

The effect of nitrogen and phosphorus supply on the competition between *Cenchrus biflorus* and *Alysicarpus ovalifolius*

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Summary

The effect of N and P supply on competition between the grass *Cenchrus biflorus* and the legume *Alysicarpus ovalifolius* was measured in a replacement experiment on sand culture in a climate room. Two levels of N and P were applied in all possible combinations, resulting in four treatments: P_0N_0 , P_1N_0 , P_0N_1 and P_1N_1 . In monoculture the grass responded to both P_1N_1 and P_0N_1 , but not to P_1N_0 . The legume responded in monoculture only to P_1N_0 . In all treatments relative yield total exceeded unity. Only in the P_1N_0 treatment some mixtures yielded more than the highest-yielding monoculture, namely those mixtures where *Alysicarpus* dominated. *Cenchrus* was the stronger competitor in all treatments. When N was limiting, the weights per plant of the grass in mixtures were greater than those in monoculture, whereas the weights per plant of the legume were close or equal to those in monoculture (in the P_0N_0 and P_1N_0 treatment respectively). This indicates that the grass experienced hardly any competition for N from the legume, which was self-sufficient in its N supply. However the severe N limitation prevented the grass from depressing the legume in the competition for other resources. The positive response of the legume to P (in P_1N_0) was just enough to consolidate its position and to enable stable coexistence. Where N was applied the grass had a strong advantage in competition for P (in P_0N_1) or in light competition (in P_1N_1). It was concluded that the rapid growth of *C. biflorus* enabled it to capture resources early, making it the stronger competitor. Although *A. ovalifolius* grew more slowly it was adapted to survive in conditions of low nitrogen availability.

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Introduction

The experiment reported here was set out within the general framework of a co-operative study of the biology of the grazing lands of the Sahel by the Netherlands and the Mali government called the 'Primary Production Sahel Project'.

The Sahel zone of Africa has a tropical climate with low rainfall and a dry season of six to seven months. The vegetation in the region supports nomadic grazing and the zone of transhumance is bounded by the 200 mm and 600 mm isohyets. Two species from that region are the annual grass *Cenchrus biflorus* and the annual legume *Alysicarpus ovalifolius*. These species occur together in communities surrounding villages and the legume is highly prized as a fodder. Little is known of their response to nitrogen and phosphorus fertilizers and how these nutrients might affect their competitive relation.

The present experiment was meant to examine these effects in the climate room of the Centre for Agrobiological Research, Wageningen.

Materials and methods

The experiment was arranged in a factorial design with two levels of nitrogen and two levels of phosphorus in four replicates in a randomized block. The phosphorus treatments were either 15 mg P per pot (P_0) or 300 mg P per pot (P_1). The nitrogen treatments were either 28 mg N per pot (N_0) or 700 mg N per pot (N_1).

Each of these treatments were applied to a replacement series with a total of ten plants per pot and the following ratios of the two species: *Alysicarpus/Cenchrus* = 10/0, 8/2, 6/4, 4/6, 2/8 and 0/10.

Experimental procedure

The plants were grown in 6-litre (20 cm diameter) enamel pots filled with a sand low in organic matter and all plant nutrients. A layer of soil (200 g) from Mali was spread over the surface of the pots in order to provide *Rhizobium*. Evaporation from the pots was reduced to between 10 and 13 g of water per day by covering the surface of the pots with a 1.5-cm layer of white plastic prills. All nutrients except for nitrogen and phosphorus were applied in the same proportion as a quarter strength Hoagland solution and supplied throughout the experiment based on the growth curve of the plants. The pots were watered daily to field capacity with demineralized water. The climate room was run at a day temperature of 31 °C and a night temperature of 24 °C. Daylight was 12.5 hours and the light intensity was 100 W m⁻² on pot surface. The relative humidity was by day 60 % and at night 80 %.

