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NUTRIENT AND BIOMASS ALLOCATION STRATEGIES FOR FIVE GRASS SPECIES IN AN OKLAHOMA TALLGRASS PRAIRIE

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NUTRIENT AND BIOMASS ALLOCATION STRATEGIES FOR FIVE GRASS SPECIES IN AN OKLAHOMA TALLGRASS PRAIRIE

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ABSTRACT

Analysis of biomass, nitrogen, phosphorus, potassium and magnesium allocation patterns to various portions of the plant was undertaken to determine if differences exist between Andropogon gerardii, Schizachyrium scoparium, Sorghastrum nutans, C_4 perennials; Dichanthelium oligosanthes, a C_3 perennial; and Aristida oligantha, a C_4 annual. The annual allocated 15.6% of its total plant biomass and 28.0% of its total plant nitrogen to reproduction, whereas the C_4 perennials allocated less than 2.7% total plant biomass and 5.0% total plant nitrogen to reproduction. Total plant nitrogen in the perennials remained relatively constant after an initial spring uptake. Nitrogen was conserved by being translocated belowground in the C_4 perennials during the fall and into overwintering leaves in Dichanthelium. Unlike nitrogen, phosphorus was not efficiently conserved while potassium was not conserved at all. The difference in the degree of conservation reflects the form in which these elements are found in the plant, nitrogen primarily as proteins and amino acids and potassium as an inorganic element making it more susceptible to leaching.

INTRODUCTION

In recent years, studies in resource allocation have focused largely on the allocation of biomass to various components of the plant, particularly with regards to reproductive effort. Harper and Ogden (1970) introduced a method of studying resource allocation by separating plants into component parts based on function and expressing each component as a proportion of the total biomass. Subsequent studies (e.g., Gadgil and Solbrig 1972, Abrahamson and Gadgil 1973, Anderson and Loucks 1973, Roos and Quinn 1977, Kawano and Masuda 1980, Soule and Werner 1981) in resource allocation have tested the theory of r- and K-selection originally proposed by MacArthur and Wilson (1967) to determine strategies in partitioning vegetative and reproductive production as they relate to successional properties and community stability.

Others have examined resource allocation in terms of essential plant elements but most of these studies have addressed community level questions (e.g., Johnson and Risser 1974, Grigal and Ohmann 1980, Williams and Bell 1981). Only a few studies have examined nutrient allocation within a particular species, however, these analyses have been in systems other than grasslands. For example, Drifmeyer et al. (1980) measured concentrations of several essential plant elements in various portions of eelgrass (_Zostera_ _marina_) in a North Carolina estuary, while Nilsen and Schlesinger (1981) examined seasonal allocation of nutrients in aboveground portions of Lotus scoparius, a chaparral shrub.

Detailed examinations of nutrient dynamics in an array of grassland communities are numerous. Investigators have reported on the responses of plant productivity (Jones 1963, Gay and Dwyer 1965, Graves and McMurphy 1969, Old 1969, Owensby et al. 1970, Power 1971, Wight and Black 1972), community structure (Lauenroth et al. 1978), water-use efficiency (Viets 1962, Owensby et al. 1970, Wight and Black 1972), and reserve carbohydrates (Colby et al. 1965, Bokhari et al. 1974, Pettit and Fagan 1974, Rains et al. 1975, Trlica 1977, Bokhari 1978a, 1978b) to nutrient application.

Aside from studies in which nutrients have been artificially applied, nitrogen has received considerable attention in native grasslands (Bokhari and Singh 1975, McKendrick et al. 1975, Clark 1977a, Jones and Woodmansee 1979, Woodmansee and Duncan 1980, Caldwell et al. 1981). Other elements, including phosphorus, magnesium and potassium, have received relatively little attention in perennial grasslands (however see Harper et al. 1934, Pritchard et al. 1964, Sheedy et al. 1973, White 1973, Callahan and Kucera 1981). Studies by McKendrick et al. (1975) and Caldwell et al. (1981) are the only ones to have examined nutrient allocation of individual grassland species. Consequently, a lack of data exists comparing the nutrient relations of grassland plants within a community.

The Great Plains are characterized by highly variable climatic conditions (Sims et al. 1978). Therefore this study was conducted over a two year period to compare the effect of the variability in climate on the relationships in nutrient and biomass allocation strategies, remobilization and conservation of nutrients, and phenology of five grass species in an Oklahoma tallgrass prairie to determine (1) differences in the way resources are allocated in five of the major grass species that occur in an Oklahoma grassland, (2) physiological adaptive strategies that permit the grasses to persist in nutrient-poor soils, and (3) differences in allocation patterns within a species between years.

