

Productivity of Sahelian rangelands in relation to the availability  
of Nitrogen and Phosphorus from the soil

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Summary

Annual productivity of natural rangelands with annual grasses in the Sahel is not restricted by the actual precipitation, but by the low fertility of the soils. Deficiencies of the elements nitrogen and phosphorus are predominant. Which of these two limits productivity most in a particular case can be determined from their ratio in plant tissue.

Productivity and nitrogen uptake by the vegetation of natural pastures were studied in sets of fertilization experiments on different soil types. On basis of their results a static model is developed to predict N-uptake and productivity of rangelands. Inputs for this model are the natural fertility of the soil, fertilization and its recovery, and the duration of the phase of vegetative growth. Little attention is paid to losses of N that may occur in the seed filling period and afterwards. Recovery of fertilizer N was generally fairly good. Very locally, denitrification and/or leaching may occur. Low availability of P was found to limit N-absorption, and thus plant yield, on some overgrazed soils.

Herbage production of natural pastures and soil fertility

Natural grasslands of the Sahel are rangelands of a very poor quality, except for the brief period that they carry fresh, young plants. An important aspect of the low nutritive value of these pastures is the low protein content of only 3 - 6% in the dry vegetation. Most of the biomass consists of annual grasses. In some areas, perennial grasses make up a considerable part of the biomass of natural pastures. Their quality often exceeds that of annual grasses. Trees maintain still higher levels of protein in their leaves, and so do many leguminous plants. Although consumption of these species can improve the animal diet considerably, the bulk intake of cattle, sheep and goats consists of annual grasses. This paper deals particularly with these annuals.

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Mature annual grasses in the Sahel are poor in protein because of the low natural fertility of the soils. In the southern part of the Sahel (400-600 mm annual precipitation) the natural vegetation would grow up to 3 to 5 times more biomass with a higher protein content if the availability of plant nutrients, particularly of nitrogen (N) and phosphorus (P), were higher. This would not require more water than the normal precipitation, as will be shown below. This observation agrees with similar findings in semi-arid lands of the United States (Power, 1970), of Israel (Van Keulen, 1975) and of Australia (Date, 1973). Only at very low levels of annual precipitation, water availability limits the annual herbage production. In Israel, this level is about  $150 \text{ mm yr}^{-1}$ . Some of our experiments suggest that this level is about 150-200  $\text{mm yr}^{-1}$  in the Sahel.

N is much more a mobile element in the soil-plant system than P is. Moreover, the soil-plant system is an open system for N: 1-20% of the N in the vegetation and in soil organic material enters and/or leaves the system annually. Some of the fluxes of N may be influenced or manipulated. It is therefore of special interest for the management of semi arid grasslands to be well informed about the elements of the N-cycle, and to understand the dynamics of the combined processes. The central question in this paper will thus be in what quantitative manner plant production depends on N-uptake from the soil, and how N-uptake relates to the natural fertility of the soil and to fertilization. On basis of results of field experiments, a model is proposed that can be applied outside the area where our experiments were performed. The main field observations required for application of this model are the amount of N contained by the vegetation at flowering on pastures that were not fertilized, and the duration of the growing season.

The annual gain or loss of P from the system is negligible, although local accumulation or exhaustion may occur over a sequence of years. The P available for uptake by plants is a small and variable percentage of the total P in the soil. Considerations of the dynamics of P-availability must therefore concentrate on transformations within the system. Some of these are of a biological nature, some are of a chemical nature. The last section of this paper deals with some of its aspects. Because plants need P and N in a certain ratio, one should not consider the N-cycle and P-cycle independently, particularly not on poor soils.

This paper is an interim report of a study aiming at the determination of the relative importance of various processes in the N-cycle in Sahelian grasslands. A final report (PPS, in prep.) will be available in 1980. The study is carried out in the framework of the research project "Production Primaire au Sahel" on a ranch near Niono ( $14^{\circ}\text{N}$ ,  $5^{\circ}\text{W}$ ) in Mali. The annual precipitation in Niono amounts to  $570 \text{ mm} \pm 20\%$ . The area consists of sandy dunes, clayey depressions and loamy plains. During the years of experimentation, the ranch was covered by a closed vegetation of annual

grasses with very few leguminous plants, and by a fairly open tree and shrub vegetation. Anatomical analysis showed that the grass species had all the arrangement of sheath bundle cells typical of plants with the C-4 type of photosynthesis. They will be referred to as C-4 grasses, in contrast to C-3 grasses that lack this arrangement. The composition of the vegetation had changed considerably as a result of drought in preceding years (Bremner and Cissé, 1977). Grazing on the ranch is partially controlled and at a low intensity since 1960.

#### Primary productivity and nitrogen availability

##### a. Method of analysis

The relation between N-uptake and production was analysed by Van Keulen (1977) and Van Keulen and Van Heemst (1979) for a number of agricultural crops, using data from fertilization experiments in which economic yield and total nitrogen uptake at maturity were available. Their method of analysis is illustrated in fig. 1, using data from a pot experiment, reported by Colman and Lazenby (1970). In the upper half of the graph, the relation between above ground biomass and nitrogen uptake is given, while the lower half contains the relation between fertilizer application and uptake. The data are averages of four cutting regimes, and thus of plants of different ages. In the upper half it is shown that in N-limiting conditions, the amount of biomass produced is proportional to the amount of N taken up, indicating that growth continues until a minimum concentration in the tissue is reached ( $N_{min}$ ). At higher levels of availability the N-concentration in the tissue is above the minimum level and yield increases less than proportional to the amount of N absorbed. When N is abundantly available, the tissue may reach a maximum level, above which no more nitrogen can be taken up ( $N_{max}$ ). The values of  $N_{min}$  and  $N_{max}$  vary with the age of the plant, being about 2.5 times higher in very young tissue than in mature tissue. At any moment during development, the minimum concentrations are about half the maximum values in most C-3 grasses and cereals. The results presented in fig. 1, as well as other observations suggest, that the maximum level in the tissue of C-4 grasses and cereals is similar to that of the C-3 grasses, but that their minimum value may be as low as a quarter of the maximum. When it is assumed, that these observations point to general physiological characteristics of the two groups, the range of possible N-concentrations in the tissue of C-3 and C-4 grasses can be estimated. A schematic representation of these values, as related to development stage is given in fig. 2. Comparison of N-concentrations in C-3 and C-4 grasses given by Brown (1978) support the hypothesis presented here. The data on uptake refer to total N in the plant tissue, regardless of the form in which it is present. It should be realized, that especially under heavy fertilizer application up to 10% of the total N may be in the form of nitrate, which is not part of the structural tissue. A distinction has

not been made, however, since only a very limited number of observations on  $\text{NO}_3^-$  content are available, while moreover, the standard error in the basic experimental data is considerable (10-20%).

The lower half of fig. 1, relating application and uptake, is characterized by the slope of the line, representing the fraction of the fertilizer nitrogen recovered in the above ground biomass ( $r$ ) and the intercept with the x-axis, representing the availability of soil N without fertilization ( $N_s$ ). The graphical procedure illustrated in fig. 1, which permits discrimination between uptake of applied nitrogen and the subsequent conversion into plant material will be applied to the experimental results obtained.

#### b. Experimental procedure

Five experiments were performed on small fields on soil types that predominate on the ranch and in the Sahel: a clayey, a sandy and a loamy soil, an overgrazed sandy soil and a heavy clay soil. The latter becomes briefly flooded in the growing season. For details about the plant species on these soils, see the legends of figs. 4-8. Except for a control plot,  $100 \text{ kg P ha}^{-1}$  (as triple super phosphate) was always given to avoid P-shortage. Preceding experiments showed that after such a P-dressing, N was the only element limiting plant production. No other mineral deficiencies occurred. Urea was applied broadcast at rates of 0, 75, 150 or  $300 \text{ kg N ha}^{-1}$  shortly before the growing season. On the overgrazed soil where the legume *Zornia* grew, seedlings were eliminated and the annual grass *Schoenefeldia* was sown. The surface of the heavy clay soil was slightly tilled manually, but the natural vegetation was allowed to develop. On the overgrazed sandy soil and on the heavy clay soil, a second group of experiments was performed with nitrate instead of urea. Nitrate was worked into the top 3 cm.

Yields were determined by duplicate harvests of  $10 \text{ m}^2$  subplots, approximately at the onset of flowering, and again 15 days later. Plant samples were analysed for N, P and ash at the Centre National de Recherche Zootechnique in Sotuba, Mali.

#### c. Experimental results

The marked response to fertilizer application, depicted in figs. 4-8 proves that soil fertility rather than moisture availability limited plant productivity, as was already anticipated in the introduction.

The shape of the curve relating production to N-uptake in these figures is similar to that of fig. 1, and to those reported by Van Keulen and Van Heemst (1979). The initial slope of the yield-uptake curves, representing the minimum N-concentrations at flowering, are similar in all but one graphs and conform those of fig. 2.

The results presented in fig. 6 suggest a minimum N-concentration of about 0.75%, which is attributed to the fact that the vegetation was a mixture of C-3 dicotyledons and C-4 grasses. The experiment on the heavy clay soil (fig. 8) was harvested a little before flowering, so that the maximum concentration of N is slightly higher than 2%.

