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Competition between legumes and grasses

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Contents

1 The Experiment on Competition between Glycine and Panicum

Enamel pots with a diameter of 21 cm and filled with 7 kg of soil were planted on 8 May 1964 with young seedlings of glycine (*Glycine javanica*, var. Tinaroo) and panicum (*Panicum maximum*, var. *trichoglume*). The nitrogen-poor sandy soil had an exchange capacity of 100 me./kg and was supplied with a basic dressing of 135 me. $CaCO_3$, 135 me. MgO, 21 me. $Ca(H_2PO_4)_2$ and 72 me. $KHCO_3$ per 10 kg of soil which resulted in a pH (water) of about 5.5.

The planting was done according to the replacement principle (DE WIT, 1960) with the number of plants given in table 1.

Table 1. The planting scheme

Pot	Panicum		Glycine	
	plants	rel. plant frequencies	plants	rel. plant frequencies
a	0	0	8	1
b	1	.25	6	.75
c	2	.5	4	.5
d	3	.75	2	.25
e	4	1	0	0

A set of pots a–e is called a replacement series, which is characterized by the restriction that the sum of the relative plant frequencies (see table 1) equals 1.

Four different treatments were applied. The R0N0 series were not inoculated with rhizobium and did not receive any nitrogen. The R1N1 series were inoculated with rhizobium and received nitrogen. The R0N1 series were not inoculated and did receive nitrogen and the R1N0 series were inoculated and did not receive nitrogen.

The pots were kept in a greenhouse which admitted about 75 percent of the outside light and was kept at a temperature of about 21 °C throughout. The plants were clipped at a height of 6 cm above the soil surface. The last of the seven harvests was on 4 November 1964. During winter many panicum plants died, so that the experiment had to be terminated.

R1 plants were inoculated by dipping their roots into a rhizobium suspension (strain CB 453 supplied by Dr. D. NORRIS, C.S.I.R.O., Cunningham Lab., Brisbane) at the time of transplanting. All pots were covered with a layer of gravel and watered by sub-irrigation to avoid translocation of rhizobium to the non-inoculated pots. Subsequent doses of nutrients were applied beneath the plants with a sterilised injection syringe. At the termination of the experiments all inoculated pots contained plenty of nodules whereas the glycine in the non-inoculated pots was completely free of them.

Introduction

Experiments on competition between perennial grass species have been studied by DE WIT and VAN DEN BERGH (1965). They considered the relative yields at successive harvests, which are the quotients of the yields of the species in the mixture and in monoculture. It was shown that after some period of establishment the species are often mutually exclusive, which means that the total of the relative yields is one.

In general, this simple situation does not exist in mixtures of leguminous and grass species, because of nitrogen fixation by rhizobium associated with the legume. Competition experiments between white clover and perennial ryegrass were carried out to furnish a basis for the further development of the theory.

Unfortunately it appeared that the clover suffered from soil-borne diseases, so that the results of these experiments did not seem very suitable for the purpose. Moreover, it is difficult to grow clover without rhizobium, so that the mutual interference of the clover-grass mixture in the absence of nitrogen fixation can not be determined very well.

Now it was observed that the rhizobium associated with the tropical leguminous species *Glycine javanica* is not present in the Netherlands, but that inoculation with the appropriate species is very easy. Besides, it appeared that soil-borne diseases of glycine are also absent in the Netherlands.

Since glycine is grown in association with the grass species green panic or panicum (*Panicum maximum*) in Australia, this species was chosen as the competitor in a series of competition experiments designed for a further development of the theoretical approach. These experiments and the subsequent theory are presented at first.

Based on this theory, competition experiments between white clover and grass and the complications due to soil-borne diseases of the leguminous species are discussed.

Table 2. The fertilizer applications

Date	Fertilizer treatment in me. per pot				Fertilizer
	R0N0	R1N0	R0N1	R1N1	
25 April	0	0	40	40	$Ca(NO_3)_2$
7 July	0	0	20	20	$Ca(NO_3)_2$
24 July	0	0	20	20	KNO_3
	0	0	8	8	NaH_2PO_4
	0	0	4	4	$MgSO_4$
4 August	0	40	0	0	K_2SO_4
21 August	40	10	0	0	K_2SO_4
	0	0	40	40	KNO_3
2 October	0	0	20	20	N as NH_4NO_3

The growth of the monoculture grass in the pots not fertilized with nitrogen was very poor and its content was only 1.5 percent N, which indicates severe N-starvation. The growth of the grass in the pots with the nitrogen treatments was 5 to 10 times better. Due to these large yield differences it was impossible to keep the amount of K in the soil the same throughout the experiment. Additional K was added in such amounts that excesses and shortages were avoided. The applied amounts of fertilizer in me. per pot are summarized in table 2.

Each replacement series was replicated 4 times but the 4 replicates were bulked before the determination of the N-content due to lack of material in some treatments and to save analytical work.

The herbage yields and nitrogen contents of the seven harvests are summarized in table 3. Herbage yields are also presented in figure 1 in the form of replacement diagrams. The diagrams in the four columns represent the treatments R0N0, R1N0, R0N1 and R1N1 and the four rows concern the 1st, 3rd, 5th and total harvests. The scales of the yield are the same within the rows, but differ between the rows. The photographs (plate 1 and 2) were taken at the time of the 3rd harvest.

1.1 The Total Nitrogen Yields

The nitrogen yields of the whole experimental period are given for each treatment and each mixture in figure 2, together with the total application of nitrogen to the N1 treatments.

The nitrogen uptake from the R0N0 pots was 0.4 g and indeed very low. The uptake by the R0N1 mixtures was 5.5 grams or about 55 percent of the applied amount. The nitrogen yield of the R1N0 treatment increased about linearly with the relative amount of glycine in the mixtures to a maximum of 5.8 grams. However, the nitrogen yield of the glycine in the monoculture of the R1N1 treatment was not $5.5 + 5.8 - 0.4 = 10.9$ grams, but only 6.7 grams, which shows that either the nitrogen fixation was suppressed by the fertilizer or the uptake of fertilizer by the fixation of nitrogen.

Table 3. Nitrogen contents and dry-matter yields of panicum (P) and glycine (G) in the replacement series at the seven harvests (mean of 4 replicates)

Treatment	Factor observed	Plant number per pot		8 June		30 June		23 July		17 Aug		8 Sept		1 Oct		4 Nov	
		P	G	P	G	P	G	P	G	P	G	P	G	P	G	P	G
R0N0	%N	0	8	–	2.27	–	1.83	–	1.74	–	1.57	–	–	–	1.62	–	2.18
		1	6	1.70	1.70	1.63	1.67	1.73	2.11	1.69	–	1.87	–	1.66	–	2.18	–
		2	4	1.60	1.58	1.52	1.55	1.71	–	1.57	–	1.76	–	1.53	–	2.12	–
		3	2	1.49	–	1.55	–	1.63	–	1.42	–	1.52	–	1.53	–	2.05	–
		4	0	1.39	–	1.52	–	1.79	–	1.47	–	1.49	–	1.62	–	2.10	–
	g d.m.	0	8	0	5.2	0	2.3	0	2.7	0	1.8	0	0	0	2.2	0	1.3
		1	6	2.4	2.1	2.1	0.7	2.1	0.8	2.4	0.5	1.5	0	2.3	0	1.7	0
		2	4	5.2	1.2	4.1	0.4	3.0	0.2	3.5	0	1.8	0	2.9	0	1.9	0
		3	2	4.3	0.5	2.9	0.2	2.6	0	3.1	0	2.5	0	2.5	0	3.0	0
		4	0	9.5	0	4.8	0	2.8	0	3.4	0	2.4	0	2.5	0	1.9	0
R1N0	%N	0	8	–	4.10	–	3.18	–	3.07	–	3.31	–	4.13	–	3.81	–	3.87
		1	6	2.53	3.04	1.60	3.01	1.73	2.70	2.05	2.98	2.77	3.76	2.35	3.63	2.68	3.86
		2	4	2.14	2.98	1.49	2.78	1.68	2.85	1.86	3.10	2.52	3.92	2.28	3.68	2.72	3.84
		3	2	1.84	3.71	1.57	3.34	1.74	2.62	1.73	2.85	2.30	3.78	2.19	3.49	2.76	3.63
		4	0	1.73	–	1.36	–	1.58	–	1.54	–	1.74	–	1.62	–	2.56	–
	g d.m.	0	8	0	6.9	0	12.2	0	36.2	0	47.2	0	20.5	0	25.6	0	17.9
		1	6	3.1	3.5	3.9	5.8	3.6	24.7	2.6	32.0	1.9	15.1	2.3	20.0	2.7	16.0
		2	4	4.8	2.1	4.6	5.1	3.8	21.9	3.6	24.6	2.2	13.2	2.2	16.8	2.0	14.4
		3	2	5.7	1.3	4.0	2.1	2.9	16.6	3.3	19.2	2.3	9.7	2.2	11.9	1.6	10.8
		4	0	7.5	0	4.7	0	3.2	0	3.6	0	2.3	0	2.3	0	1.9	0
R0N1	%N	0	8	–	4.32	–	2.98	–	3.39	–	2.64	–	4.80	–	2.21	–	3.70
		1	6	3.86	3.97	1.88	1.95	2.11	2.50	1.51	2.16	3.01	3.81	1.79	2.02	2.80	2.90
		2	4	3.66	3.84	1.46	1.62	2.30	2.53	1.46	1.87	2.58	2.91	1.54	1.81	2.80	2.76
		3	2	3.26	3.57	1.42	1.59	2.35	2.72	1.42	1.84	2.44	3.04	1.62	1.57	2.69	2.84
		4	0	2.70	–	1.39	–	2.45	–	1.54	–	2.43	–	1.65	–	2.44	–
	g d.m.	0	8	0	13.0	0	27.6	0	30.4	0	38.9	0	19.1	0	24.1	0	14.0
		1	6	14.2	7.2	29.2	7.2	25.5	5.5	41.5	9.8	27.9	9.7	12.3	3.1	13.9	5.7
		2	4	22.8	5.6	32.8	3.7	26.4	4.1	49.9	7.8	36.7	6.2	23.3	2.0	17.6	3.6
		3	2	30.8	3.2	31.5	1.8	29.0	1.9	55.8	3.6	48.7	3.6	20.9	1.7	22.5	1.9
		4	0	43.9	0	30.3	0	30.0	0	62.0	0	51.8	0	23.8	0	26.4	0
R1N1	%N	0	8	–	4.89	–	3.26	–	3.38	–	3.25	–	4.67	–	3.02	–	4.50
		1	6	4.19	4.45	1.66	2.34	2.04	3.32	1.62	3.29	3.02	4.11	1.83	3.32	2.84	3.62
		2	4	4.21	4.35	1.46	2.26	2.37	3.36	1.41	2.88	2.54	3.68	1.63	3.06	2.78	3.57
		3	2	3.90	4.51	1.60	2.43	2.24	3.04	1.41	2.94	2.62	3.66	1.55	2.88	2.67	3.36
		4	0	3.58	–	1.44	–	2.43	–	1.51	–	2.30	–	1.63	–	2.76	–
	g d.m.	0	8	0	8.6	0	30.3	0	37.4	0	44.4	0	18.3	0	31.1	0	17.7
		1	6	11.7	7.5	27.6	12.8	24.9	20.0	41.6	24.9	28.3	15.1	16.9	17.8	16.0	14.9
		2	4	17.1	4.1	39.6	7.9	24.4	11.8	52.1	21.0	34.9	11.4	23.2	14.7	17.4	12.9
		3	2	22.0	1.7	41.2	2.1	35.6	4.5	60.4	7.5	39.1	5.6	28.1	8.4	22.2	7.0
		4	0	31.1	0	38.5	0	36.0	0	60.6	0	51.6	0	26.8	0	26.8	0