The experiment was established by planting three seeds at each of ten predetermined locations in each pot. After germination the seedlings were thinned to one per location. The phosphorus treatments were applied at planting and all pots supplied with 28 mg nitrogen. Additional nitrogen was supplied to the N_1 treatments throughout the experiment based on the growth curve of the plants

measured by daily transpiration. As the plants grew taller they were confined to the space of each pot area by cylindrical supports.

Measurements

The penetration of light into the canopies at the top of the legume (i.e. 10 cm) was measured on one replicate after 31 days of growth using a nickel cadmium light meter with a small probe (1 cm²).

The pots were harvested after 42 days of growth when all plants had reached flowering and the rate of transpiration had reached a plateau. At harvest the height, number of tillers or main lateral stems, and number of flowers were recorded on each individual plant. The dry matter yield of each species component was measured after oven drying (90 °C for 48 hours). In one replicate the plants were clipped at stratified heights of 0-10, 10-20, 20-30, 30-40, 40-60, 60-80, and > 80 cm. The leaf area of the component species was measured for each of these layers using an area measuring machine. The roots of the monocultures were washed from the soil and dry weight was determined. The dry matter of the replicates was bulked and ground. Concentrations of total nitrogen and phosphorus were determined.

Data analyses

Competition between the species was measured by the model of de Wit (1960). Curves were hand-fitted according to the hyperbolic equation:

$$O_a = \frac{k_{ac} \cdot z_a}{k_{ac} \cdot z_a + z_c} M_a \text{ and } O_c = \frac{k_{ca} \cdot z_c}{k_{ca} \cdot z_c + z_a} M_c,$$

with frequency independent relative crowding coefficients (k_{ac} for *Alysicarpus* and k_{ca} for *Cenchrus*). M_a and M_c were the yields in monoculture of either *Alysicarpus* or *Cenchrus*, O_a and O_c their respective yields in mixture and z_a and z_c their relative planting frequencies. A look at the points in Fig. 1 reveals that there is no reason to apply Sigmoid curves.

Relative yield total (RYT) is taken from de Wit & van den Bergh (1965) as the sum of relative yields (r). The following applies

$$RYT = r_c + r_a = O_c/M_c + O_a/M_a$$

where plants compete for the same 'space' the RYT must be unity. Where RYT is greater than unity the plants do not compete for exactly the same space.

The relative reproductive rate (α) defined by de Wit (1960) is given by:

$$\alpha_{ca} = (O_c/Z_c)/(O_a/Z_a)$$

in which Z_a and Z_c are the numbers of seeds sown and O_a and O_c the numbers of seeds harvested of *Alysicarpus* and *Cenchrus* respectively. Because the amount of seeds per gram of dry matter produced is more or less the same for both species (Breman, pers. comm.), the dry matter yields of the species can be used

instead of the seeds harvested (Fig. 4).

It therefore follows that

$$\log O_c/O_a = \log \alpha_{ca} + \log Z_c/Z_a$$

so that if the relative reproductive rate is independent of the plant frequency the observations will be arranged in a straight line parallel to the diagonal when $\log O_c/O_a$ is plotted against $\log Z_c/Z_a$ in a so-called ratiodiagram (Fig. 4). If the relative reproductive rate is frequency dependent and intersects the diagonal from left above to right below a stable equilibrium ratio occurs at the intersection.

Results

Response of the monocultures

The responses of both species to nitrogen and phosphorus are shown in Table 1. The dry matter yield of *Alysicarpus* was increased ($P < 0.01$) by phosphorus and there was no effect for nitrogen. In *Cenchrus* there was a significant nitrogen and phosphorus interaction ($P < 0.01$). The highest grass yield was obtained with the application of both nitrogen and phosphorus; there was a response to nitrogen alone but not to phosphorus alone.