The total N-uptake and the biomass produced at the highest fertilization levels vary considerably in different experiments. This is attributed to differences in the duration of the vegetative period, as will be discussed below. Comparison of the results of the first and of the second harvest of the same treatment shows that biomass increases after flowering, whereas the total N-uptake remains constant or diminishes, thus leading to an upward shift of the uptake-yield curve.

The lower halves of figs. 4-8 show the availability of N without fertilization ( $N_s$ ) and the recovery fractions ( $r$ ).  $N_s$  varies from 10 to 35 kg N ha<sup>-1</sup> yr<sup>-1</sup> in these experiments. Such values are not characteristic for the soil types, but are strongly influenced by differences in long term exploitation between the sites. The values of  $N_s$  are quite low when compared to those found by Van Keulen and Van Heemst (1979) in their survey, but are normal for sahelian pastures. Mineralization is the most important process that makes N and P available for plant growth on unfertilized soils. Use of radioactive tracers in rice fertilization studies showed that the amount of N provided by mineralization is independent of the level of fertilization (FAO, 1970). This is supposed to be similar in sahelian soils, although no direct evidence supports this assumption. The N in precipitation and N<sub>2</sub>-fixation contribute also to the availability of N on unfertilized soils. The relative importance of the latter process is probably affected by application of N, but its contribution was not substantial in the experiments described. Hence, it seems reasonable to assume that the amount of N available to the plants without fertilization will also be available when fertilizers are applied. The proportionality between supply of N and its absorption by the vegetation therefore reflects a constant recovery fraction. The value of  $r$  was between 0.4 and 0.65 in these experiments for the first year after fertilizer application. These values are in the middle of the range reported by Van Keulen and Van Heemst (1979).

Because the vegetation at flowering contains 2% N at most, there is a limit to how much N can be absorbed. The recovery fraction is thus only a constant up to a certain rate of fertilization. This is shown clearly in figs. 5 and 7. The recovery fraction is similar for both the early and the late harvests, or seems to decrease in time, particularly at high levels of productivity.

d. Interpretation of experimental results

For the prediction of herbage yields in response to treatments, it is useful to be able to construct graphs like those of figs. 4-8 for a particular situation, with only a minimum of experimental information to be collected in the field. The results of the experiments presented will be analysed below to this end. We will concentrate on four aspects:

1. the amount of biomass at flowering and at maturity under conditions where nitrogen is non-limiting;
2. the N-concentration at flowering in conditions of N-deficiency and of ample N-supply;
3. the natural fertility of the soil;
4. the recovery fraction.

The amount of N in the above ground parts of the vegetation attains a maximum around flowering. This is shown in fig. 3, which presents results of one of many similar experiments (PPS, in prep.). This phenomenon was found at all levels of herbage production. The observation that the amount of N in the vegetation does not increase after flowering is most valuable, because it provides a clue for the calculation of N-uptake: when nitrogen is non-limiting, the concentration of N at flowering is 2% (cf. fig. 2), and the amount of N taken up can be related directly to the amount of biomass present at that moment. The latter quantity is a function of the rate of growth and the duration of the period of vegetative growth. The natural vegetation of annual grasses grows at rates of about 220 and about 150 kg dry matter ha<sup>-1</sup> day<sup>-1</sup> on clayey and sandy soils respectively, under optimum conditions of plant nutrients and soil moisture. This was found in field experiments with periodic harvests in conditions which were identical to those at the highest fertilization level of the experiments of the figs. 4-8. Results of one series of periodic harvests are given in fig. 3; results of other experiments are summarized in table 1. A sudden acceleration of the growth rate, following a drastic change in the weather, marks the beginning of a period of vigorous, vegetative growth, which ends at flowering. The duration of this period, indicated in table 1, is only slightly longer with heavy fertilization than without it, so that in practice, the period of vigorous, vegetative growth can be established in unfertilized pastures. Alternatively, the date of growth acceleration can be derived from the actual precipitation pattern, accounting for local run off and run on. The date of flowering of most Sahel grasses is partially controlled by daylength (PPS, in prep.) and may be estimated when observations are lacking. The values of table 1 show that the amount of biomass at flowering is clearly related to the number of growing days. The lower maximum growth rates at the sandy soils are probably due to a lower availability of soil water.

In the experiments described, the vegetation was usually strongly dominated by one species. If two or more species are present, that differ considerably in their

dates of flowering, the analysis of the data may be more complex, but not necessarily so. If the species are thoroughly mixed, the longer living species may finally dominate the vegetation and thus determine its herbage production. If both species are in monospecific patches, the analysis can be done for both species separately.

After flowering, the vegetation grows for another 10-20 days until the plants mature. The growth rate drops to zero over that period, so that on the average it is half of that during the vegetative phase.

For the time being, the amount of N available to the vegetation from unfertilized soil cannot be predicted from basic data. It needs to be determined in the field by harvesting vegetation on unfertilized plots at flowering. As mineralization proceeds only when the soil is humid, a relation between  $N_s$  and the length of the period that the top soil is wet is to be expected. There are indications of such a relationship in sahelian soils, as in the Negev (Harpaz, 1975), and they will be discussed in a later report (PPS, in prep.). It means that  $N_s$  needs to be determined in an average year, or adjusted when determined in relatively wet or dry years.

Experimental determinations of the recovery fraction of the N applied requires careful field experimentation, since there is not yet a good theoretical basis to calculate the value of  $r$  for particular conditions. However, when plotting  $r$  versus  $N_s$  from figs. 4-8 and some other PPS data, a relation between  $N_s$  and  $r$  seems to exist (fig. 9). The data points suggest that  $r$  is inversely related to  $N_s$ . This relation could provide an estimate of  $r$  when only  $N_s$  has been determined. Although this relation is supported by only a few data points, there is an additional argument, based on competition for available N in the soil between plants and soil microorganisms. If plants would be grown on pure and sterile sand to which nutrient solution is added, the recovery of N would be complete and the 'natural fertility' zero. But in soil with some organic matter, decomposition makes inorganic N available for uptake by microorganisms and by plants. Microorganisms will absorb part of this N because the soil organic matter has often a high C/N ratio (20-35) and its decomposition does then not provide sufficient N for microbial growth. The more microorganisms are active, the higher the 'natural fertility' of the soil, but also the stronger their competitive power for N. This suggestion would support an inverse relation between  $r$  and  $N_s$ . It also implies that recovery of fertilizer N in sahelian pastures will be quite high in the long run since the fertilizer N fixed by soil organic matter will be released in due course when the organic matter decomposes.

It is not yet known over what range of soil fertilities this relation is valid nor is investigated whether it changes at higher or lower rainfall levels. For British soils, Brockman et al. (1971) found a positive correlation between  $r$  and  $N_s$ . Such a relation can be expected whenever fixation of fertilizer N by soil organic matter is relatively unimportant, compared to denitrification and leaching.

A limited number of observations suggests that the size of the root system of a mature vegetation of annual grasses is 700-1400 kg dry matter  $\text{ha}^{-1}$  and is only to a limited extent dependent on the amount of above ground biomass. Also the N-concentration of the roots is quite constant: 1.1 to 0.2%. Hence, there is always about 10 kg N  $\text{ha}^{-1}$  contained in the root system, at least in our experiments. This is quite an appreciable proportion of the total N absorbed under N-deficient conditions, but since this quantity seems so invariable, it does not affect the above considerations.

e. A simulation model

Based on the evidence presented above, a static simulation model is developed. It enables one to calculate the biomass present at the end of the growing season for pastures in the southern part of the Sahel, and the amount of N that it contains. Its application is restricted to vegetations of annual grasses, and to situations where P-deficiency is not severe. For each situation in which the model is used, the duration of the period of vigorous, vegetative growth, the amount of N in the vegetation at flowering on unfertilized field, and the rate of fertilization need to be specified. The minimum and maximum concentration of N at flowering are supposed not to vary with conditions. The value of the recovery fraction may be based on its relation to  $N_s$  (cf. fig. 9), or it may be determined experimentally in case of doubt about the validity of this relation for the specific case. The model is presented graphically in fig. 10.

The amount of biomass at flowering is calculated first for a situation with an ample supply of plant nutrients. It is found by multiplying the growth rate of 220 or 150 kg dry matter  $\text{ha}^{-1} \text{day}^{-1}$  on clayey or sandy soils respectively, with the length of the period of vigorous, vegetative growth. In the example of fig. 10, this period is 30 days. The N-concentration at flowering is 2%. During seed fill, the biomass increases at about half the preceding rate, without further uptake of N. In fig. 10, this lasts for 15 days. The biomass of the mature vegetation and the N contained in it, are thus calculated for a condition with abundant nutrients. The curvilinear relation between the productivity and the N taken up by the vegetation at lower levels of N-availability can now be approximated by drawing a line through the origin at a slope equal to the minimum concentration of N at maturity, and approaching the uptake-yield point determined for optimum conditions.

Plotting the relation between the supply of N by fertilization and its uptake is very straightforward once  $N_s$  and  $r$  are known.