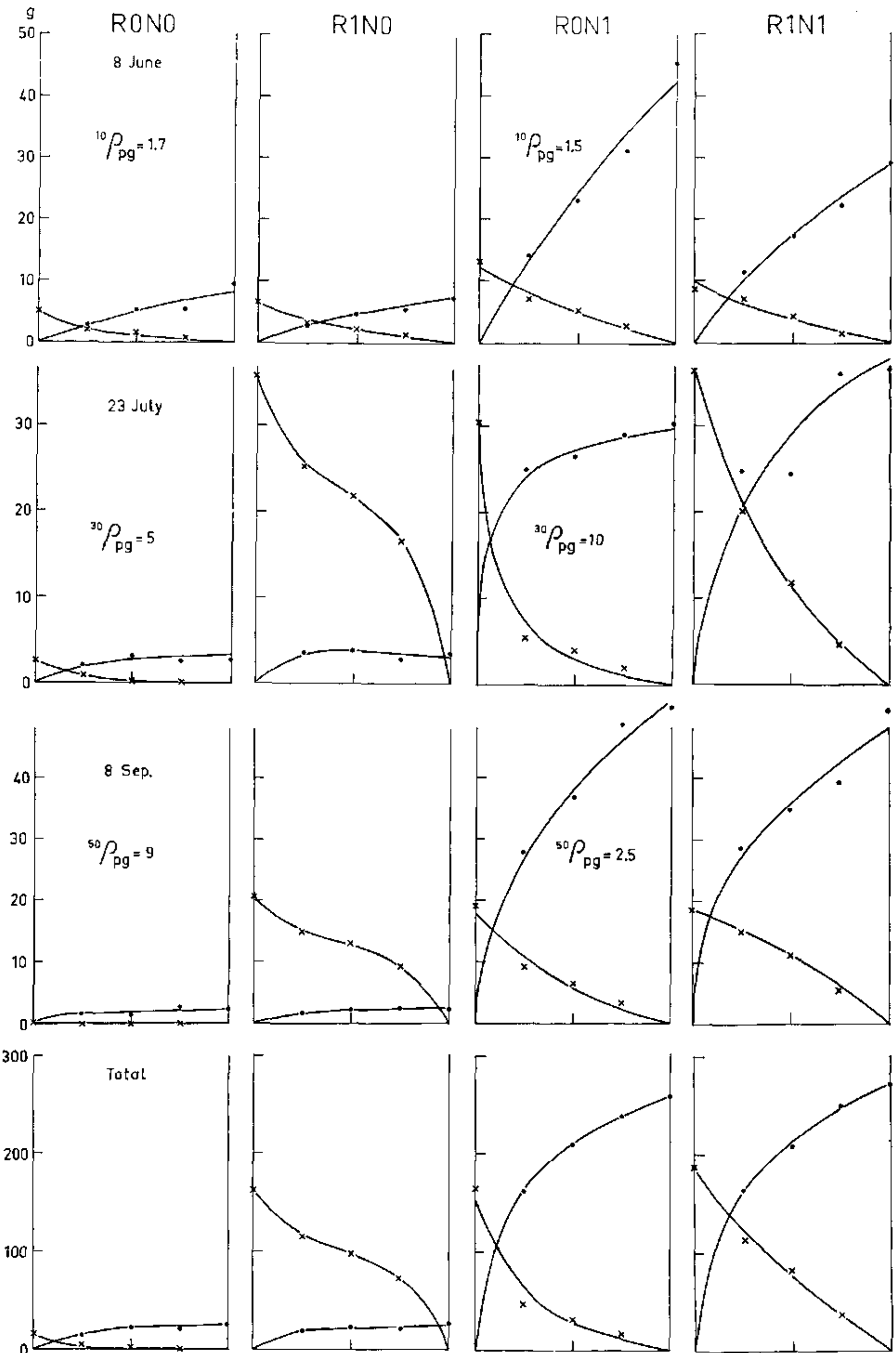

Fig. 1. The dry matter yields of panicum (P) and glycine (G) at the 1st, 3rd and 5th harvest and the total dry matter yields of the seven harvests

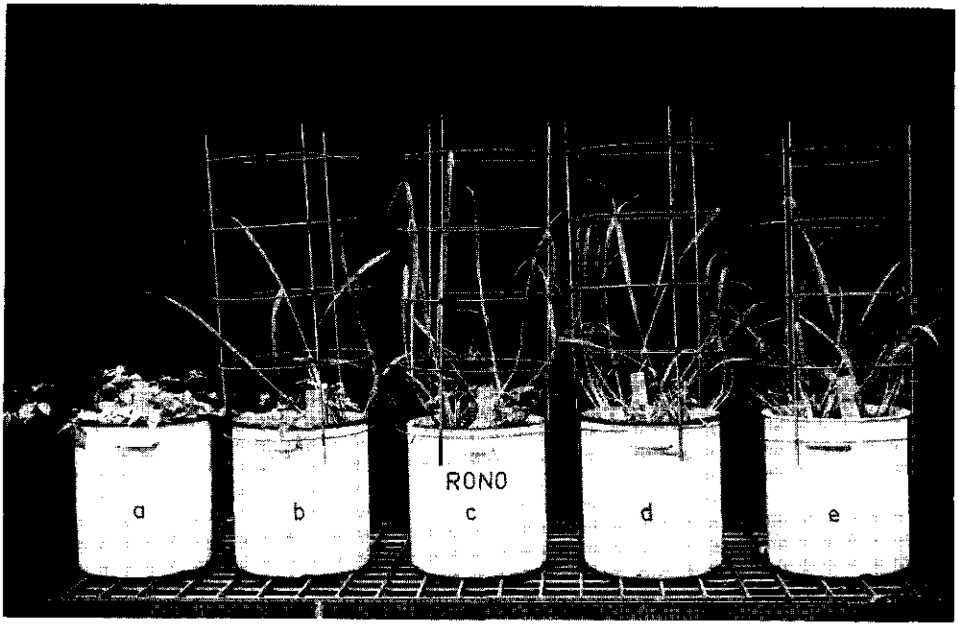

Plate 1. The glycine-panicum series at the third harvest in the treatments without nitrogen application. Planting scheme as in table 1

Plate 2. The glycine-panicum series at the third harvest in the treatments with nitrogen application. Planting scheme as in table 1

The nitrogen yield was highest with a relative plant frequency of 0.75 for glycine, but even there the yield of 7.6 grams was considerably lower than the amount of $5.2 + 4.2 - 0.4 = 9.0$ grams, which would have been found without negative interaction.