In earlier experiments (Bink & Wolters, 1981, not published) it was found that the nitrogen concentration of *Alysicarpus* without nitrogen fertilization was approximately 4 % in young plants, decreasing to 3 % and rising again to 4 % when nodulation was succeeded. Without *Rhizobium* the N concentration may de-

Table 1. Dry matter yield (g/pot), %N, %P, shoot/root ratio and transpiration coefficient (ml/g DM) for *Alysicarpus ovalifolius* and *Cenchrus biflorus* in monoculture.

	Dry matter	%N	%P	Shoot/root	Transpiration coefficient
<i>Alysicarpus ovalifolius</i>					
P ₀ N ₀	3.57	3.1	0.12	4.6	428
P ₁ N ₀	6.31	3.9	0.32	8.6	573
P ₀ N ₁	3.22	5.0	0.31	8.0	450
P ₁ N ₁	6.51	5.0	0.46	7.8	429
Level of significance	**			*	N.S.
LSD	2.24			3.65	
<i>Cenchrus biflorus</i>					
P ₀ N ₀	5.07	0.6	0.10	5.9	183
P ₁ N ₀	5.61	0.5	0.14	6.0	190
P ₀ N ₁	14.81	2.6	0.08	4.9	257
P ₁ N ₁	29.98	2.3	0.33	7.9	241
Level of significance	**			*	**
LSD	2.14			1.92	54

* $P < 0.1$; ** $P < 0.01$; N.S. = non-significant.

crease to 1.5 %. In other experiments a concentration of organic nitrogen of 4 % was found with nitrogen fertilization and also with P fertilization. In the present experiment the N concentration was 3.1 % in the P_0N_0 , 3.9 % in the P_1N_0 and 5.0 % in P_0N_1 and P_1N_1 . In the latter treatments there probably was 1 % nitrate nitrogen present in the samples.

The nitrogen concentration of *Cenchrus* was extremely low in the treatments without nitrogen (P_0N_0 and P_1N_0): 0.6 and 0.5 respectively. On the treatments receiving nitrogen (P_0N_1 and P_1N_1) the N concentration in *Cenchrus* was higher, though still lower than the lowest concentration ever found in *Alysicarpus*. The phosphorus concentration of *Alysicarpus* was highest in the P_1N_1 treatment. P levels in the P_1N_0 and P_0N_1 were similar. The P concentration of *Cenchrus* was lowest in the treatments without phosphorus (P_0N_0 and P_0N_1), highest in the P_1N_1 treatment and intermediair in the P_1N_0 treatment but in each treatment lower than the P concentrations of *Alysicarpus*. Because there were no replicates of the chemical analyses it was not possible to subject these data to statistical analyses.

The P:N ratios suggest that *Alysicarpus* was limited by phosphorus in the P_0 treatments (Dijkshoorn & Lampe, 1981). *Cenchrus* was limited by nitrogen in the treatments without nitrogen and by phosphorus in the P_0N_1 treatment.

There was a trend towards a lower shoot:root ratio in *Alysicarpus* in the P_0N_0 treatment ($P < 0.1$). Transpiration coefficients of *Alysicarpus* were not significantly different but there was a significant effect ($P < 0.01$) in *Cenchrus* of adding nitrogen.

Competitive relationships

In Fig. 1 the dry matter yields of *Alysicarpus* and *Cenchrus* of the individual pots are plotted against the plant frequencies. Fig. 2 shows the replacement diagrams for the relative dry matter yields and nutrient contents. The RYTs in all treatments including the P_1N_1 where nutrients were not limited, are greater than unity. This means that the species were not mutually exclusive and occupied some different 'space'. Only in the P_1N_0 treatment some mixtures yielded more than the highest-yielding monoculture. The advantage was 20 % and occurred in mixtures dominated by *Alysicarpus* (see Fig. 1). Bink & Wolters (1981) found in the P_1N_0 treatment of a competition experiment with these two species without *Rhizobium* that the RYT was unity. Both species excluded each other in competition for nitrogen. In their case the relative crowding coefficient for *Alysicarpus* (k_{ac}) was only 0.27 while that of *Cenchrus* was more or less the same as in the present experiment. Obviously the effect of nodulation was an improvement of the performance of *Alysicarpus* but did not result in a greater competitive pressure on *Cenchrus*.