This simple, static model is not very accurate. However, it takes into account essential growth processes, and thus improves our understanding of the system. It



may also improve considerably our factual knowledge of productivity and N-uptake, as may be concluded from the reasonable agreement between predicted and measured productivity (fig. 10).

f. Other conclusions from the experiments

The total amount of N in the biomass often drops after flowering, though not always (fig. 3-8). The magnitude of such losses is positively correlated with the rainfall after flowering and with the amount of N in the vegetation. Various processes have been suggested to explain this phenomenon, but further analyses are needed before general conclusions can be drawn. It is clear, however, that for the determination of the actual uptake of N by the vegetation, harvest should be around flowering, particularly if productivity is high, and lodging of herbage occurs before the end of the rainy period. This situation occurred in the experiments of fig. 3, 4 and 8, where rotting became very intensive.

In one experiment (fig. 8) a value of  $r$  (0.21) was found well below the one expected (0.44) on basis of fig. 9 and its value of  $N_s$  (25). This was the case on the heavy clay soil, fertilized with nitrate which was flooded for some time. The low recovery is ascribed to denitrification and/or leaching. On basis of fig. 8, one cannot discriminate between the two. When the recovery of urea is used as a standard, one or both processes seem to have caused the loss of just over half the N supplied. Since urea is usually nitrified within a relatively short time, the large difference between urea and nitrate fertilization was unexpected. It seems as if nitrification was slow in this experiment. We have no indication why, and further research will be conducted on this point. Incubation experiments are being executed to ascertain the potential for denitrification during flooding in heavy soils from a few sites in the Sahel.

It seems contradictory to assume the occurrence of denitrification and/or leaching and still to find a relatively high value of  $N_s$ , since exhaustion of soil N would make  $N_s$  very low. It is suggested that  $N_s$  can remain fairly high because most of the N is already absorbed by the plants before flooding occurs in these N-deficient conditions. Only when more N is present than can be absorbed before flooding, i.e. in some of our experimental conditions, denitrification and/or leaching could occur. Also here the recovery fraction is constant only up to a certain level of fertilizer application and declining at increasing rates. On basis of such considerations, it is expected that denitrification and leaching may only rarely and very locally be of importance in natural vegetation of the Sahel because soils are generally very poor. When intensive fertilization is practised, one or both processes can become important locally.

Whenever severe deficiency of soil water during the main growth period or of available P occurs, the above approach to productivity and N-uptake is not valid anymore. How P-deficiency influences productivity is the topic of the next chapter.

### Primary productivity and availability of phosphorus

#### a. The P/N ratio

Annual productivity is more limited by the low availability of N than by that of P on many soils in the Sahel. E.g., in the experiments cited above, the amount of herbage produced and the amount of N taken up on the control plot without P was the same or only slightly below that on the fields with only P-fertilizer. A situation will now be presented where P limited productivity severely. It presents a fine example of fertilization with P only, which has the same effect as that usually caused by supply of P and N together. Before the results of experiments will be interpreted, the rational of the relation between N and P concentrations in plants will be discussed.

N and P are functionally closely linked. Both are parts of essential components of functioning cells: the N in enzymes and P in compounds that provide energy for many enzymatic reactions. Moreover, the biochemical maintenance of cell proteins requires the presence of nucleic acids, which contain P. It may thus be expected that the ratio between N and P is of particular importance. The hypothesis is put forward that the ratio of total P over total organic N may be used to determine whether N or P limited plant productivity in a particular case, provided that no other deficiencies occur. This hypothesis is based on experimental work by Dijkshoorn (pers. comm.), who varied the nutrient supply to some plant species over a wide range and found that the P/N ratio (in  $\text{g P g}^{-1}$  organic N) in vegetative tissue did reflect such variations, but only within certain limits:

species	P/N minimal	P/N maximal
<i>Lolium perenne</i> (C-3 grass)	0.045	0.18
<i>Schoenefeldia gracilis</i> (C-4 grass)	0.029	0.12
<i>Helianthus annuus</i> (C-3 dicot.)	0.041	0.16
<i>Cassia tora</i> (C-3 dicot.)	0.060	0.24

Accumulation of the element which is not in short supply to values beyond the P/N range indicated, is apparently avoided. The differences between the species are not very large (with the possible exception of *Cassia*), and part of the variation may be due to experimental errors. *Cassia tora* not being an important species, the minimum and maximum value of the P/N ratio used in this paper, will be the average of the first three species. Old, and well fertilized plants show sometimes a P/N

ratio that exceeds 0.15 considerably. Still we suggest, as a first approximation, that if the P/N ratio of an annual plant is  $0.038 \text{ g P g}^{-1} \text{ organic N}$ , one must conclude that this plant is very P-deficient. Fertilization with P will then be most effective, while fertilization with N will not enhance productivity. If the P/N ratio equals 0.15, P-fertilization will have no effect, while N-fertilization will be most effective. When the P/N ratio is close to one of these boundaries, growth will be severely retarded, but is not always halted: the plant can still grow by dilution of P and N simultaneously, maintaining the P/N ratio at a constant value, till the minimum value of N (cf. fig. 2) or that of P is reached. (The absolute minimum value of P in flowering C-4 grasses is probably about 0.05% P). A common situation in the Sahel is that the P/N ratio of plant tissue is not extremely high or low, but that P- and N-uptake proceed slowly because their availability is low. Fertilization with one element increases its uptake, and makes the other element the limiting factor. The limiting element becomes then diluted to a lower concentration than it would have been without fertilization, so that application of either element stimulates the herbage production. Results of such experiments are presented elsewhere (PPS, in prep.).

When collecting plant samples for determination of its P/N ratio, one should be aware that this ratio often changes during the growing season, particularly in plants grown on poor soils: N is more available to a small root system than P because of the higher mobility of nitrate (Van Keulen et al., 1975). Young plants are thus more susceptible to P-shortage than old plants. To characterize quickly the P-status of the soil relative to N, it may thus be useful to determine the P/N ratio of quite young plants. This idea is supported by other PPS-data (unpublished), showing that the productivity of a vegetation, with young grass plants, only a few cm high, having a P/N ratio of less than 0.06, was stimulated more by P-fertilization than that of vegetations with young plants having higher P/N ratio's.

#### b. Nitrogen uptake and availability of phosphorus

Large areas of the Sahel are covered with a vegetation of almost pure stands of Zornia glochidiata, an annual N-fixing legume. This vegetation occurs especially where overgrazing has taken place or takes place, or where land has been cultivated for some time. A sandy soil on the ranch, for many years covered with such a vegetation, was fertilized with P and its effect on productivity of some grass and legume species was studied. The experiment of fig. 6 was performed on a run off area of the same soil type. Zornia seedlings were removed, and by sowing, pure stands were obtained of the annual C-4 grasses Cenchrus biflorus, and Schoenefeldia gracilis, and of the annual legumes Cassia mimosoides, Alysicarpus ovalifolius, Zornia glochidiata (all  $\text{N}_2$ -fixing) and Cassia tora (not  $\text{N}_2$ -fixing). Subplots of  $1 \text{ m}^2$  were harvested at the full flowering stage.

Upon addition of P, the uptake of P, the uptake of N and dry matter yields of grasses and legumes increased considerably (fig. 11), the responses being similar in different species. The P/N ratio ranged from 0.049 in plants on non-fertilized plots to 0.140 in plants on the soil fertilized with P. This suggests that plants grown on the unfertilized soil had taken up the maximum amount of N per unit of P absorbed, and that the plants on the fertilized plots contained the maximum amount of P per unit of N. This implies also that without fertilization, much available N was probably left in the soil, which with P-fertilization was absorbed by the plants. About  $20 \text{ kg NO}_3 \text{ ha}^{-1}$  was indeed found in the top 20 cm at the end of the rainy season on a plot nearby. The possibility exists that P-fertilization stimulated mineralization, but this phenomenon is extremely rare. The total amounts of N absorbed by grasses and by legumes capable of  $\text{N}_2$ -fixation were not significantly different. Fixation of  $\text{N}_2$ , if any, did thus not increase the total amount of N in the vegetation, irrespective of P-fertilization. This is not surprising as their N-concentrations are at a maximum level.

Although the amounts of P in vegetations on the unfertilized plots were small, they are not smaller than those on surrounding sandy soils, where P-fertilization had little effect on the yield. The P-response was thus not primarily due to an extremely low availability of P in the unfertilized soil, but by a deficiency of P relative to N.

Another situation in which plant productivity was completely limited by P-availability was found by a colleague (Cissé, pers. comm.), who studied regeneration of loamy soils that are barren due to overgrazing. He found that such soils near Niono released about  $40 \text{ kg N ha}^{-1}$  after tillage (to enable rain to infiltrate) and sowing C-4 grasses (Schoenefeldia gracilis and Digitaria exilis). The P/N ratios of these plants were about 0.038 at an early stage, indicating severe P-deficiency. P-fertilization ( $30 \text{ kg P ha}^{-1}$ ) increased N-uptake to  $100\text{-}150 \text{ kg N ha}^{-1}$ , and P/N to 0.078. The availability of N in the soil was even so high that additional fertilization with N gave almost no response. Harvests the following year, without further fertilization, showed that N-uptake decreased only little on the unfertilized plot, but was down to  $20 \text{ kg N ha}^{-1}$  on the field that received P previously. The P/N ratio was adequate in all cases. On the plot that received fertilizer, all available N had apparently been taken up by the vegetation in the first year of the experiment. These experiments show that P-fertilization may be quite advantageous for one year, and provides possibilities for complete regeneration of a vegetation. But it also shows that when overgrazing of the restored area is resumed, the soil has lost a considerable portion of its N-stock, and will be in a worse condition than it was before. A description of experiments and results concerning regeneration of heavily overgrazed soils is in preparation by Cissé.