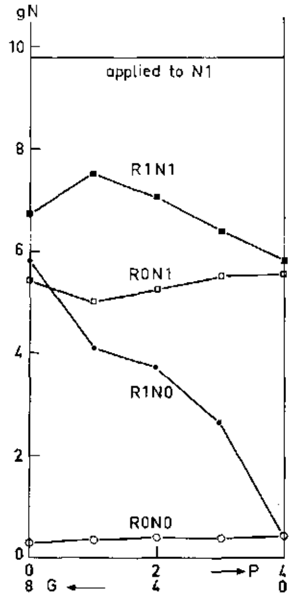

Fig. 2. The total nitrogen yields of the seven harvests of panicum and glycine. The horizontal line represents the nitrogen applied to the N1- treatments

1.2 The Relative Yield Total

The relative yield (r) of a species is obtained by taking the quotient (O/M) of the yield of the species in the mixture (O) and in the monoculture (M). The relative yield total (RYT) of two species grown together is the sum of their relative yields. It has been found (DE WIT, 1960, DE WIT and VAN DEN BERGH, 1965) that the RYT is often 1, i.e. that

$$\mathrm{RYT} = O_1/M_1 + O_2/M_2 = 1 \qquad (1)$$

When this is the case it is said that the two species are mutually exclusive (DE WIT and VAN DEN BERGH *op. cit.*).

The RYT of each harvest of each replacement series was calculated and the average RYT's for the seven harvests are presented in figure 3. Figure a concerns the dry matter yields and figure b the nitrogen yields.

The RYT of the R0N0 mixtures appears to be somewhat smaller than 1, but the absolute yields (figure 1) are so low in this case and to such a large extent affected by slight variations in growth habit that the deviations are of little importance. The result of the R0N1 treatment shows indeed without any doubt that the RYT of the two species is 1 when there is no rhizobium in the soil. The RYT of the mixtures is considerably larger than 1 in the presence of rhizobium, and the more so in the replacement series without N-fertilization. The obvious reason for this is the additional source of nitrogen in the pots with rhizobium and with glycine.

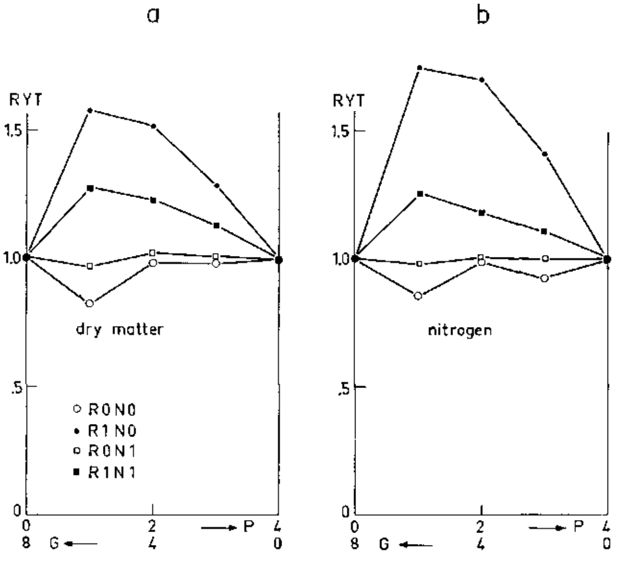

Fig. 3. The average relative yield totals (RYT) of panicum and glycine based on dry matter yields (fig. a) and nitrogen yields (fig. b)

1.3 Competition in the Absence of Rhizobium

The relative replacement rate (RRR) of glycine with respect to panicum at the *n*th harvest with respect to the *m*th harvest is defined as

$$ {}^{nm}\rho_{gp} = \frac{{}^{n}r_{g}/{}^{n}r_{p}}{{}^{m}r_{g}/{}^{m}r_{p}} \tag{2} $$

in which ${}^{n}r_{g}$ is the relative yield of glycine in the mixture at the *n*th harvest, and the other symbols have a similar meaning. Glycine gains when the *n*th harvest is later than the *m*th harvest and ρ is greater than one.

Combining equations (1) and (2) gives:

$$ {}^{n}O_{g} = \frac{{}^{nm}\rho_{gp}\,{}^{m}r_{g}}{{}^{nm}\rho_{gp}\,{}^{m}r_{g} + {}^{m}r_{p}}\,{}^{n}M_{g} \tag{3a} $$

$$ {}^{n}O_{p} = \frac{{}^{m}r_{p}}{{}^{nm}\rho_{gp}\,{}^{m}r_{g} + {}^{m}r_{p}}\,{}^{n}M_{p} \tag{3b} $$

Now it was found by DE WIT (1960) and DE WIT and van DEN BERGH (1965) that experimental results were not at variance with the supposition that ρ is independent of the relative yields when RYT = 1. This means that a species should gain at any frequency when it gains at one frequency, but this has not been tested for extreme relative frequencies. It was also shown that in the case of planted replacement series relative plant frequencies can be substituted for the relative yields (r) of the equations (3) provided there has been good establishment of the plants.

Methods to estimate ρ from experimental data are discussed by DE WIT (1960). The curves for R0N0 and R0N1 treatments in figure 1 were drawn according to the equations (3) by using the values of ρ shown with the graphs.

In the case of the R0N1 treatment the curves fit closely enough for the conclusion that equation (3) can be used to describe the results. However, the data for the R0N0 treatment in table 3 show that the yield of glycine in the pots which contained small amounts is systematically too small, an effect which can not be seen in figure 1 due to the small scales. This is because under such conditions a relatively large amount remained in the pot when clipped at a height of 6 cm. This is confirmed by the observation that the glycine of the monoculture was absent in the 5th harvest, but present again in the 6th and 7th harvest.

At the relative plant frequency of 0.75 for glycine in the R0N1 series the yield of glycine was in general systematically too low and the yield of panicum systematically too high. Since RYT is 1 (figure 3), this is due to the relatively bad establishment of glycine in some of these pots.

The mutual interference of both species is completely characterized by the RRR, and in a most convenient way represented by means of course lines, which are obtained (DE WIT and VAN DEN BERGH *op. cit.*) by plotting the RRR for each harvest on a logarithmic scale against time and joining the points. This is done in figure 4a for the

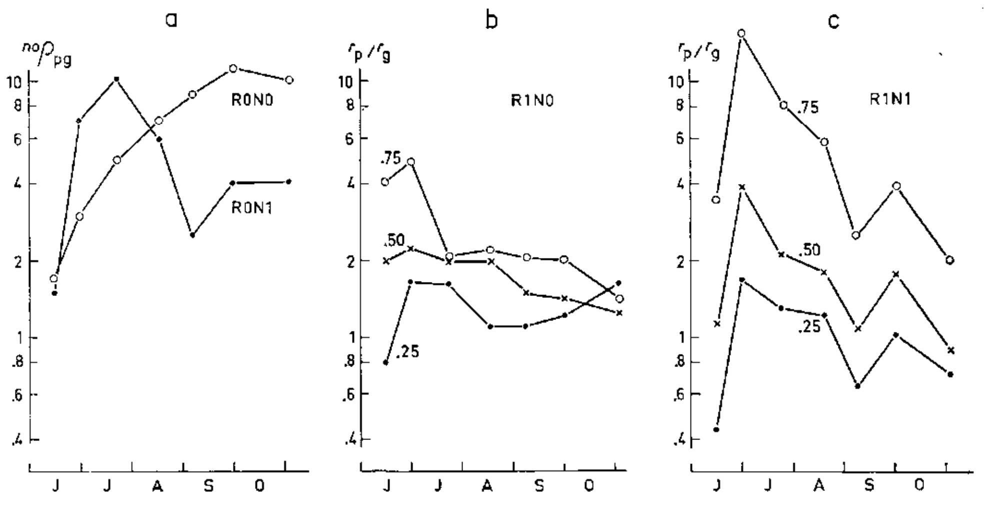

Fig. 4. The course lines of RRR for the treatments without rhizobium (fig. a) and the course lines at relative plant frequencies for panicum of 0.75 (○), 0.50 (×) and 0.25 (●) in the treatments with rhizobium (fig. b and c)

R0N1 and R0N0 series. Without nitrogen, the course line slopes upward and the magnitude of the slope indicates the rate at which panicum gained on glycine. With nitrogen, panicum gained at first at an even faster rate, but from the end of July onwards glycine started to recover, so that eventually the glycine in the nitrogen series was much better off than that in the series without nitrogen.

It follows from equation (2) that the course line which is obtained by plotting the ratio of the relative yields at successive harvests is the same as the one obtained by plotting RRR, when the relative yields of the species in the *m*th harvest, i.e. the reference harvest, are equal. Course lines parallel to this one are found when the ratios of the relative yields are plotted for other relative yields of the reference harvest and RRR is independent of the composition of the mixture. The course lines are not parallel when RRR is not independent of this composition, as will be discussed in the next section.

1.4 Competition in the Presence of Rhizobium

The RYT of the mixtures is larger than 1 in the presence of rhizobium so that equation (3) cannot be used to describe the results and the RRR (equation 2) depends on the relative plant frequency. To judge which species gained, the three course lines for the R1N0 treatment, obtained here by plotting the quotient of the relative yields at relative plant frequencies for panicum of 0.75, 0.50 and 0.25 against the time of harvest are presented in figure 4b. Obviously, in mixtures with a relatively large amount of panicum, glycine gained and in mixtures with a relatively large amount of glycine, panicum gained. At the last harvest the course lines are so close together that the situation is reached where the mixtures are practically the same.

The course lines for the R1N1 treatment are given in figure 4c. These are practically parallel for the first two harvests which indicates that during that period the species were still mutually exclusive (compare also figure 1). But ultimately the three course lines converge also, although at a slower rate.

The course lines are very useful for judging whether and then at what rate the mixtures approach each other and whether an equilibrium is reached, but they appear unsuitable for a further quantitative analysis of the mutual interference.