The convex curves and high relative crowding coefficients for the grass show that it was the stronger competitor in all treatments.

In most cases the relative crowding coefficients calculated for uptake of nitrogen and phosphorus were approximately equal to the relative crowding coefficients calculated for dry matter yields. Only in the P_0N_1 treatment there was a

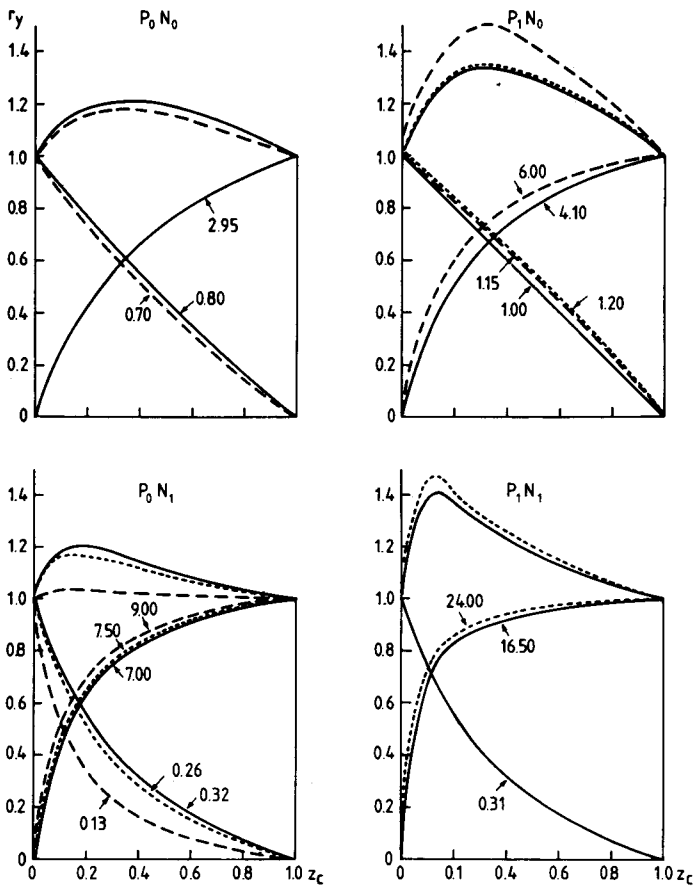


Fig. 1. Replacement diagrams presenting dry matter yield of *Alysicarpus* (×) and *Cenchrus* (●) and total yield (---) for the four treatments. Notice the different scales by $P_1 N_1$.

difference, k_{ac} calculated for P content being lower than k_{ac} for dry matter yield. The grass had a strong advantage in competition for P because of the rapid growth. In monoculture the legume can still dilute the phosphorus to the same content as in the mixtures and in that case the relative crowding coefficient for phosphorus will become the same as for dry matter. The P contents and the P:N ratio suggest that both species are limited by phosphorus.

In the $P_0 N_0$ treatment *Alysicarpus* was limited by phosphorus while the internal concentrations and the P:N ratio suggest that *Cenchrus* was limited by nitrogen (Table 1). When phosphorus only was applied ($P_1 N_0$), the limiting factor for *Alysicarpus* was eliminated resulting in higher k values, while *Cenchrus* was still limited by nitrogen. This resulted in a stable equilibrium, as can be seen in Fig. 4. Where both nutrients were applied ($P_1 N_1$), the k values in