METHODS

Species Descriptions

The five species analyzed included an annual, old-field threeawn (*Aristida oligantha*) and four perennials, big bluestem (*Andropogon gerardii*), little bluestem (*Schizachyrium scoparium* var. *frequens*), Indian grass (*Sorghastrum nutans*)and Scribner's dichanthelium (*Dichanthelium oligosanthes* var. *scribnerianum*). Old-field threeawn is a native, C_4 (Brown 1977) grass that reproduces only by seed. Its culms are 15-50 cm tall and branched. It is most commonly associated with disturbed areas and is an important species in old-field succession in Oklahoma (Booth 1941, Wilson and Rice 1968, Perino and Risser 1972). Big bluestem and Indian grass, dominant members of the tallgrass prairie, are tall (0.8-2 m), rhizomatous, C_4 (Downton 1975, Krenzer et al. 1975) grasses. Little bluestem, also a dominant member of the tallgrass prairie, is a midsized (0.5-1.5 m) bunchgrass which exhibits C_4 photosynthesis (Brown and Gracen 1972, Downton 1975). Scribner's dichanthelium is a small (15-30 cm), C_3 grass (Moss et al. 1969) and an inconspicuous but important (high constancy) member of the tallgrass prairie.

Species Composition and Plant Phenology

Species composition of the research area was determined by estimating percent aerial cover of herbaceous and woody species. Thirty 1 m^2 quadrats were placed in a stratified random design along three parallel lines transecting the study area on 24 June 1980 and 17 July 1981. Field observations for phenological data of the five species were made along the transects at approximately two week intervals during the growing season and at irregular intervals throughout the remainder of 1980 and 1981.

Biomass and Nutrient Analyses

All plant material was collected at irregular intervals in 1980 and 1981 to a depth of 30 cm from eight randomly located points. Monoliths were excavated from 0.25 m^2 quadrats subjectively placed as close to the points as possible to insure maximum sampling of a particular species. Plant material was first separated by species into roots, crowns (including rhizomes and culm bases), foliage, and sexual reproductive parts, then oven-dried at 80 C for 48 hr and weighed. Underground parts were freed of soil by shaking or, when necessary, using a fine water spray. The material was ground in a Wiley mill to pass a 40-mesh sieve. Undoubtedly, root biomass was underestimated with a monolith dept of only 30 cm. However, Old (1969) and Dahlman and Kucera (1965) found that between 75-80% of all roots occurred in the upper 25 cm of tallgrass prairies in Illinois and Missouri.

Nitrogen, phosphorous, potassium and magnesium concentrations were determined by species for the different plant fractions. Nitrogen was determined via a modified semi-micro Kjeldahl method (Nelson and Sommers 1973) with colorimetric determination of ammonia using the modified method of Cataldo et al. (1974). Determination of phosphorus was made using a modified Fiske and Subbarow (1925) method with perchloric-nitric acid (1:6 v/v) digestion. Potassium and magnesium were analyzed on a Perkin-Elmer Model 303 Atomic Absorption Spectrophotometer after digestion in a perchloric-nitric acid (1:6 v/v) mixture. Strontium (1%) was added before determination of magnesium to avoid interferences (Slavin et al. 1963).

Decomposition

Plant decomposition was measured by placing approximately 20 g of dried standing dead foliage by species in fiberglass wire mesh bags (pore size = 0.26 cm^2). After initial weights were recorded, the mesh bags were placed in the study area on 13 November 1980 and sampled at irregular intervals for one year. At each sample, five mesh bags for each species were dried for 48 hr at 80 C, then weighed. The difference between the initial and final weights was used to express percent weight loss.

Soil Analyses

A soil pit was excavated on 27 June 1980 to bedrock at a location subjectively determined to be representative of the study area to measure solum thickness. Ten randomly placed soil samples were taken from the upper 15 cm of the A_1 horizon for textural analysis using the Bouyoucos hydrometer method (Bouyoucos 1951). These samples were analyzed for ammonium nitrogen by steam distillation with MgO (Bremner 1965) and for nitrate nitrogen by a specific ion electrode, after extracting the soil with distilled water (1:2 soil:water ratio) for 1 hr with occasional stirring. Exchangeable potassium and magnesium and available phosphorus were analyzed colorimetrically after extraction with ammonium acetate and 0.02 N sulfuric acid, respectively.

RESULTS

Study Site Description

The University of Oklahoma Grassland Research Area is located 12.8 km southwest of Norman, Oklahoma in McClain County (T8N, R4W, Sec. 12). The study plot, located on a gentle, north-facing slope is composed of dark reddish brown loamy-sand soils in the Nash-Lucien-Grant Association (USDA 1979). These soils are well-drained and underlain by sandstone. Depth of the A_1 horizon was approximately 30 cm, solum thickness and depth to bedrock was 81 cm. The A_1 horizon was 77% sand, while silt and clay fractions totaled 9% and 14%, respectively. Mean concentrations of soil ammonium nitrogen and nitrate nitrogen were 2.68 and 1.75 ppm, respectively. Available soil phosphorus averaged 7.3 ppm and mean concentrations for exchangeable potassium and magnesium were 154.0 and 69.1 ppm, respectively.