1.5 The Transfer of Nitrogen to Panicum, and its Consequences

The nitrogen yields of the 4th harvest of the R1N0 series are given in figure 5. The curves 1 in figures a and b represent the yields of glycine and panicum, respectively. At first the yield of panicum increases somewhat with decreasing relative plant frequency and the yield curve of glycine is S-shaped. This suggests that with increasing amounts of glycine more nitrogen was transferred to the panicum and that the panicum was more competitive because of this. It is immaterial in this discussion whether

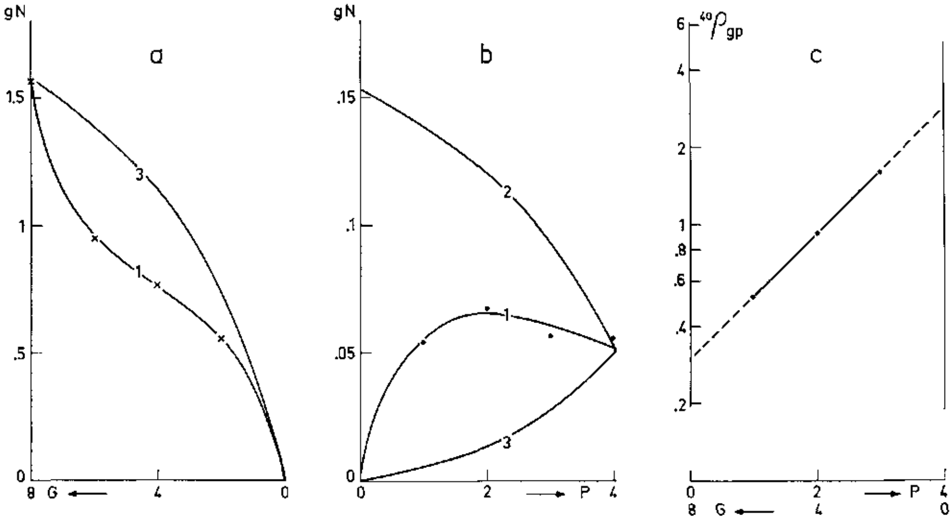

Fig. 5. Nitrogen yields of the 4th harvest of glycine (fig. a) and panicum (fig. b) in the R1N0 treatment in the presence (curve 1) and absence (curve 3) of nitrogen transfer. Curve 2 represents the yield of the monoculture panicum which would have been obtained at the nitrogen status of the panicum in the mixture. Fig. c shows how the RRR calculated from curve 1 for glycine depends on the relative plant frequency

the transferred nitrogen originates from fixation by the rhizobium or has been taken up by the grass directly from the soil or fertilizer.

It is seen in figure 1 and table 3 that the yield of glycine with rhizobium was about the same with and without nitrogen, which means that the yield of glycine was hardly affected by the nitrogen status of the soil and that the lower yields of glycine in the mixtures were not caused by differences in the nitrogen status of the glycine.

Accordingly, the nitrogen yields of glycine can be used to calculate, with equation (3a), how RRR varies with plant frequency. The result of this calculation is presented in figure 5c. It appears that the RRR of glycine with respect to panicum increased linearly with the relative plant frequency of panicum when presented in a semi-logarithmic graph.

It appeared in the experiments without rhizobium that both species are mutually exclusive, irrespective of the nitrogen status. Hence, both species are also mutually exclusive at the nitrogen status of panicum caused by the nitrogen fixation, so that equation (3b) and the values of RRR in figure 5c can be used to calculate the yield of the monoculture of panicum which would have been obtained at the nitrogen status of panicum in the mixture. These yields are represented by curve 2 in figure 5b.

By extrapolating the line through the points in figure 5c to the axis, where the relative frequency of glycine in the mixture is zero, the RRR of glycine with respect to panicum is obtained for the situation where there is no transfer of nitrogen to panicum in the mixture. The yield curves of glycine and panicum calculated with this RRR are represented by the curves 3 in figures a and b.

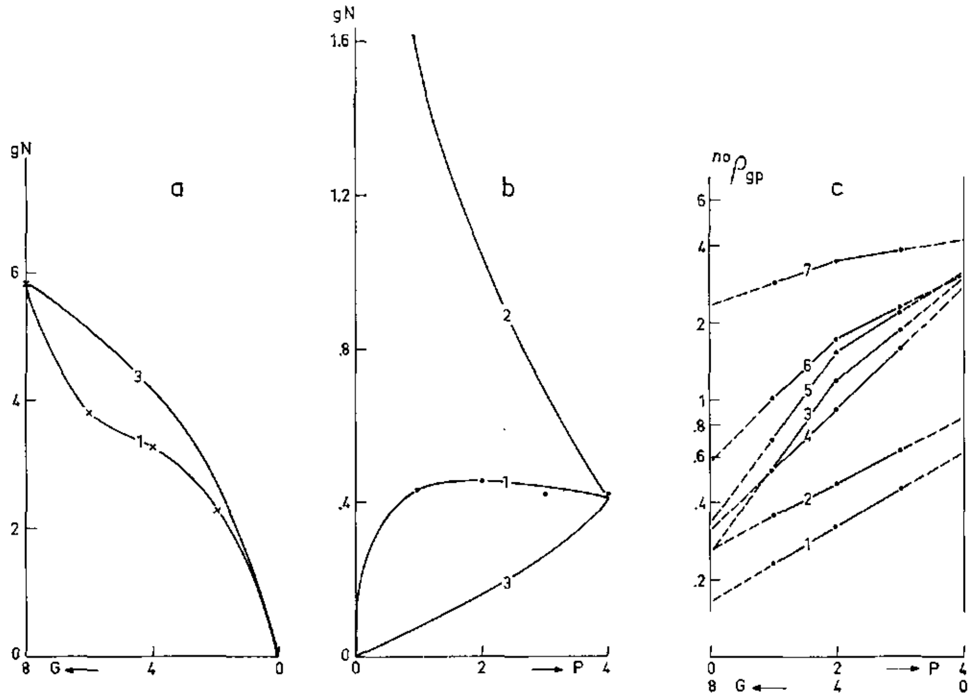

Fig. 6. As fig. 5, but for the total of the seven harvests of the R1N0 treatment

Similar curves were calculated for each other harvest of the R1N0 treatment, and the total nitrogen yields obtained from the seven harvests are given in figures 6a and b. Figure 6c gives the relation between RRR and the relative plant frequency for each harvest separately.

Curve 2 in figure 6b for the calculated yields of panicum in monoculture shows that panicum profited considerably from its association with glycine. However, in all cases the yield was still considerably lower than the yield of 6 g N which was obtained in the case of nitrogen fertilization.

It appears from curves 3 and 1 in figure 6b, that due to nitrogen transfer the yield of panicum increased by 0.3 g N at a plant frequency of 0.5. This caused greater competition, and by comparing curves 1 and 3 in figure 6a it is seen that because of this the nitrogen yield of the glycine was decreased by 0.9 g. Obviously the transfer of nitrogen caused a decrease in total N-yield instead of an increase. The corresponding results for the R1N1 treatment are given in figure 7.

Curve 2 in figure 7b shows that at a plant frequency of 0.5 the calculated monoculture yield is 2 g N higher than the N-yield of the monoculture proper. This is considerably higher than the difference of 0.5 g in the case of the R1N0 treatment. Obviously, the fertilization with N improved the transfer of nitrogen to the panicum. This is also illustrated by the absolutely large difference between curves 1 and 3 in figure 7b. On the other hand it is seen that the lines in figure 7c are horizontal which

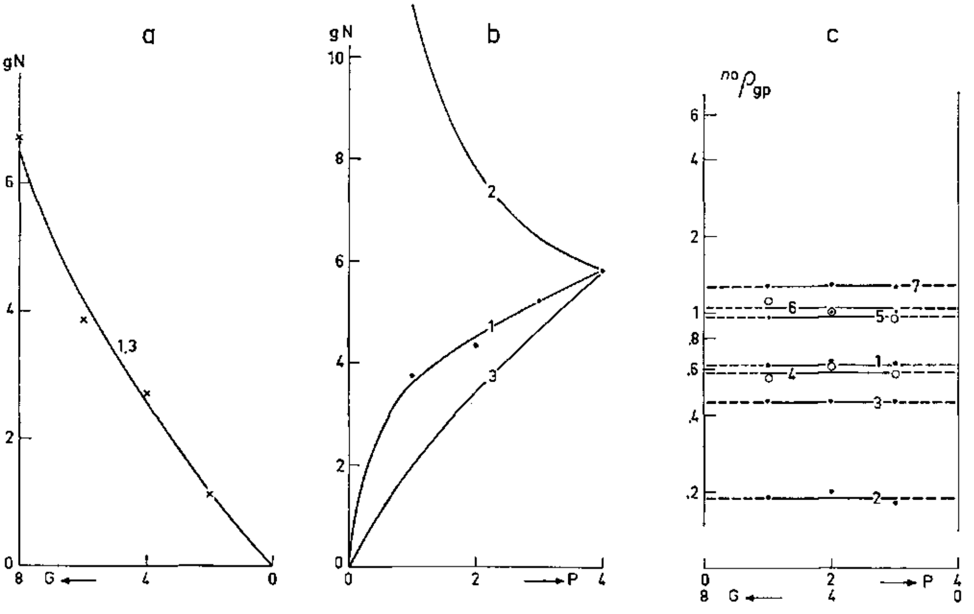

Fig. 7. As fig. 5, but for the total of the seven harvests of the R1N1 treatment

means that the glycine fertilized with N did not suffer from any increased competition due to nitrogen transfer. For this reason curves 1 and 3 coincide in figure 7a. The increased nitrogen yield of the panicum was therefore not off-set by a decreased yield of the glycine.