It is not surprising to find that the tilled, barren soil contained such a large amount of available N. Mineralization will take place whenever these soils

become moist even though this period will be brief because of very considerable run off. Since no plants are present to absorb the N released, it will accumulate. Hence the soil shows a fallow effect after reclamation. It is however not obvious why P is relatively unavailable, since mineralization releases both P and N. As a possible explanation it is suggested that, as a result of overgrazing, not sufficient plants are present to absorb the N and P released by decomposition of the soil organic matter. Available N and P accumulate as a result. When the soil dries out at the end of the rainy season, N and P precipitate. N becomes readily available when the soil is moistened the next year, but this may not be so for P, since its precipitation can occur in highly insoluble forms. If this suggestion is correct, under-exploitation of the available nutrients by over-exploitation of the vegetation would lead to fixation of P by the soil, and to accumulation of available N. The latter process is sometimes reinforced by  $N_2$ -fixation by legumes. The strong P-deficiency is then the resultant of these processes.

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Table 1. The duration of the period of vigorous vegetative growth, the amount of biomass at flowering and the amount at maturity in some experiments on fertilized, natural pastures in Niono, Mali. Annual grasses dominated strongly the vegetation in all cases. Fertilization was  $300 \text{ kg N ha}^{-1}$  (as urea),  $100 \text{ kg P ha}^{-1}$  (as triple super phosphate) plus  $225 \text{ kg K}_2\text{SO}_4 \text{ ha}^{-1}$ . Biomass data are averages; the standard error of the average is about 10%.

description of the site			results		
soil type	year	run off/run on	vigorous vegetative growth (days)	biomass at flowering (kg dry matter $\text{ha}^{-1}$ )	biomass at maturity (kg dry matter $\text{ha}^{-1}$ )
clayey soil	1976	none	45	10.000	11.500
" "	1977	"	30	6.750	8.500
" "	1978	"	35	7.500	9.500
vertisol	1978	run on	25	3.500	5.000
loamy soil	1977	none	25	5.000	6.500
sandy soil	1976	run off	30	5.000	6.000
" "	1977	none	40	4.750	6.000
" "	1978	run off	20	3.250	5.000

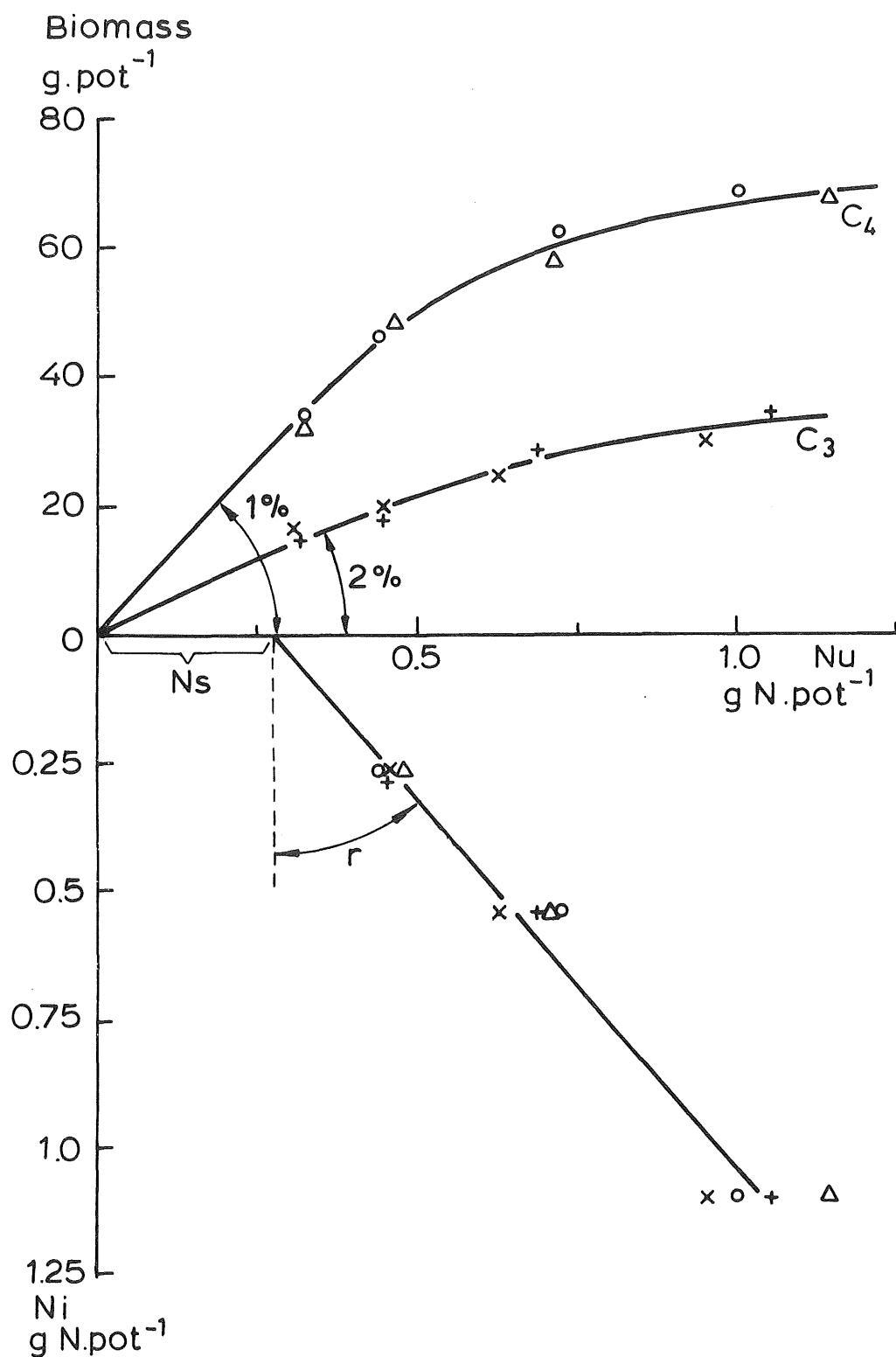


Fig. 1

Results of a growth experiment in pots with different levels of fertilization with ammonium nitrate at  $24-35^{\circ}\text{C}$ , with 2 C-3 grasses (Phalaris (x), and Lolium (+)) and 2 C-4 grasses (Digitaria (o) and Paspalum ( $\Delta$ )). The upper part shows the above ground dry matter versus the N that it contains ( $N_u$ ), the lower part  $N_u$  versus the N-supplied as fertilizer ( $N_i$ ). Experiment by Colman and Lazenby (1970).



