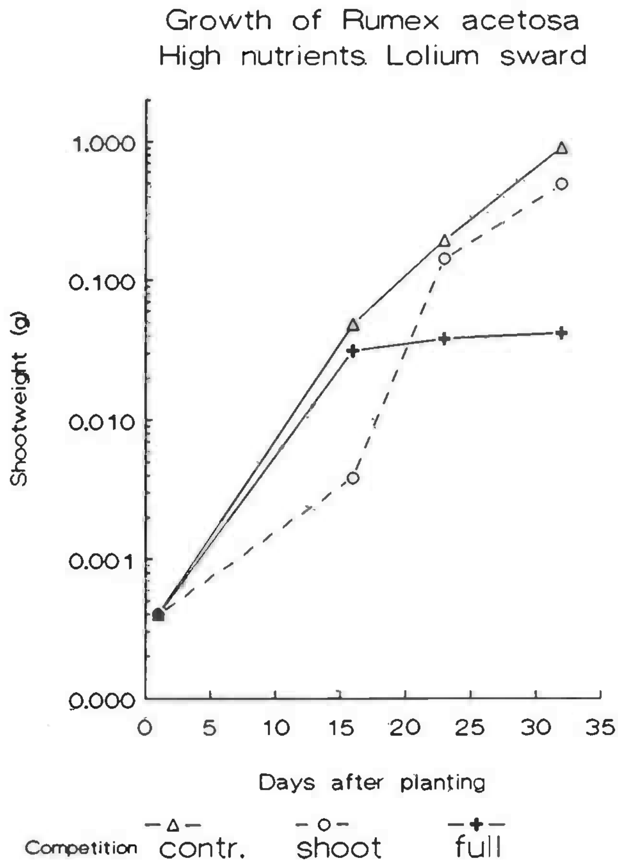
Growth of Rumex acetosa
High nutrients Anthoxanthum sward