2 The Experiment on Competition between Perennial Ryegrass and White Clover

To study the effect of water level on competition between grass and clover plastic cylinders of different length and a diameter of 20 cm, filled with soil and open at the bottom, were placed in water so that water levels were obtained at 12, 26, 41, 70 and 99 cm below the soil surface (figure 8). At each water level, six cylinders were planted on 13 January 1960 with perennial ryegrass (*olium perenne*, var. Engels raaigras weide-type Barenza) and white clover (*Trifolium repens*, var. Witte cultuurklaver C.B.), according to replacement series given in table 4. Each grass plant was reduced to one tiller of 5 cm length of which the roots were almost completely cut back. The clover plants were reduced to a few centimeters of stolon with 1 or 2 leaves and hardly any roots. The existing experimental set-up (VAN DEN BERGH, 1963) was not large enough to introduce replicates.

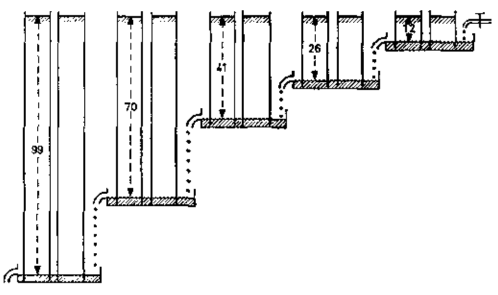

Fig. 8. The maintenance of the different water levels in the grass-clover experiment

The sandy soil had an exchange capacity of 140 me./kg, a pH (water) of about 5.2 and an organic matter content of 4.5%. Two weeks after planting and after each cut 2.5 me. KH_2PO_4, 6 me. K_2SO_4 and 8 me. $MgSO_4$ dissolved in 100 ml water were given per container. The soil contained some nitrogen and no additional nitrogen was given, in order to retain a reasonable amount of clover in the containers as long as possible.

The experiment was carried out in a greenhouse which transmitted about 75 percent

Table 4. The planting scheme

Container	Ryegrass		Clover	
	plants	rel. plant frequencies	plants	rel. plant frequencies
a	0	0	31	1
b	6	.19	25	.81
c	12	.39	19	.61
d	19	.61	12	.39
e	25	.81	6	.19
f	31	1	0	0

Table 5. Nitrogen contents, nitrogen yields and frequencies of tillers and stolons of ryegrass (R) and white clover (C) in the replacement series at the 2nd to 8th harvest

Water level	Factor observed	Plant number per pot		24 Febr		15 March		6 April		26 April		17 May		8 June		29 June	
		R	C	R	C	R	C	R	C	R	C	R	C	R	C	R	C
12 cm	% N	0	31	–	3.14	–	4.32	–	4.14	–	3.86	–	3.94	–	3.34	–	2.77
		6	25	2.06	3.73	2.59	4.27	2.82	4.30	2.61	4.08	2.70	4.22	4.10	3.38	–	2.77
		12	19	1.73	3.52	2.03	4.05	2.56	4.02	2.35	4.11	2.61	4.56	3.50	3.60	2.83	3.02
		19	12	1.73	3.10	1.89	3.86	2.59	3.79	2.40	3.94	2.43	3.82	2.32	3.38	2.19	2.88
		25	6	1.52	3.46	1.79	3.46	2.18	3.47	2.16	3.73	2.32	3.42	2.16	2.94	1.98	2.86
		31	0	1.46	–	1.74	–	2.27	–	2.19	–	2.43	–	2.18	–	2.00	–
	mg N	0	31	0	160	0	354	0	497	0	212	0	209	0	84	0	39
		6	25	21	186	21	312	28	331	8	155	5	190	4	118	0	64
		12	19	38	123	33	255	44	414	14	247	18	301	4	151	3	79
		19	12	60	40	40	112	34	228	12	173	7	294	5	165	4	81
		25	6	49	24	34	76	28	174	17	116	9	199	6	183	2	109
		31	0	61	0	38	0	36	0	20	0	22	0	26	0	28	0
	tiller and stolon freq	0	31	0	164	0	326	0	444	0	411	0	481	0	441	0	350
		6	25	53	141	42	214	38	283	20	348	15	332	8	360	6	264
		12	19	69	126	70	219	59	255	46	293	38	361	19	331	19	245
		19	12	123	38	101	117	74	206	56	298	32	380	30	382	19	285
		25	6	94	34	101	96	78	183	63	228	48	382	28	389	19	347
		31	0	204	0	159	0	129	0	109	0	135	0	123	0	144	0
26 cm	% N	0	31	-	4.08	–	3.86	–	3.81	–	3.66	–	3.07	–	2.69	–	2.83
		6	25	3.82	3.98	1.86	4.08	2.46	3.81	2.70	3.62	2.64	3.07	3.15	2.48	2.40	2.77
		12	19	3.09	3.30	1.73	3.92	3.14	4.00	2.38	4.14	2.16	3.62	2.35	2.69	2.19	2.37
		19	12	3.62	3.23	1.76	3.94	2.38	3.66	2.46	3.86	2.62	3.92	2.67	3.42	2.51	2.96
		25	6	3.41	3.14	1.65	3.87	2.10	3.47	2.26	3.55	2.40	3.66	2.05	3.39	2.02	2.94
		31	0	2.19	–	1.54	–	2.35	–	2.29	–	2.19	–	2.08	–	2.10	–
	mg N	0	31	0	384	0	335	0	327	0	132	0	77	0	48	0	45
		6	25	126	207	48	261	47	209	32	51	32	31	9	32	10	36
		12	19	185	132	50	192	88	212	64	87	43	65	47	54	39	26
		19	12	253	74	72	51	60	92	32	58	26	71	24	55	23	38
		25	6	276	34	69	46	57	80	34	50	31	55	29	44	22	29
		31	0	256	0	71	0	82	0	50	0	35	0	31	0	36	0
	tiller and stolon freq	0	31	0	227	0	292	0	357	0	335	0	314	0	249	0	142
		6	25	64	159	64	200	57	185	62	178	50	127	35	84	31	61
		12	19	138	112	120	160	91	174	94	167	83	183	79	146	75	90
		19	12	244	44	189	65	125	125	80	156	72	207	54	187	54	166
		25	6	325	29	241	49	202	105	134	128	116	135	90	119	80	99
		31	0	287	0	221	0	183	0	164	0	129	0	120	0	120	0
41 cm	% N	0	31	–	4.86	–	3.66	–	3.58	–	4.10	–	3.71	–	3.07	–	3.07
		6	25	5.15	4.98	3.44	3.36	2.30	3.47	3.87	3.90	4.64	3.86	3.74	3.04	3.65	3.15
		12	19	4.37	4.38	1.87	3.23	2.02	3.54	2.86	4.27	3.49	3.94	3.65	3.30	2.85	3.23
		19	12	3.94	4.06	1.97	3.23	2.18	3.70	2.40	4.14	2.30	3.97	2.72	2.74	2.27	2.74
		25	6	3.92	4.34	1.86	3.20	1.78	4.10	2.24	4.22	2.29	4.67	2.21	3.71	2.03	2.75
		31	0	4.58	–	1.86	–	1.94	–	2.43	–	2.74	–	2.48	–	1.94	–
	mg N	0	31	0	282	0	249	0	276	0	131	0	141	0	123	0	86
		6	25	118	234	138	168	71	187	35	82	51	73	37	76	11	66