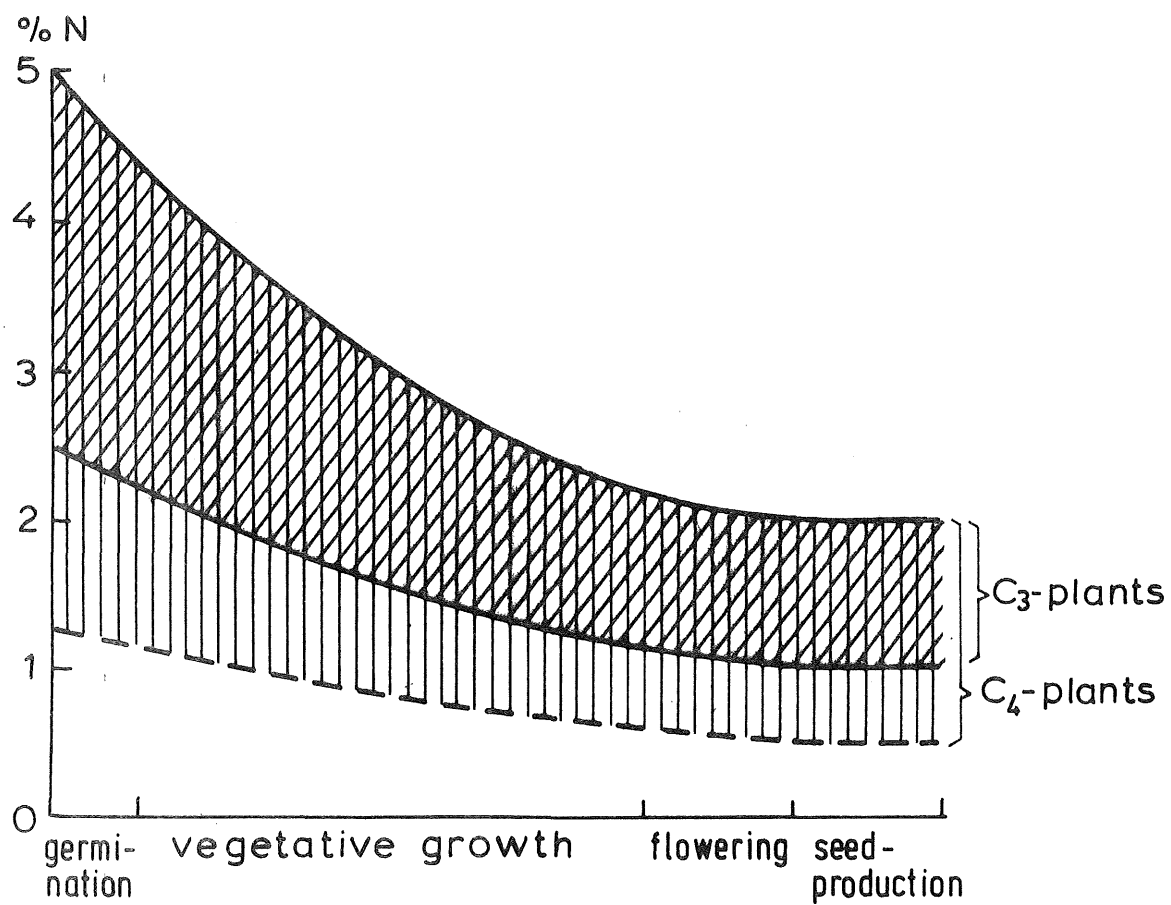


Fig. 2 Maximum and minimum N concentrations of total above ground biomass in C-4 and C-3 grasses as a function of their development stage.

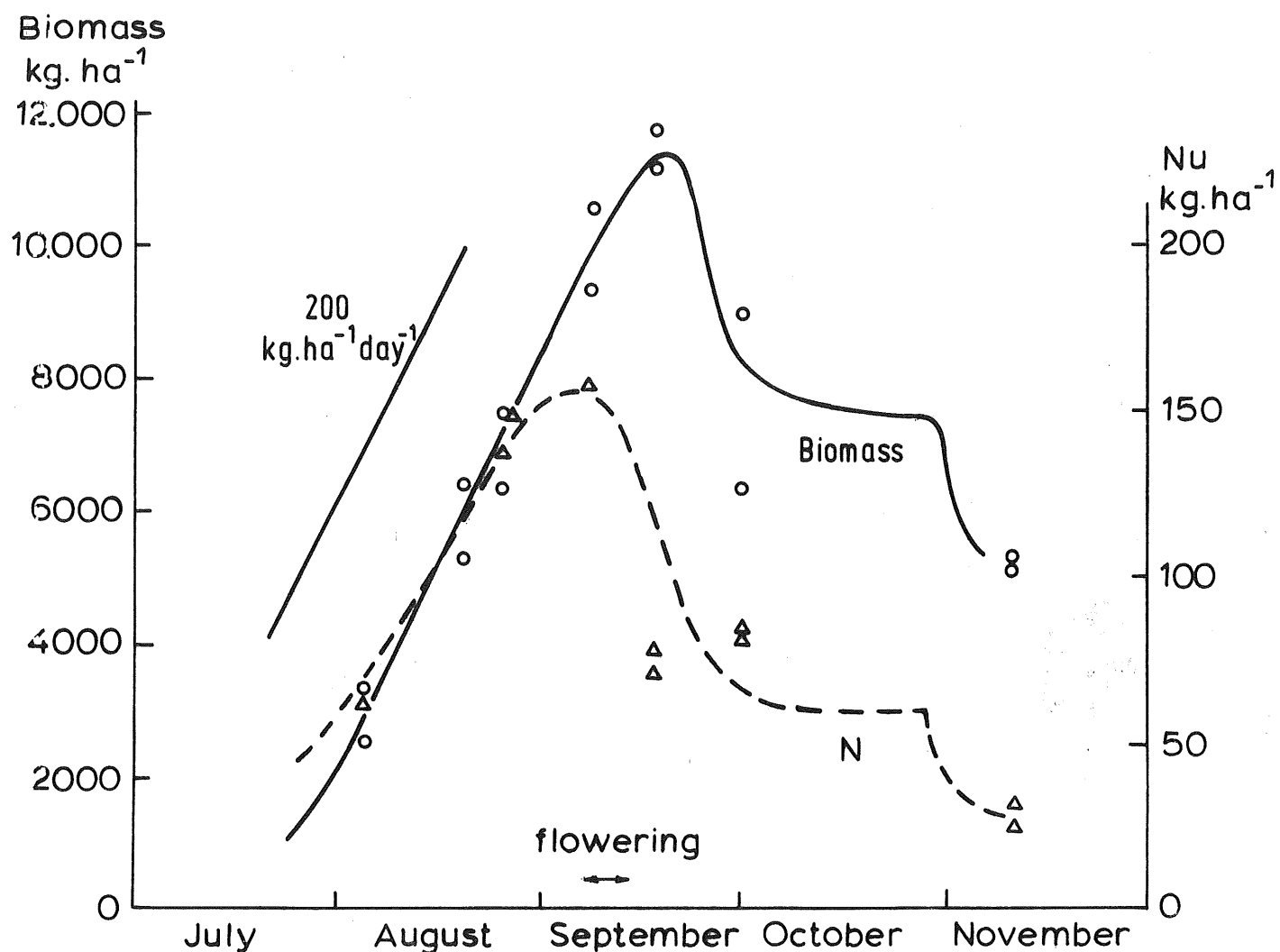


Fig. 3

Primary productivity and N-uptake of a natural vegetation, strongly dominated by the C-4 grasses *Diheteropogon hagerupii* and *Loudetia togoensis* on a clayey soil in Niono in 1976. Each data point represents one harvest. The vegetation grew for almost 50 days at a rate of  $200 \text{ kg ha}^{-1} \text{ day}^{-1}$ . Heavy and exceptionally late rains caused extra losses of biomass and of N in October.

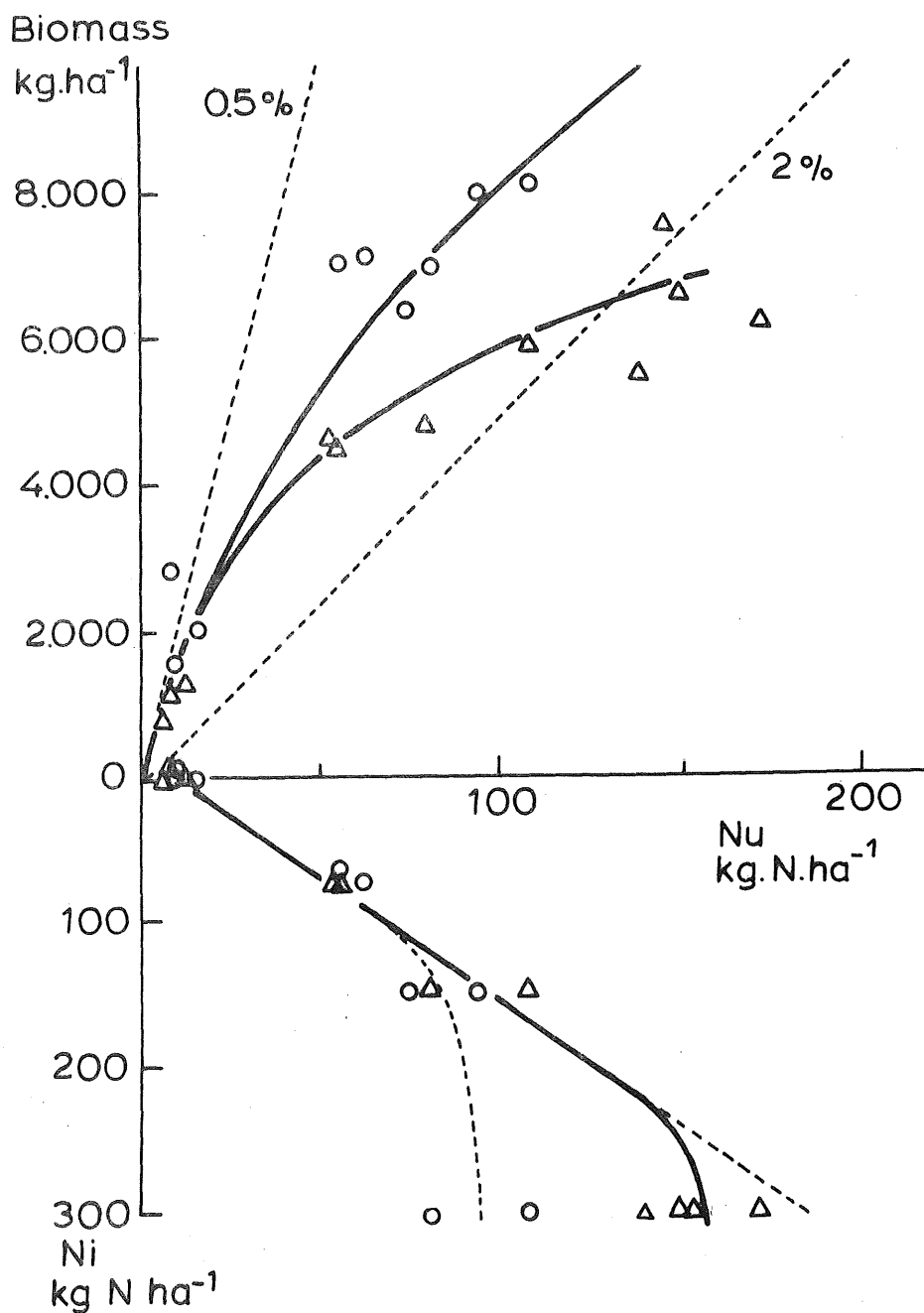


Fig. 4

Fertilization with urea on a clayey soil, strongly dominated by the C-4 grasses *Diheteropogon hagerupii* and *Loudetia togoensis*. The lines representing the minimum and maximum N-concentrations at flowering are shown. The triangles correspond with the harvest on 31/8/77 just before flowering, the circles with the harvest on 14/9/77 during flowering and seed production.