The study site contained numerous grasses, forbs and woody species (Table 1). Big bluestem, little bluestem, Indian grass, Scribner's dichanthelium, switchgrass (_Panicum virgatum_) and old-field three-awn were the most abundant species in the prairie for both 1980 and 1981 although percent cover varied between the two years. Forbs were of minor importance in the prairie with an aerial cover of 10-15%, although they occurred in 93% of the quadrats. Some of the more important forbs included _Ambrosia psilostachya_, _Psoralea tenuiflora_, _Liatris punctata_, *Schrankia nuttallii* and *Thelesperma filifolium*. Seven woody species were sampled although two other species (*Prunus angustifolia* and *Rubus* sp.) were also found in the study area. This area was moderately grazed until 1949, has never been cultivated, and has rarely burned.

Temperature and precipitation profiles for 1980 and 1981 represent climatic patterns for the study area (Fig. 1). During 1980, precipitation totaled 619 mm which was approximately 200 mm below normal. Spring precipitation dominated the moisture regime for 1980, accounting for approximately 50% of the annual total. This same year was also characterized by a severe summer drought where less than 76 mm of precipitation fell for the three month period of June - August. In contrast, precipitation was above normal for 1981 with a total of 895 mm. Rainfall was also more equitably distributed throughout the year with no summer drought.

Phenology

Scribner's dichanthelium was the first species to initiate growth and to flower in the spring (Table 2). Unlike the other species, it underwent a period of summer dormancy in which all aboveground plant material was senescent. Additionally, Scribner's dichanthelium reinitiated growth in the fall by producing a small rosette of leaves that remained green throughout the winter. Scribner's dichanthelium is known to flower twice during the year (Steyermark 1963), however I never observed the fall flowering period.

Of the other perennial species, little bluestem showed the first visible signs of vegetative growth on 31 Mar 1980. Big bluestem and Indian grass initiated growth a few days later on 9 Apr 1980. Major flowering periods for big bluestem, little bluestem, and Indian grass occurred after 13 September and were all within a few days of one another. The annual, old-field threeawn, was the last of the five species to intiate growth by seed germination. Its major flowering period occurred between 7-24 Aug.

Phenological results for 1981 were similar to 1980 with a few exceptions. For all species, intitation of growth in the spring was from 2-9 days earlier in 1981 than in 1980. Also, the major flowering periods were slightly advanced in 1981. The most notable difference was the intitation of regrowth of Scribner's dichanthelium in the fall which occurred almost seven weeks earlier in 1981.

Biomass Allocation

Allocation patterns of aboveground foliage and belowground roots and crowns were similar in all five species for the two study years (Figs. 2 and 3). At the end of the growing season (November sample) the percent of total biomass allocated to roots ranged from a low of 11.9% in old-field threeawn to 14.8% in Indian grass. In 1981, Indian grass again allocated more biomass to roots (15.7%) than the other four species. Allocation to crown production ranged from a low of 17.4% in old-field threeawn to 30.4% in little bluestem for 1980. In 1981, little bluestem again allocated the greatest amount of biomass to crowns (32.2%) with old-field threeawn allocating the least (14.6%). The range of foliage biomass allocation was from 48.4%-64.0% for old-field threeawn and Indian grass, respectively in 1980 and 50.8%-61.7% for little bluestem and Indian grass, respectively in 1981.

Reproductive effort (percent of total biomass allocated to sexual reproduction) was similar in old-field threeawn and Scribner's dichanthelium for both years (Table 3). Significantly less biomass was allocated for reproduction in big bluestem, little bluestem and Indian grass. Also, big bluestem and Indian grass were the only species to show a significant increase in reproductive effort from 1980 to 1981, although all species did increase.

Nitrogen Allocation

The percent of total nitrogen by plant part for 1980 and 1981 was similar to the percent biomass allocation for old-field threeawn, but differs considerably for big bluestem, little bluestem and Indian grass (Figs. 4 and 5). Unlike the biomass allocation, where allocation to roots and crowns decreased, the percent of nitrogen belowground (roots and crowns) increased during the fall and winter. During this time nitroten levels allocated to foliage decreased. Scribner's dichanthelium showed two peaks (early summer and late winter) in the percent nitrogen in the foliage fraction. Similar to the other perennials, belowground nitrogen allocation increased during the fall.