Table 5. Continued

Water level	Factor observed	Plant number per pot		24 Febr		15 March		6 April		26 April		17 May		8 June		29 June	
		R	C	R	C	R	C	R	C	R	C	R	C	R	C	R	C
41 cm	mg N	12	19	271	145	105	90	71	141	54	73	45	83	66	49	54	32
(continued)		19	12	350	98	100	65	67	89	55	54	46	32	92	19	77	11
		25	6	423	26	137	16	78	16	49	8	41	14	71	11	89	6
		31	0	467	0	161	0	64	0	39	0	36	0	82	0	77	0
	tiller and	0	31	0	193	0	250	0	244	0	270	0	280	0	253	0	200
	stolon freq	6	25	77	152	127	249	82	302	40	289	47	277	41	263	11	229
		12	19	168	111	135	150	96	171	48	180	66	172	78	141	71	73
		19	12	250	68	208	75	185	108	170	78	155	86	170	65	164	35
		25	6	271	26	230	25	191	35	155	43	154	42	168	37	176	26
		31	0	374	0	342	0	248	0	181	0	178	0	215	0	221	0
70 cm	% N	0	31	–	4.94	–	4.62	–	4.19	–	4.29	–	4.14	–	3.62	–	2.94
		6	25	4.64	4.43	4.35	4.18	3.42	3.63	3.55	4.29	3.60	3.82	2.91	3.09	2.90	3.07
		12	19	4.43	4.58	4.16	4.08	3.22	3.49	3.46	3.97	3.36	3.55	2.94	3.12	2.85	2.96
		19	12	4.66	4.90	4.08	4.40	3.46	3.90	3.47	4.32	3.17	3.52	2.69	3.71	2.80	3.97
		25	6	4.45	4.38	3.92	4.70	3.18	3.70	3.09	4.02	2.50	3.73	2.21	4.03	2.40	3.49
		31	0	4.45	–	3.84	–	3.12	–	2.74	–	2.35	–	1.95	–	2.50	–
	mg N	0	31	0	227	0	291	0	361	0	244	0	186	0	65	0	53
		6	25	107	191	174	188	229	218	149	103	79	69	61	34	67	15
		12	19	253	92	295	106	302	101	104	52	67	50	53	34	46	30
		19	12	321	88	355	75	325	70	167	30	89	35	62	22	48	12
		25	6	458	26	388	9	363	18	161	4	77	4	55	8	41	10
		31	0	503	0	480	0	371	0	156	0	61	0	41	0	32	0
	tiller and	0	31	0	191	0	306	0	357	0	346	0	327	0	327	0	206
	stolon freq	6	25	69	122	80	169	105	197	84	189	72	175	87	118	106	72
		12	19	162	85	202	116	184	123	99	141	77	144	67	162	56	122
		19	12	218	76	237	84	213	103	168	104	122	78	83	78	79	42
		25	6	300	20	315	14	284	20	225	16	190	28	154	24	126	27
		31	0	313	0	289	0	270	0	219	0	225	0	200	0	183	0
99 cm	% N	0	31	–	4.48	–	4.45	–	4.62	–	4.53	–	4.42	–	3.38	–	3.42
		6	25	4.78	4.69	4.69	4.56	4.32	4.43	4.24	4.26	4.11	4.27	4.53	3.44	–	3.17
		12	19	3.89	4.34	4.67	4.51	4.27	4.10	4.34	4.16	4.05	3.68	3.49	3.10	3.39	3.01
		19	12	4.45	4.32	4.42	4.74	3.73	3.95	3.82	4.48	3.44	3.38	2.74	2.99	2.80	2.51
		25	6	4.70	4.30	4.43	4.35	4.02	4.42	4.22	–	4.06	3.79	3.89	3.62	3.44	3.39
		31	0	4.42	–	4.27	–	3.62	–	3.95	–	3.57	–	2.93	–	2.83	–
	mg N	0	31	0	139	0	156	0	254	0	235	0	380	0	304	0	147
		6	25	86	103	131	96	203	137	119	119	90	184	14	179	0	114
		12	19	128	100	294	63	389	98	234	37	166	52	94	50	54	48
		19	12	294	43	393	19	470	28	298	9	224	7	137	9	67	13
		25	6	362	26	483	13	406	4	232	0	171	0	97	4	45	7
		31	0	406	0	436	0	485	0	257	0	239	0	141	0	79	0
	tiller and	0	31	0	134	0	172	0	217	0	248	0	354	0	336	0	293
	stolon freq	6	25	65	84	84	118	95	157	61	135	37	182	10	220	3	225
		12	19	130	66	175	75	174	102	139	110	116	127	74	151	65	141
		19	12	223	29	253	39	271	38	254	46	232	43	203	45	130	57
		25	6	313	24	353	24	241	24	158	23	166	31	96	31	83	32
		31	0	272	0	305	0	285	0	251	0	241	0	203	0	150	0

of the outside light and was kept at a temperature of 20 °C. Before April additional light was supplied with HPL lamps to a total daylength of 17 hours.

The containers were harvested every three weeks by cutting at a height of 3 cm. The eighth and last harvest was at 29 June.

Until the first cut on 3 February the plants were watered from above to ensure a good establishment. Thereafter no water was supplied from above, apart from the nutrient solution. The yields of this first cut were low (about 2 g dry matter per container) and the same for each treatment. They will not therefore be discussed and the first yields to be considered are those of the second cut on 24 February.

At each cut the dry matter yields and the nitrogen yields of each species were determined for each container. Moreover the tiller frequency of the ryegrass was determined by counting the tillers per container, and the stolon frequency of the clover by counting the number of intersections of the stolons and the threads on a frame which was placed on the container (ENNIK, 1960). The nitrogen contents, nitrogen yields and frequencies of tillers and stolons of the 2nd to 8th harvest are summarized in table 5.

2.1 Competition at a Water Level of 99 cm

The results at the 2nd, 4th, 6th and 8th cut of the replacement series at a water level of 99 cm are presented in figure 9. The graphs in the upperpart of the figure present the stolon frequency for white clover and the tiller frequency for grass. The curves through the observations concerning the frequencies are drawn according to the equations (3) with the values of ρ given at the top of the graphs. The scattering is considerable because each point represents the yield of only one container, but by and large it may be concluded that the curves fit reasonably well, so that both species appear to exclude each other at this water level. This is confirmed by the value of 1 for the average relative yield total (RYT) based on the nitrogen yields and presented in figure 13a.

It was assumed by DE WIT and VAN DEN BERGH (1965) that the value of ρ in the equations (3) is independent of the relative plant frequencies when both species are mutually exclusive. The dotted lines in the graphs of the N-yields are calculated on the basis of this assumption. As in the case of the R0N0 treatment of panicum and glycine, it appears that the N-yield of the legume in the cylinders which contain small amounts is systematically too small. It is likely that here again this is caused by the relatively large amount which remained on the containers after clipping small yields, a conclusion which is confirmed by the absence of the effect where stolon frequency was determined. Fortunately it appears that at other water levels the white clover was maintained to such an extent that it is not necessary to consider this complication.

The fact that both species are mutually exclusive indicates that at the water level of 99 cm there was no nitrogen fixation by the legume.

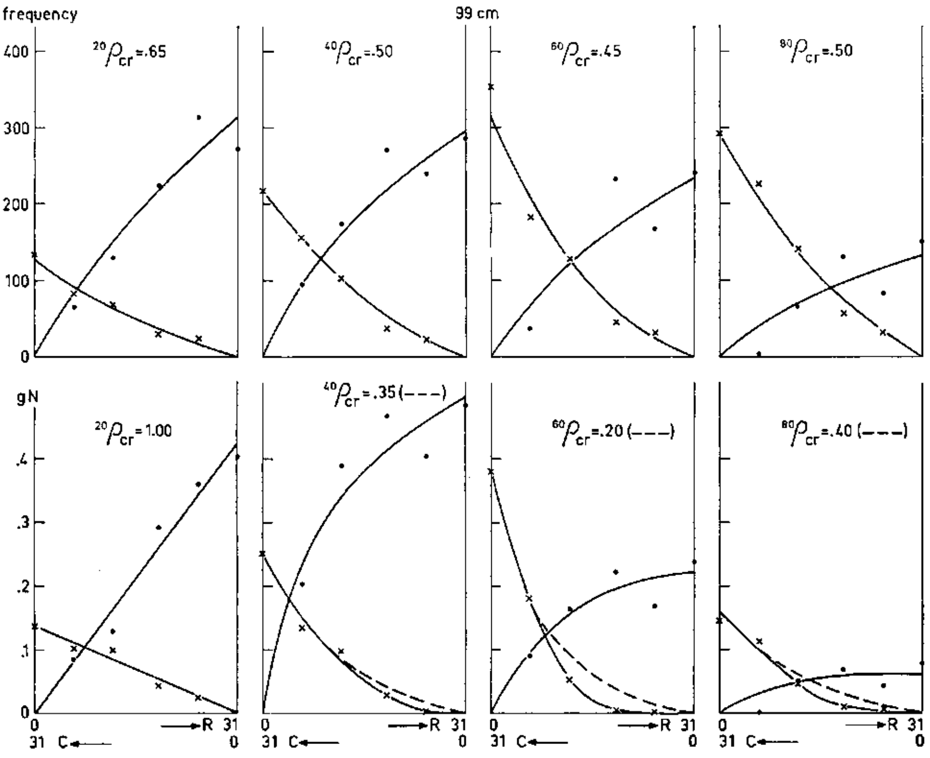

Fig. 9. The stolon and tiller frequencies (above) and the nitrogen yields (below) of clover (C) and ryegrass (R) at the 2nd, 4th, 6th and 8th harvest (from left to right) at the 99 cm water level

2.2 Competition at Water Levels of 70 and 41 cm

The nitrogen yields at the 2nd, 4th, 6th and 8th cut of the replacement series at a water level of 70 and 41 cm are given in figure 10. The species were mutually exclusive at the 2nd and 4th harvests with the water level of 70 cm and at the 2nd harvest with the water level of 41 cm. But for the other harvests the yield of ryegrass increased somewhat with decreasing relative plant frequency which indicates that nitrogen was transferred from the clover to the grass. This is also illustrated by the shape of the RYT-curves in figure 13a for these water levels.

The calculations explained in section 1.5 were applied to each harvest and the totals of the seven harvests for the water levels of 70 and 41 cm are presented in figure 11d and c. The curves 2 for the calculated yields of ryegrass in monoculture show that the grass profited from its association with clover, and a comparison of curves 1 and 3 shows that at a relative plant frequency of 0.5, amounts of 0.1 and 0.2 g N were transferred to the grass at the water levels of 70 and 41 cm, respectively.