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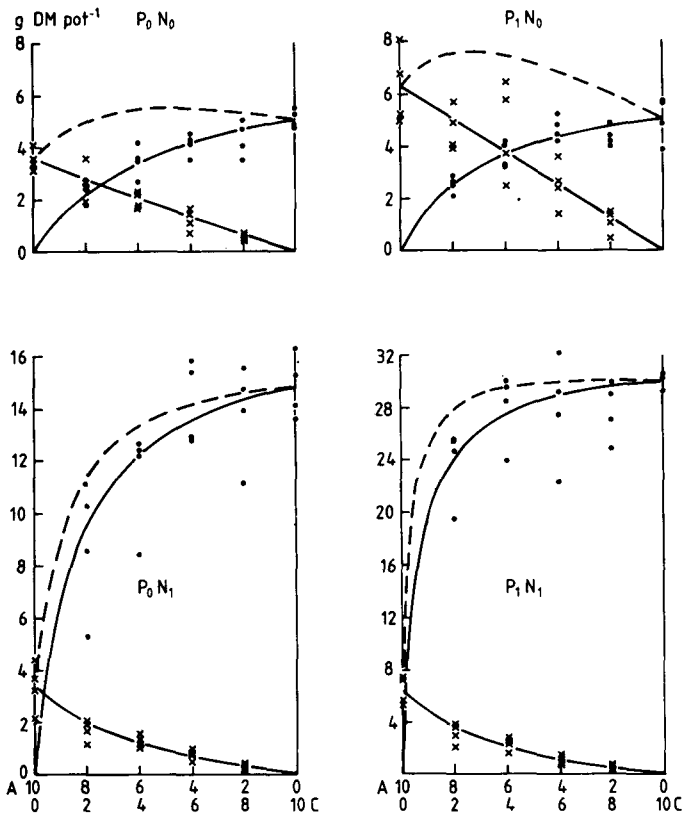


Fig. 2. Replacement diagrams of relative yields of *Alysicarpus* and *Cenchrus* of g dry matter (—), nitrogen (---) and phosphorus (- - -) in the four treatments. Monocultures of *Alysicarpus* on left and of *Cenchrus* on right. RYT's are superimposed at the top. k values of the curves are given in the figures. Missing k values for P and/or N are in that case the same as for dry matter.

the legume for nitrogen and phosphorus were equal to that for dry matter. The low k value for legume dry matter shows that there was considerable interference from the grass.

The response of the grass to nitrogen resulted in an increase in size and it seems probable that this could confer an advantage. A method of illustrating size is the leaf area profile for the several treatments shown in Fig. 3.

Clearly in the treatments to which nitrogen had been applied (P_0N_1 and P_1N_1) the grass was able to shade the legume. Measurements taken 31 days after planting showed that the penetration of light to the legume canopy in the mixtures were as follows:

Treatment	P_0N_0	P_1N_0	P_0N_1	P_1N_1
Light penetration (%)	73	62	58	32

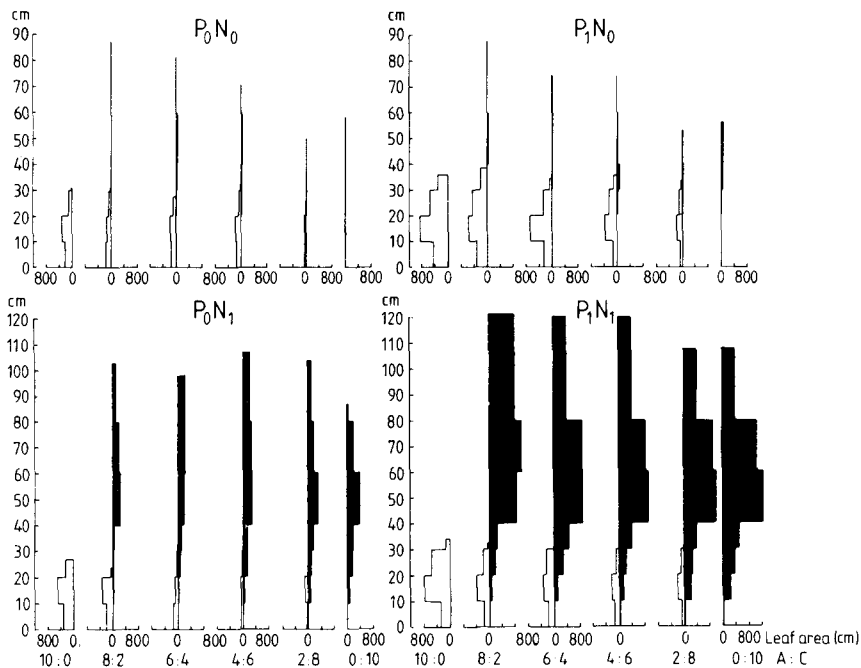


Fig. 3. Leaf area profiles of *Alysicarpus* and *Cenchrus* in monocultures and mixtures for the four treatments. Unshaded on left represents *Alysicarpus*, shaded on right *Cenchrus*.

There can be little doubt that a reduction in the light received by the legume would have contributed to a reduction in its yield in the P_1N_1 treatment. However, there was little difference in the values recorded for the P_1N_0 and P_0N_1 treatments.

In Fig. 4 the relative replacement rates (α) for the four treatments are presented. This figure shows that the legume/grass competition approached equilibrium when phosphorus only (P_1N_0) was applied. In the treatments where nitrogen was applied the legume was suppressed severely.

Flowering of *Alysicarpus* was significantly increased by phosphorus supply (2.8 flowers per plant at P_0 compared with 4.3 flowers per plant at P_1 ; $P < 0.001$).

There was also a significant interaction of nitrogen supply with the planting frequency ($P < 0.001$): with nitrogen there were 5.5 flowers per plant in monoculture reducing as planting frequency decreased to 2.0 flowers per plant at a planting frequency of 20%. Without nitrogen there was no effect of planting frequency with a mean of 3.9 flowers per plant. In *Cenchrus* there was a significant interaction of nitrogen and phosphorus supply ($P < 0.001$). When both nutrients were supplied flowering was increased to 1.7 flowers per plant compared to a mean of a single flower per plant in all other treatments.

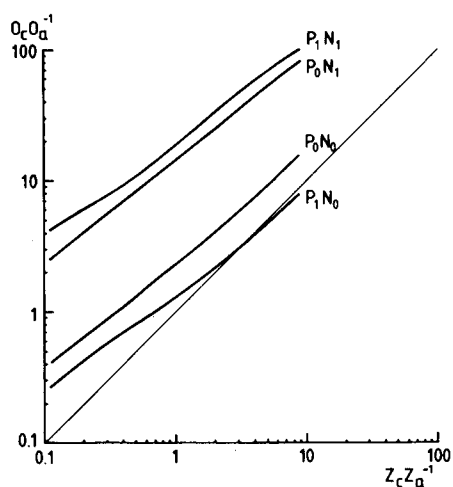


Fig. 4. Ratio diagram in which the ratio of the initial plant frequencies are plotted against the yield ratio for the four treatments.

Tiller numbers of the grass remained at one per plant in the P_0N_0 and P_1N_0 treatment. However, in the treatments with nitrogen (P_0N_1 and P_1N_1) there were more tillers per plant and also an effect of planting frequency. In the following table the number of tillers per plant are shown for these two treatments:

Number of plants per pot		2	4	6	8	10
Number of tillers per plant	P_0N_1	3.5	5.5	2.3	2.0	1.9
	P_1N_1	7.0	4.0	3.5	3.4	2.5

These results confirm the competition between the grass plants in the treatments supplied with nitrogen.

Discussion

The two species studied in this experiment had quite different responses to nitrogen and phosphorus. In mixtures there was an interaction between these responses and competition effects. We speculate as to the mechanism of the co-existence of these species in nature.