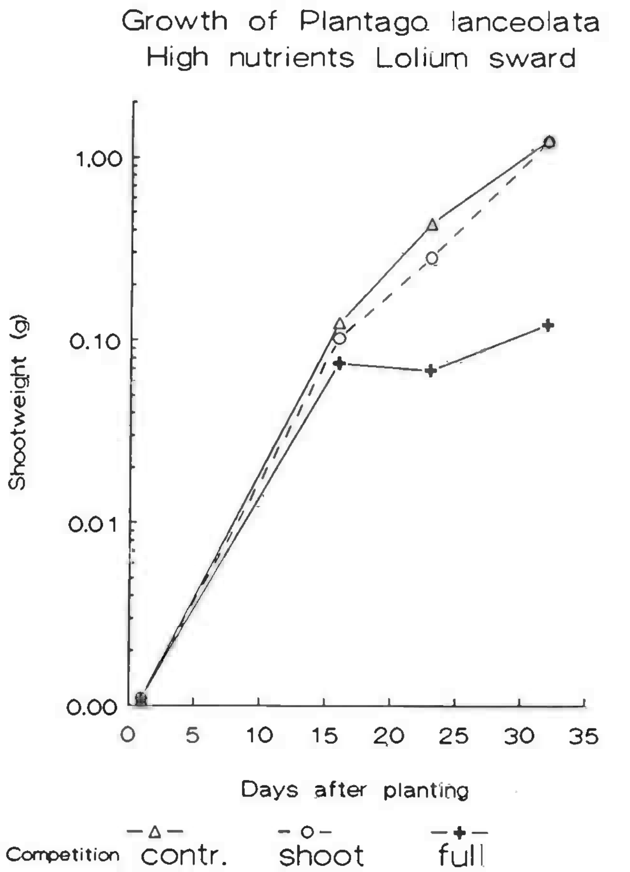


Growth of Plantago lanceolata
High nutrients Anthoxanthum sward

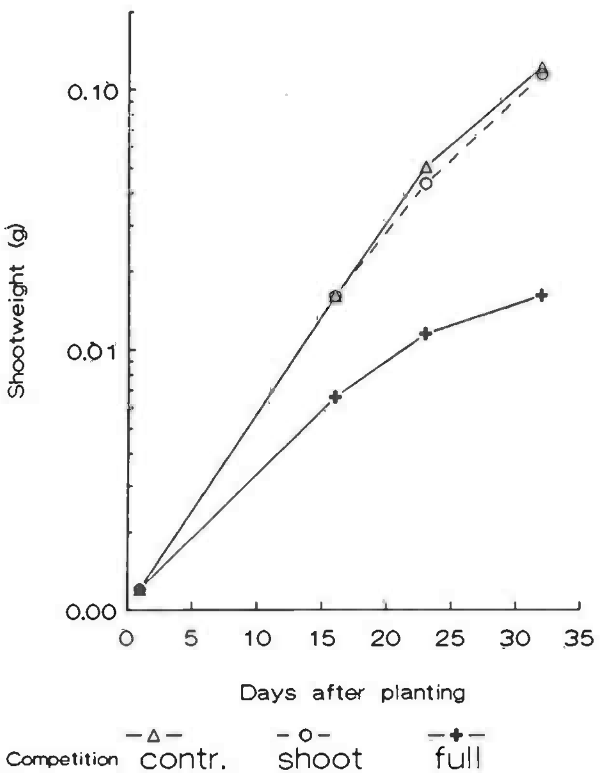



Growth of Anthoxanthum odoratum
High nutrients Lolium sward
Shootweight (g)
1.00
0.10
0.01
0.00
0
5
10
15
20
25
30
35
Days after planting
Competition
contr.
shoot
full

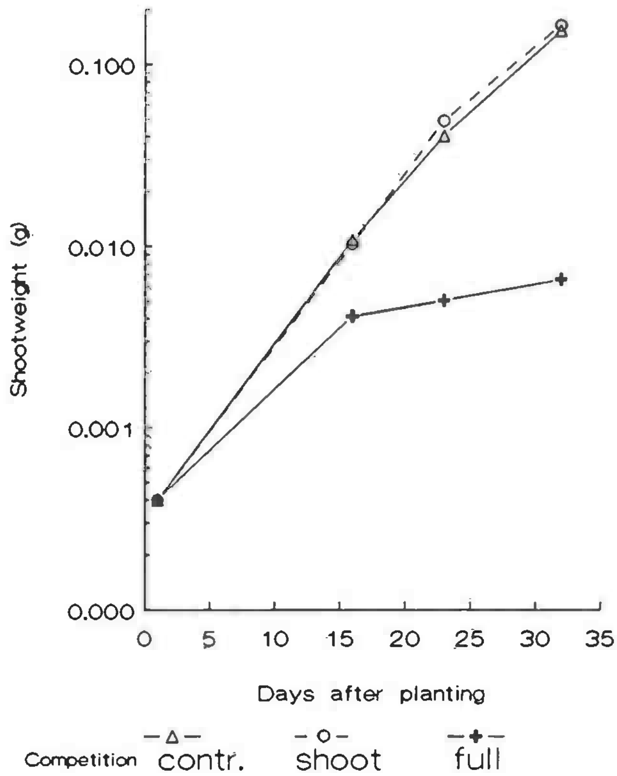

Growth of Rumex acetosa
High nutrients Lolium sward
Shootweight (g)
1.000
0.100
0.010
0.001
0.000
0
5
10
15
20
25
30
35
Days after planting
Competition
contr.
shoot
full


Growth of Plantago lanceolata
High nutrients Lolium sward
Shootweight (g)
1.00
0.10
0.01
0.00
0
5
10
15
20
25
30
35
Days after planting
Competition
contr.
shoot
full

Growth of Anthoxanthum odoratum
Low nutrients Lolium sward



Growth of Rumex acetosa
Low nutrients Lolium sward



Growth of Plantago lanceolata
Low nutrients Lolium sward