The curves 1 and 3 for the white clover coincide, which shows that the ryegrass was not more competitive in spite of the transfer of nitrogen to the grass. The mutual

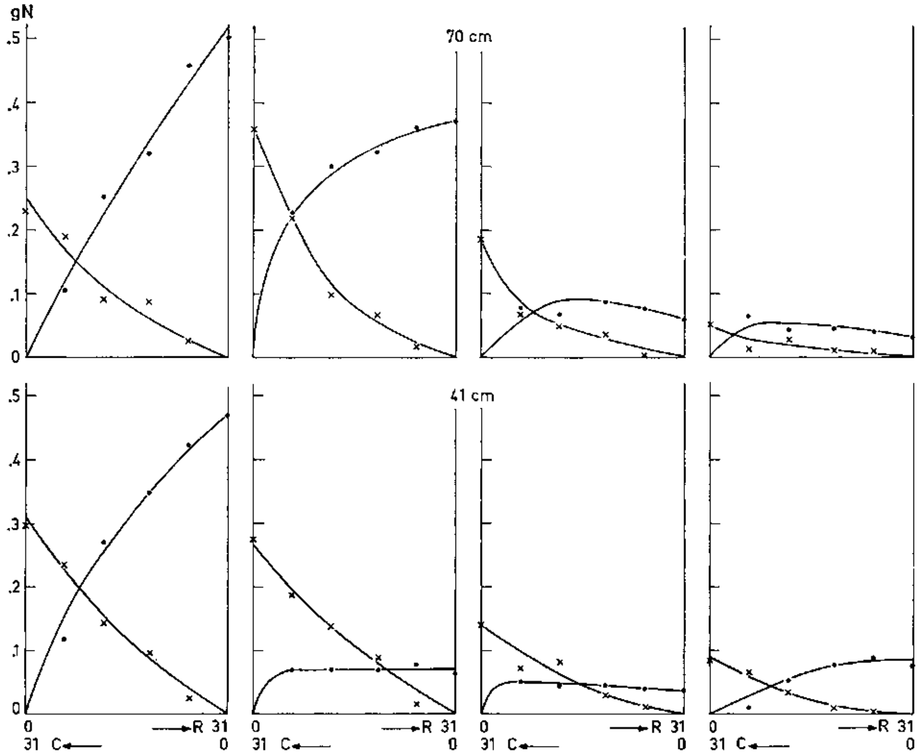

Fig. 10. The nitrogen yields of clover and ryegrass at the 2nd, 4th, 6th and 8th harvest (from left to right) at the water levels of 70 and 41 cm

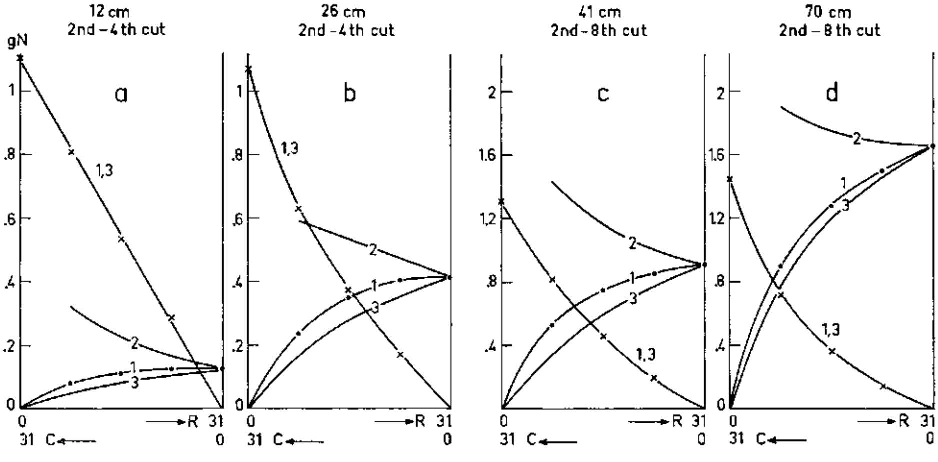

Fig. 11. The nitrogen yields of clover (C) and ryegrass (R) in the presence (curve 1) and absence (curve 3) of nitrogen transfer for the water levels of 12, 26, 41 and 70 cm. Curve 2 represents the yield of the monoculture ryegrass which would have been obtained at the nitrogen status of the ryegrass in the mixture

interference is here the same as in the case of the R1N1 treatment of the panicum-glycine replacement series (figure 7).

2.3 Competition at Water Levels of 26 and 12 cm

The nitrogen yields at the 2nd, 4th, 6th and 8th harvests of the replacement series at a water level of 26 and 12 cm are presented in figure 12.

The patterns for the 2nd and 4th harvest are similar to those with a water level of 41 cm. At the other harvests the picture is complicated by low clover yields at high plant frequencies. Inspection shows that the yield of clover was especially low in the containers which yielded the highest at first. As will be discussed later on, this is probably due to soil-borne diseases. Whatever the cause, application of the theory has to be restricted here to the results of the 2nd, 3rd and 4th cut.

The calculations in section 1.5 have been again applied, and the totals of the three harvests at both water levels are presented in figure 11b and a. At a relative plant frequency of 0.5, amounts of 0.1 and 0.05 g N were transferred to the grass at the water levels of 26 and 12 cm. The curves 1 and 3 for the clover coincide, again showing that the ryegrass was not more competitive in spite of the transfer of nitrogen to the grass.

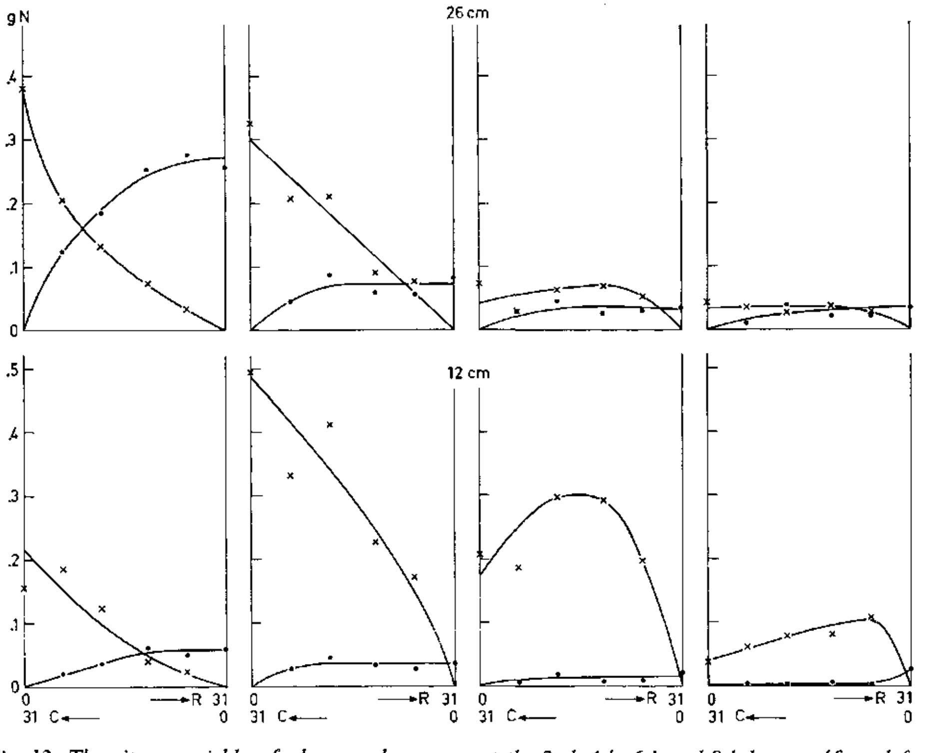

Fig. 12. The nitrogen yields of clover and ryegrass at the 2nd, 4th, 6th and 8th harvest (from left to right) at the water levels of 26 and 12 cm

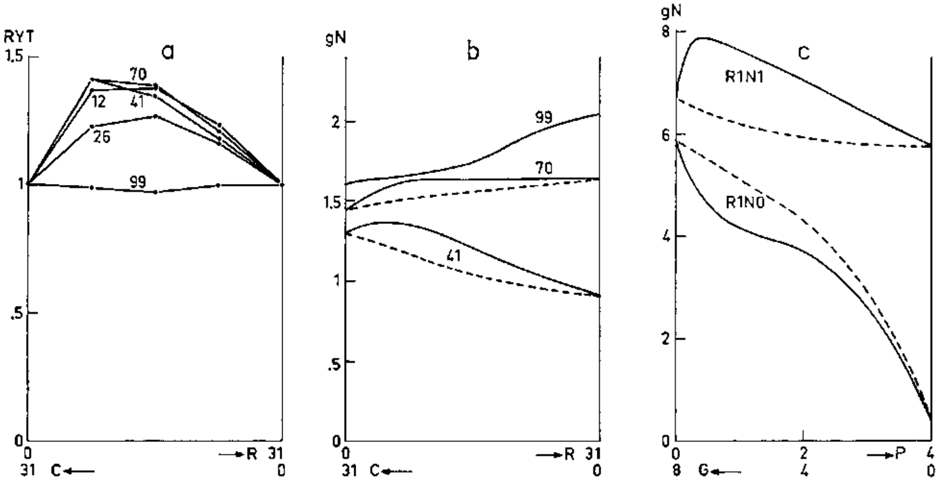

Fig. 13. a. The average relative yield totals of ryegrass and clover based on nitrogen yields. The curves for the water levels of 12 and 26 cm concern the 2nd to 4th harvests and the other curves the 2nd to 8th harvests

b. The total nitrogen yields of the ryegrass-clover mixtures at three water levels in the presence (——) and absence (----) of nitrogen transfer

c. The same for the panicum-glycine mixtures in the treatments with rhizobium

3 Discussion

The better growth of grass due to the transfer of nitrogen did not affect the shape of the yield curves for the clover. This is shown by the constancy of the ρ calculated from the clover yields. The course lines constructed by means of the values for ρ are given in figure 14. The lines in figure a are based on nitrogen yields of the clover and those in figure b on stolon frequency.