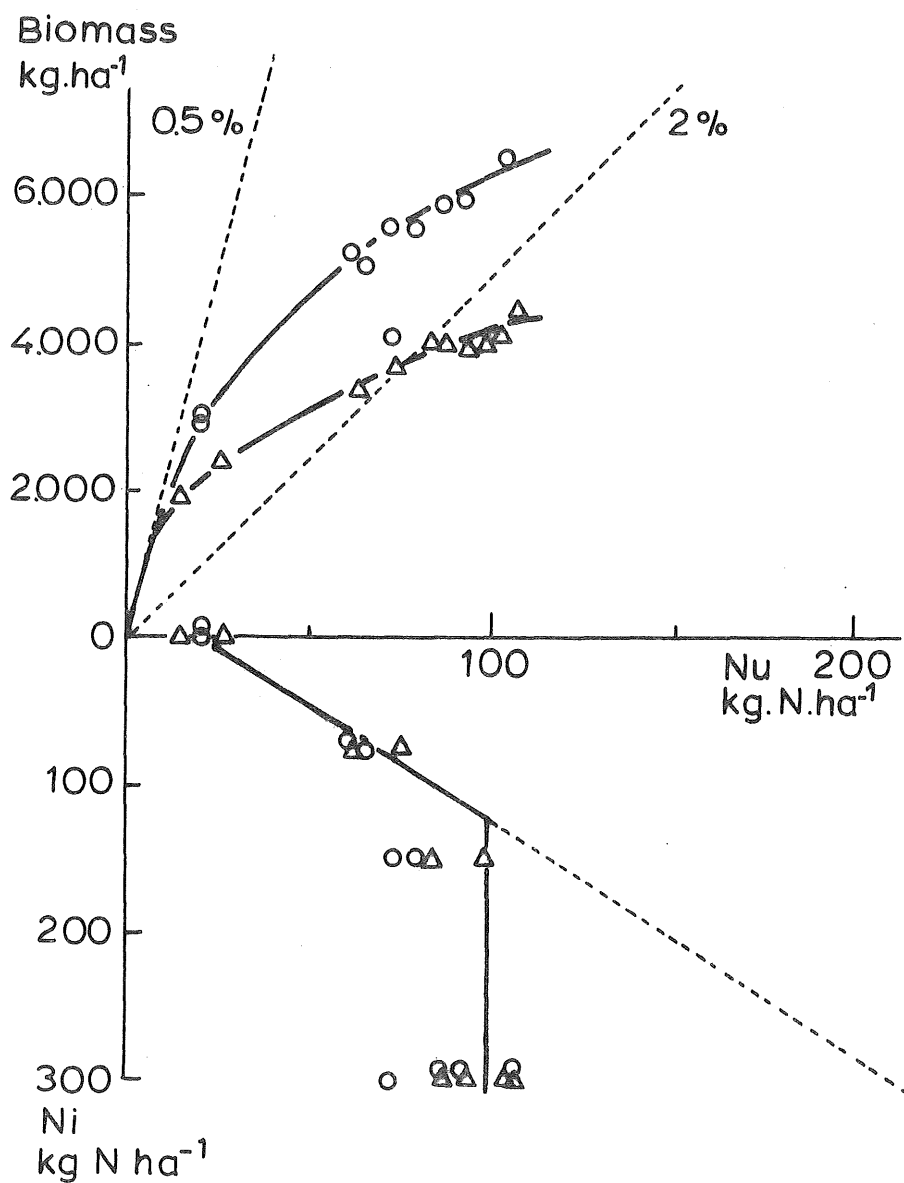


Fig. 5

Fertilization with urea on a sandy soil, strongly dominated by the C-4 grass *Schoenefeldia gracilis*. The triangles correspond with the harvest on 27/8/77 when the vegetation was in a late vegetative stage, the circles with the harvest on 10/9/77 when all plants flowered.

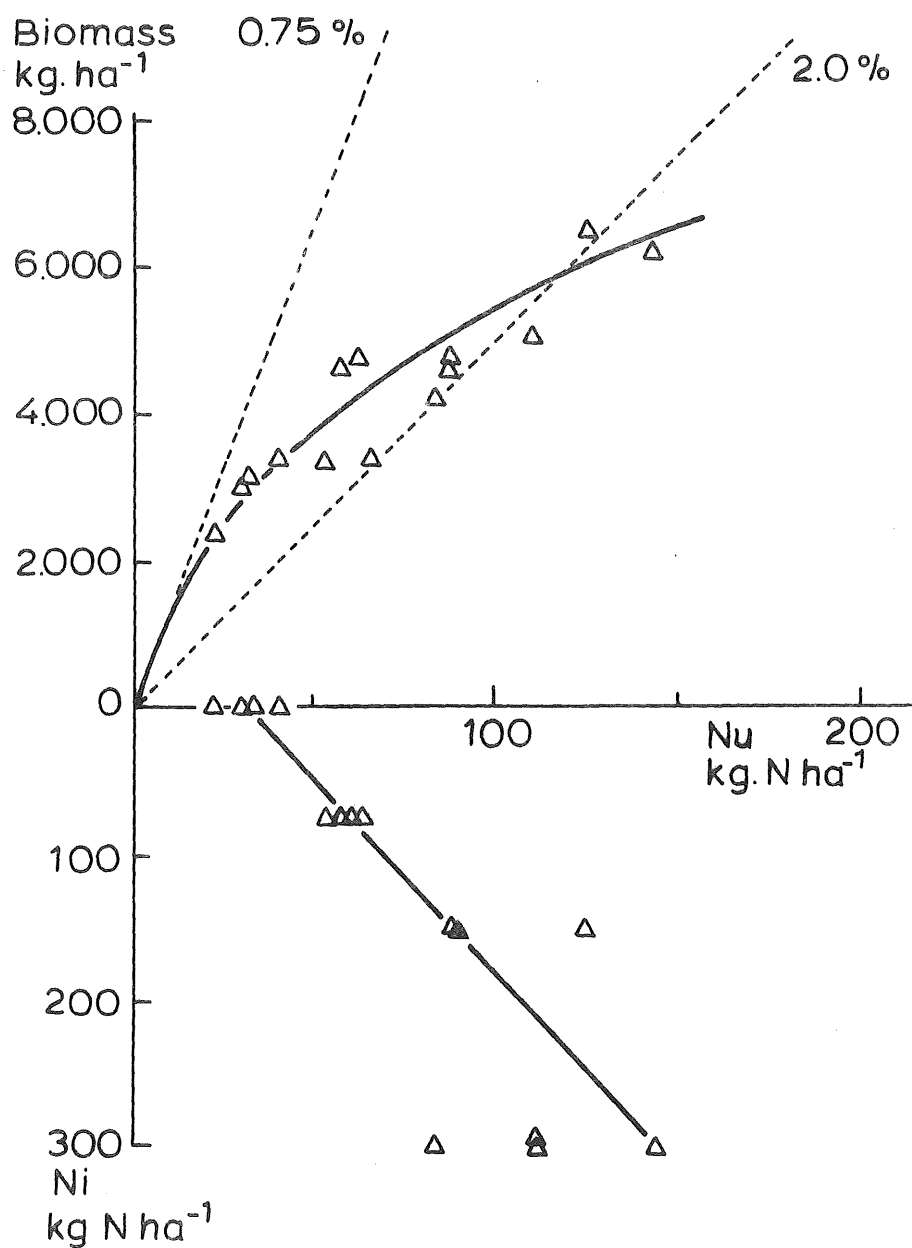


Fig. 6

Fertilization with urea on a loamy soil, dominated by the C-4 grass *Dactyloctenium aegyptium* and the C-3 dicotyledons *Borreria* spp and *Blepharis linearifolia*. All data are obtained from the harvest on 21/9/77, when all plants were flowering and/or producing seeds.