Alysicarpus nodulated well and was able to grow almost without a source of soil nitrogen. Its response to phosphorus was a yield increase by a factor of almost 2, which was smaller than that reported for some other tropical legumes (Andrew & Robins, 1969). It is possible to think of the response in an inverse way; for example the reduction in yield in a deficient soil was only half that of maximum yield potential. This could suggest that *Alysicarpus* is adapted to growing in soils where phosphorus is deficient. Another characteristic of plants adapted to nutrient deficient soils is a slow growth rate (Chapin, 1980). It is

possible to infer slower growth rate in *Alysicarpus* both from its smaller yield and high transpiration coefficient. In contrast the response of *Cenchrus* to nutrient supply, particularly nitrogen, together with its larger yield and smaller transpiration coefficient, suggests that it is adapted to higher soil fertility.

As expected, the grass had a large competitive advantage where nitrogen was applied. In the situation where nitrogen was ample but phosphorus was limiting, the grass competed vigorously for phosphorus and the RYT_{max} for phosphorus of 1.04 showed that the species came close to being mutually exclusive. Where nutrients were not limiting, legume yields in the mixtures were reduced and we conclude that shading by the taller grass was responsible. Experiments by others (for example Stern & Donald, 1962) have shown that competition for light in grass-legume swards becomes important when soil fertility is high. Ironically the RYT_{max} in this situation of non-limiting nutrients was 1.4; a possible explanation for this is that the mixtures utilized light more efficiently than the monocultures with the legume surviving on the 32 % of light not intercepted by the grass, partly coming from aside. There is doubt whether this effect would have occurred in a continuous sward.

Without applied nitrogen the yield and the competitive ability of the grass was reduced. We had expected that in this situation the legume's ability to fix nitrogen would make it the stronger competitor. Instead the weights per plant of the grass in mixtures were larger than in monoculture, while the weights per plant of the legume in mixtures were at best only equal to the monoculture. With the legume self-sufficient for nitrogen, competition in the nitrogen-deficient soil will have occurred mainly between the individual grass plants. Consequently fewer plants in the mixtures had more nitrogen available per plant than in the monocultures. This resulted in an increase in height of the grass plants as planting frequency decreased (Fig. 3). The values for RYT_{max} (1.2 without phosphorus and 1.35 with phosphorus) in these treatments exceeded unity, because *Alysicarpus* is not limited by soil nitrogen.

The question arises as to how these species are adapted to coexist in nature. One model for coexistence suggested by Braakhekke (1980) involves the competitive advantage of one species for one nutrient and of another species for a different nutrient. In this experiment we have shown *Cenchrus* to be a strong competitor for both nitrogen and phosphorus and also for light. It would seem that *Cenchrus* is adapted to grow rapidly and therefore seize available resources first. Even in infertile situations, this was evident and allowed the plant to survive even though only one flowering tiller per plant was produced. *Alysicarpus* being independent of soil nitrogen was best adapted at low nitrogen levels where light competition from the grass was reduced. In the N_0 treatments *Alysicarpus* profits from P fertilization whereas *Cenchrus* cannot respond to P because it suffers from severe N limitation. This advantage of *Alysicarpus* in monoculture yield is just enough to balance the advantage of *Cenchrus* in overall competitive ability and enables *Alysicarpus* to survive the competition from *Cenchrus* and to subsist in mixtures at low A/C ratios (Fig. 4) in a homogeneous environment when some phosphate is given. It seems probable that plants adapted to infertile situa-

tions are not subjected to the rigorous selection for competitive advantage and we could perhaps think of *Alysicarpus* as a 'survivor'. Although differences in rate and pattern of germination can change the amount of *Alysicarpus* from year to year depending on the rainy season (Breman et al., 1980) an equilibrium shown in Fig. 4 for the P_1N_0 plus the higher yield for mixtures dominated by *Alysicarpus* make a fertilizing with phosphorus still interesting.

Admittedly the results from phytotron experiments do not encompass the full range of conditions experienced by plants in nature. In nature soils are not homogeneous and pockets of higher fertility may exist in depressions for example. A mosaic of environmental differences has been shown to account for the coexistence of another tropical grass-legume mixture (Torsell, 1973) and could also occur in Mali.

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