The course lines in figure a at water levels of 99 and 70 cm indicate that at first the clover lost, but that this loss was regained later on, whereas this was not the case at higher water levels. It will be shown later on that this was due to the availability of nitrogen. It is seen in figure b that this change was not reflected in the course lines calculated from the stolon frequency.

This is in agreement with DE WIT and VAN DEN BERGH (1965) who found that the course lines for grass based on tiller frequencies were much more sluggish than those on dry matter yields. The fact that no minimum occurs in the course lines in figure b is due to the rapid recovery of the clover. Which set of course lines is the most useful depends on the purpose required. Short-term effects can be studied only by course lines based on yields. Those based on frequencies may be preferred when long-term changes are studied because longer time intervals between determinations are then sufficient.

DE WIT and VAN DEN BERGH, taking into account the accuracy of the experimental results, assumed that the relative replacement rate (RRR) is independent of the relative plant frequency when the relative yield total (RYT) of two species is 1.

There are hardly any experiments available to study whether this independence is maintained at extreme relative yields, but the present experiments with legumes and

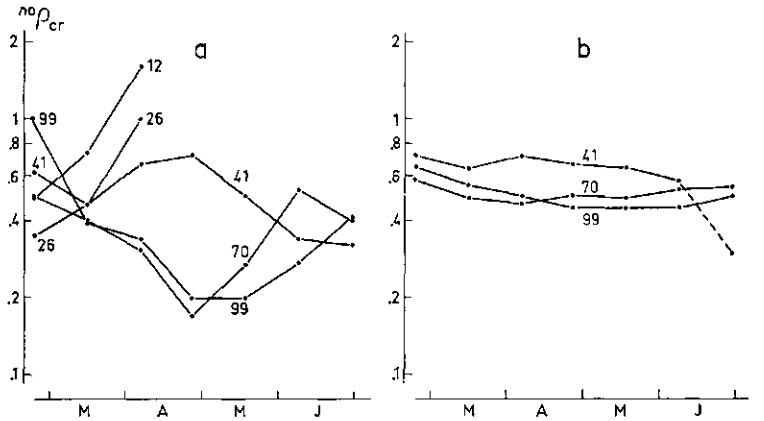

Fig. 14. Course lines for various water levels based on nitrogen yields of clover (fig. a) and stolon frequencies (fig. b)

grasses seem to indicate that this is not always the case. It was found that in those cases where the RYT of legumes and grasses was 1, the low legume yields were systematically too low compared with the yields calculated by means of a constant RRR. It could be concluded from this that the legumes vanished very rapidly as soon as they were present in relatively small amounts. However, the reason that hardly any legume was found in the yield is that the plants produced very little growth above the level of clipping under these conditions. Hence they escaped defoliation, and this has helped them to live on, rather than vanish completely.

3.1 The Transfer of Nitrogen

The RYT is greater than 1 in the case of panicum and glycine treated with rhizobium (figure 3), and of clover and ryegrass at all but one water level (figure 13a). Under these conditions the legume produces nitrogen, so that the amount of harvested nitrogen depends on the relative plant frequency, as is illustrated in figure 13b and c.

It has been calculated in section 1.5 what the nitrogen yields would have been in the absence of a transfer of nitrogen to the grass. The total nitrogen yields under these conditions are represented by the dotted lines in figure 13b and c. At the water levels of 70 and 41 cm these calculated yields are lower than the yields actually obtained, and it is seen in figure 11 that this is also the case at the two highest water levels.

At the water level of 41 cm this increase caused the total nitrogen yield of a mixture with 80 percent clover at the time of planting to be higher than the yields of either of the monocultures.This latter favourable situation can only develop when the yields of the grass and legume monocultures are about the same. The same phenomenon occurred in the case of the R1N1 treatment of glycine and panicum (figure 13c).

In these cases the transfer of nitrogen caused an increase in yield because the resulting better growth of grass did not adversely affect the growth of the legume. Such an adverse effect did, however, occur with the R1N0 treatment, and a comparison of the two lines in figure 13c for this case shows that the ultimate result of the transfer of nitrogen was a yield decrease instead of a yield increase. BAKHUIS and KLETER (1965) observed the same phenomenon in grass-clover mixtures.

3.2 The Effect of Nitrogen Application

The absence of the adverse effect discussed at the end of the previous section indicates that the competitive power of the glycine was higher with nitrogen application. This appears also from a comparison of the course lines for the R0N0 and R0N1 treatments (figure 4) and for the R1N0 and R1N1 treatments.

This is a very favourable situation, because the grass profits from the nitrogen fixation, and the legume can be maintained in sufficient proportion in the mixture by occasional nitrogen applications. This feature could be of large practical importance.

Unfortunately there are very few published data concerning grass-glycine mixtures, but it is noteworthy that at the Kairi Research Station in North Queensland very highly productive and balanced panicum-glycine pastures have been maintained since 1955 (11 years) without any management except for regular rotational grazing. As far as this can be used as an example, it supports the contention that glycine is not discouraged by a high level of mineral N availability. However, as indicated in the present experiments, as well as in practice, heavy grass growth can occur at the beginning of the season, before glycine is firmly established, and this growth can suppress glycine in the early stages.

It is a well-known practical experience that in mixed pasture white clover is depressed by nitrogen application. This is also illustrated by the results of the present experiment.

The release of nitrogen in the soil at the different water levels can be followed by considering the nitrogen uptake by the grass in monoculture during the experimental period, which is presented in figure 15a.

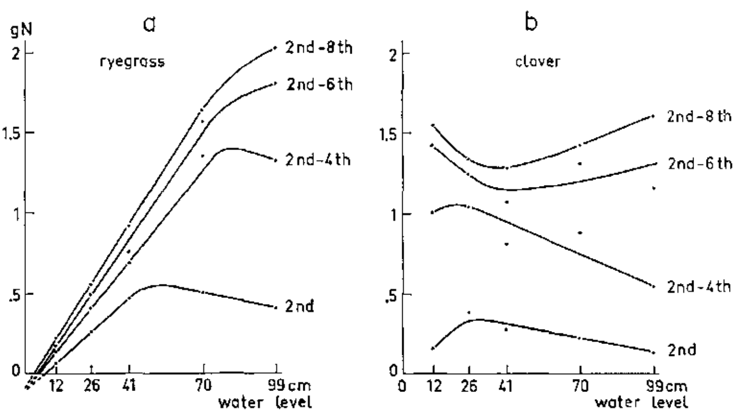

Fig. 15. Integrated nitrogen yields at successive harvests for the monoculture of ryegrass (fig. a) and clover (fig. b) in dependence of the water level

It is seen here that at the 70 and 99 cm water levels the readily available mineral nitrogen was exhausted around the 4th to 5th cut, and that after that time the grass obtained only nitrogen which mineralized during growth. Figure 14a shows that during the period of liberal N supply, the grass gained on the clover, but that after this, the clover recovered.

At the water levels of 12, 26 and 41 cm the readily available nitrogen was already exhausted at the second cut so that the clover could maintain itself, at least as long as diseases did not interfere.

3.3 Diseases

At the water levels of 12 and 26 cm the yield of clover dropped sharply after the fourth cut on those containers which had previously yielded the highest amounts of the clover.

Theoretically such a result can be expected when harvesting eventually exhausts the supply of some element in the soil especially needed by the clover. However, in a previous competition experiment at two light intensities, a similar effect was noticed in the replacement series at the low light intensity, which yielded the least (ENNIK, 1960); so that this cannot be the explanation.

The phenomenon has been studied thoroughly during recent years (ENNIK *et al.*, 1962, 1964, 1965, 1966) and from the observations that

a. the root system of clover deteriorates rapidly in course of time,
b. the deterioration is coupled with the presence of parasitic organisms,
c. this deterioration can be prevented by disinfection of the soil with D-D or steaming,
d. plants with a deteriorated root system recover after treatment with compounds known to control soil parasites,

it is concluded that in the present experiment also, the decrease in clover yield was caused by soil-borne diseases.

Summary

The grass species *Panicum maximum* and the leguminous species *Glycine javanica* were grown together in pots according to the replacement principle. The treatments were with and without rhizobium, and with and without nitrogen in all four combinations. The plants were harvested seven times during the experimental period of six months.

The species appeared to be mutually exclusive in the absence of rhizobium, but in the presence of rhizobium complicated interrelations occurred. A theory has therefore been developed enabling an estimation to be made of the yields of panicum and glycine which would have been obtained in the absence of nitrogen transfer. A comparison with the actual yields showed to what extent panicum profited from the presence of glycine when rhizobium was present and to what extent glycine suffered from the better growth of panicum. This latter phenomenon did not occur in the presence of nitrogen.

Replacement series of perennial ryegrass and white clover were grown in containers at various water levels. Both species were mutually exclusive at a water level of –99 cm. At the higher water levels of –12, –26, –41 and –70 cm the ryegrass profited from the presence of the clover, but the clover did not suffer from this better growth. This picture was complicated after the fourth harvest at the water levels of –12 and –26 cm because of the development of clover diseases.

It has often been observed that in a grass-clover mixture nitrogen application stimulates especially the grass. The present experiment confirmed this observation. However, in the panicum-glycine mixtures nitrogen application proved in several ways to stimulate especially the glycine, i.e. the leguminous species.

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