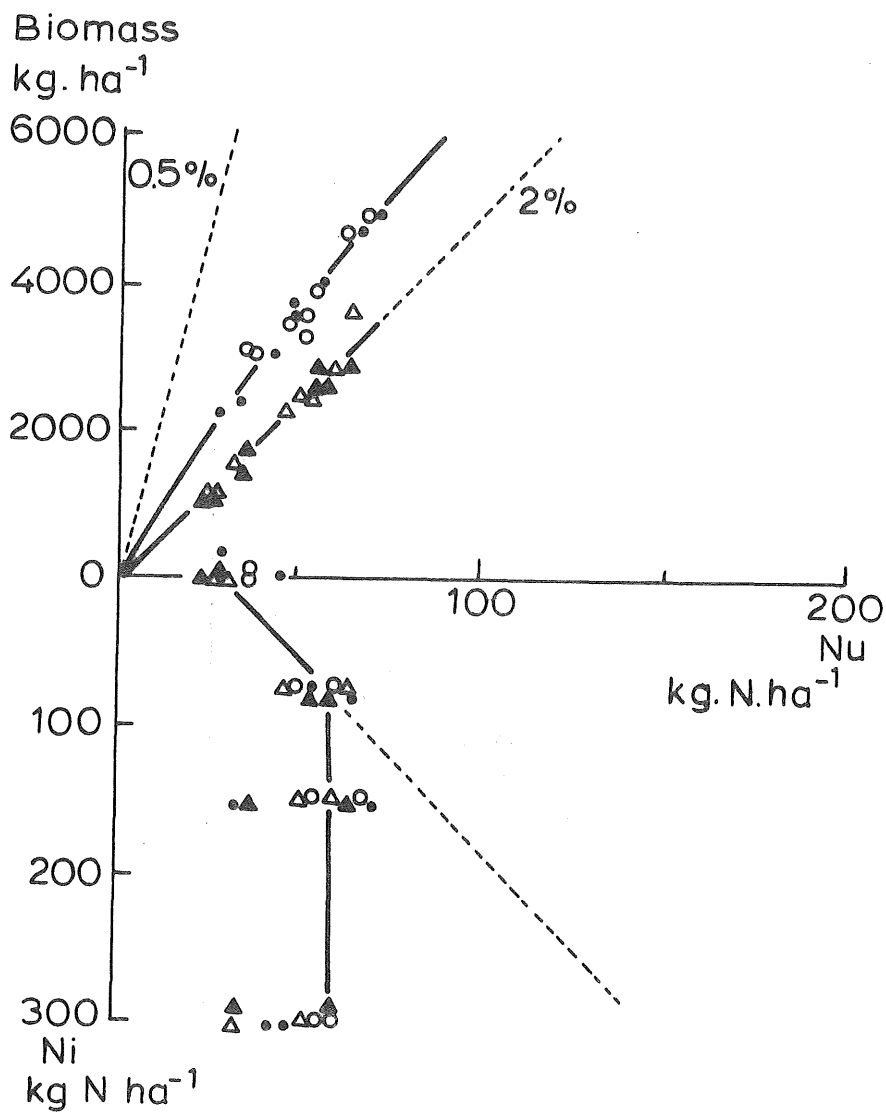


Fig. 7

Results of an experiment on a sandy soil, that used to be occupied by *Zornia glochidiata*, but that was sown to the C-4 grass *Schoenefeldia gracilis*. The open symbols represent the plots fertilizer with nitrate, the closed symbols those fertilized with urea. The triangles indicate the harvests of 5/9/78, the circles the harvests of 20/9/78.

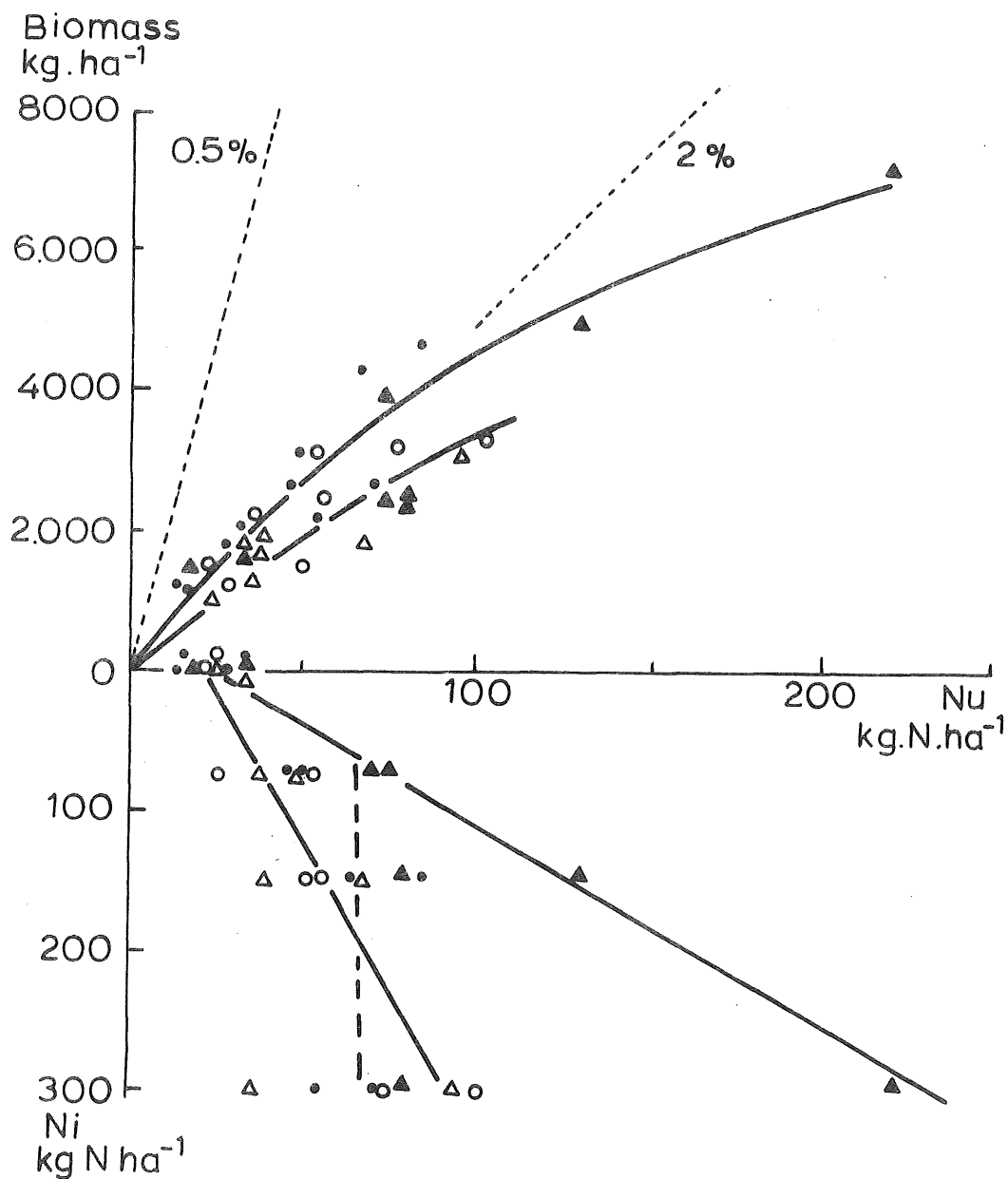


Fig. 8

Results of an experiment on a heavy clay soil, dominated by the C-4 grass *Echinogloa colona*. The open symbols represent plots fertilized with nitrate, the closed symbols those fertilized with urea. The triangles indicate the harvests on 28/8/78, the circles the harvests on 9/9/78 when most plants flowered.

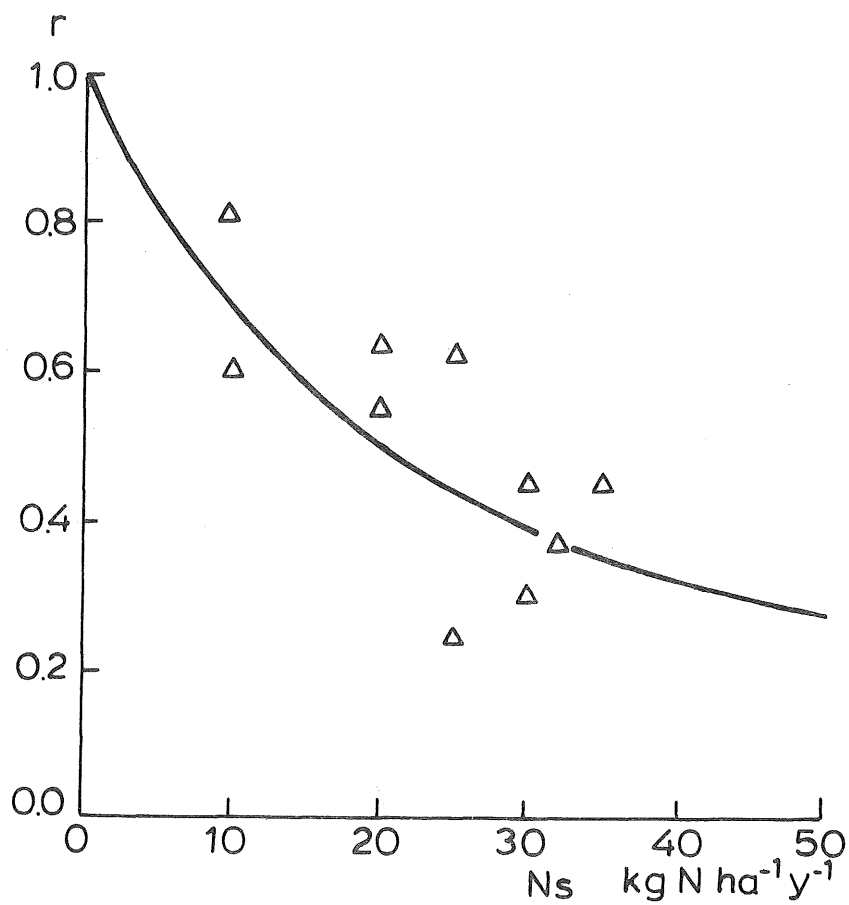


Fig. 9

The fraction ( $r$ ) of N applied as fertilizer recovered in above ground biomass versus the fertility of soils without fertilization ( $N_s$ ).



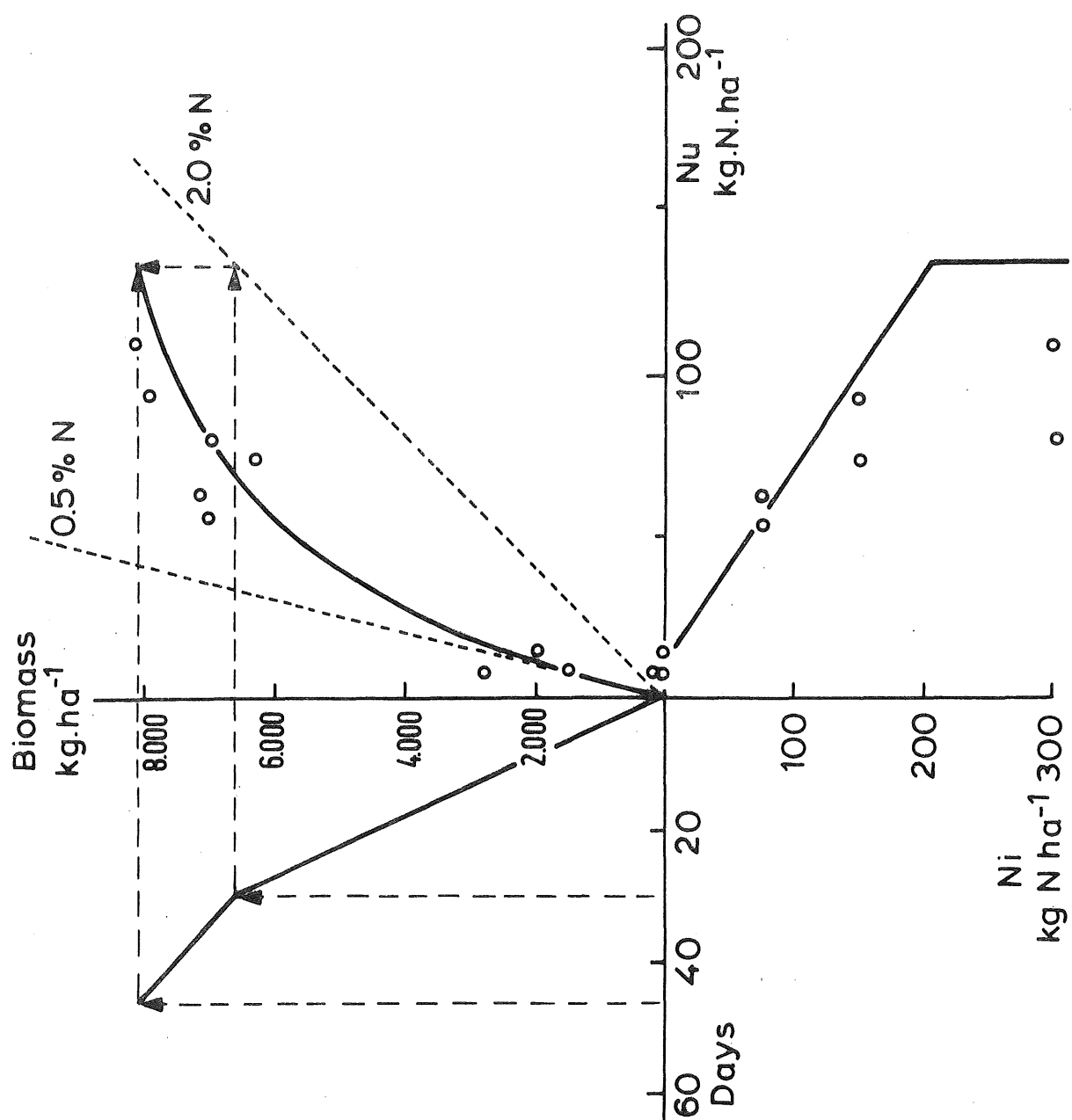


Fig. 10

A graphical presentation of the procedure explained in the text to calculate productivity and N-uptake by annual pastures at various levels of fertilization. The procedure is here applied for the conditions of the experiment of fig. 4. The results of this experiment, second harvest, are included for comparison.

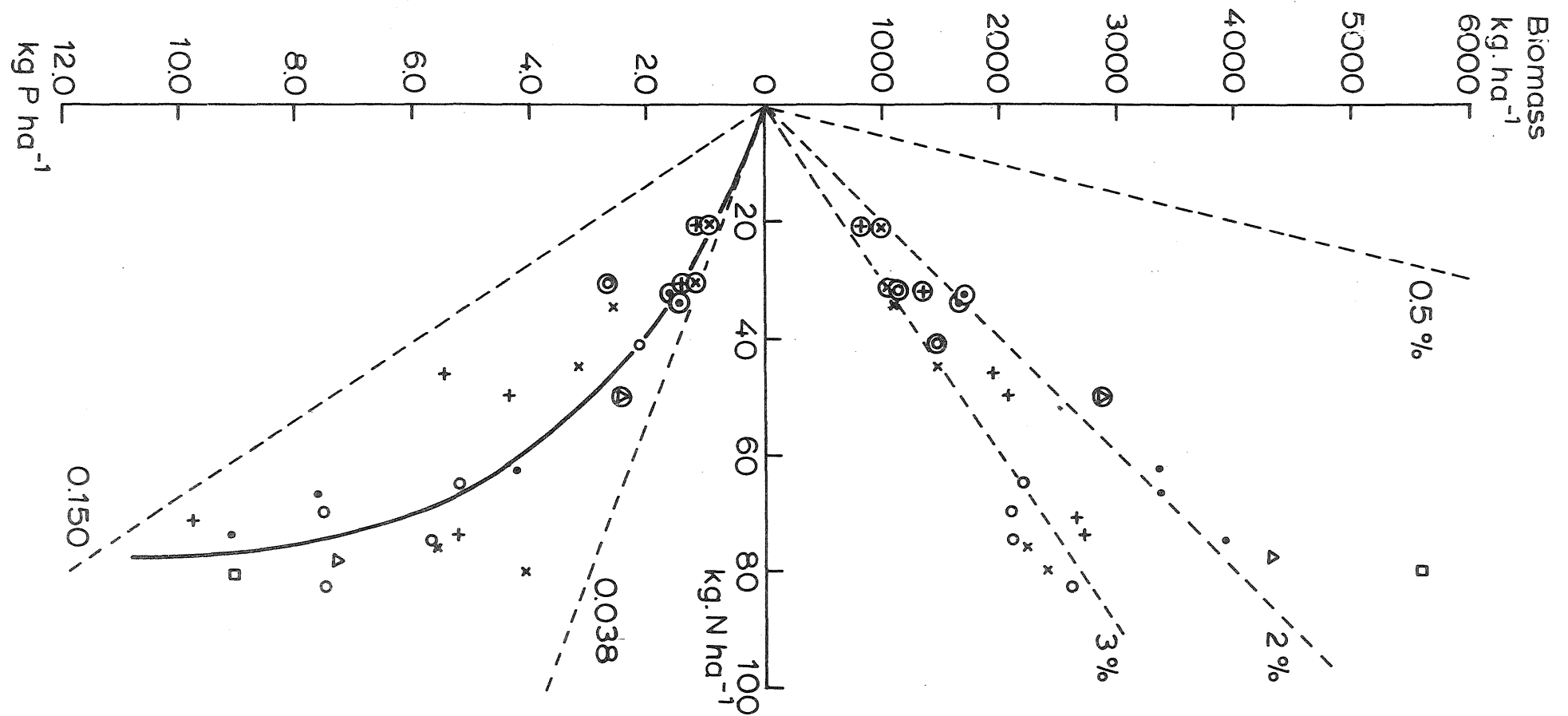


Fig. 11

The relation of dry matter production, N-uptake and P-uptake of some annual grasses and legumes on an overgrazed sandy soil. Each point represents one harvest at a fully flowering stage. Symbols:  $\Delta$  *Cenchrus* (sown 19/7, harvested 7/9),  $\square$  *Schoenefeldia* (19/7-7/9),  $\circ$  *Alysicarpus* (20/6-24/8),  $\times$  *Cassia mimosoides* (20/6-24/8),  $+$  *Zornia* (20/6-24/8) and  $\bullet$  *Cassia tora* (20/6-24/8). The encircled symbols represent non-fertilized plots.