Old-field threeawn allocated 29% in 1980 and 25% in 1981 of its total plant nitrogen to reproduction. Big bluestem, little bluestem and Indian grass never allocated more than 10% total plant nitrogen to sexual reproduction for the two years. Scribner's dichanthelium was intermediate with 16% and 24% for 1980 and 1981, respectively.

In order to account for the fluctuations in the aboveground and belowground fractions, especially in the perennials, the total plant, aboveground and belowground nitrogen content were examined by species for the two years (Figs. 6 and 7). Aboveground component represents both foliage and sexual reproduction fractions while the belowground component corresponds to the root and crown fractions. These values are the product of biomass times nitrogen concentration (ppm) expressed on a per square meter basis.

Total plant nitrogen content for old-field threeawn increased steadily throughout the growing season until the August sample, after which a decline occurred. Both aboveground and belowground portions exhibited a similar pattern. Total nitrogen content in big bluestem, little bluestem and Indian grass increased during the spring and early summer then remained relatively constant in the following months. After the peak nitrogen content was reached in these plants, a shift occurred with nitrogen aboveground being translocated belowground. Scribner's dichanthelium appears to translocate some nitrogen belowground during late summer and fall, but ultimately stores most of the nitrogen in overwintering leaves at the base of the old stems. Therefore, aboveground nitrogen content increased with a concomitant decrease belowground after November when the overwintering leaves were produced.

Total nitrogen content and the percent of nitrogen in the aboveground and belowground fractions were compared for all species at the time of flowering (Table 4). These samples do not represent the same sample date, but rather similar phenological stages. Statistical analyses were not performed on the total plant nitrogen content since it would be a function of the plant's abundance and size, but rather were performed on percentage allocation. The important comparison was to determine the plant's strategy involved in the percent allocation to aboveground and belowground plant parts. Old-field threeawn and Scribner's dichanthelium each allocated a significantly greater percent of the total plant nitrogen to aboveground parts than did the other species. Big bluestem and Indian grass allocated the least amount aboveground in 1980 and, therefore, more belowground on a percent basis. Little bluestem was intermediate in 1980 while big bluestem was intermediate in 1981.

Three of the five species (old-field threeawn, big bluestem and Indian grass) had significant increases in the percent of total nitrogen allocated aboveground and decreases in the percent allocated belowground from 1980 to 1981. Little bluestem and Scribner's dichanthelium showed no significant difference in allocation of nitrogen in the two fractions for the two years.

The amount of nitrogen remaining in the above and belowground fractions at the end of the growing season also differed among species (Table 5). Old-field threeawn and Scribner's dichanthelium had over 60% of the plants' total nitrogen remaining aboveground for 1980 and 1981. The other species had significantly less nitrogen remaining aboveground for the two years. Big bluestem and Indian grass were the only species to have a significant increase in the amount of nitrogen remaining aboveground from 1980 to 1981. The other species showed no difference between sample years.

The three warm-season perennials had similar patterns of nitrogen allocation, therefore, a comparison was made of their apparent nitrogen translocation efficiencies. This was calculated by expressing as a percent the decrease in the amount of nitrogen aboveground (export) from the time of peak aboveground concentration to the January sample. Import to belowground parts is a measure of the percent increase in that fraction and was calculated during the same time period. Big bluestem remobilized

50% of its aboveground nitrogen in 1980 (Table 6). Of this, 77% entered the belowground fraction. In 1981, only 36% aboveground nitrogen was remobilized with 85% of it entering belowground roots and crowns. Little bluestem did not vary between years as to the percent nitrogen remobilized, however only 24% of it entered the belowground fraction in 1980 while 61% was translocated belowground in 1981. Indian grass remobilized the least amount of nitrogen from aboveground for both years and less nitrogen entered the belowground fraction in 1980 than 1981.

Nitrogen in the foliage not consumed by herbivores and not translocated to younger leaves or to belowground parts becomes nitrogen in the aboveground standing dead compartment upon senescence. Because a large portion of nitrogen (30-55% of total) remains in foliage at the end of the growing season, an attempt was made to determine the rate at which this nitrogen was returned to the soil through decomposition and to see if differences in decomposition rates existed between the five species. Samples of standing dead foliage from the 1980 growing season were used in the decomposition study. Nitrogen content varied from 7230 ppm in old-field threeawn and 6831 ppm in Scribner's dichanthelium to 3295, 3128 and 2156 ppm for little bluestem, Indian grass and big bluestem, respectively. The higher the initial nitrogen content in the foliage, the faster was the decomposition rate (Fig. 8). Analysis of covariance was used to determine whether or not the slopes of the decomposition results were significantly different from one another. The slopes of the regression lines for old-field threeawn and Scribner's dichanthelium were not different. ($F=1.21$, $P > 0.05$) while both were different ($P < 0.01$) from the remaining species which, as a group, showed no statistical difference. According to these rates, it would take 4-7 yr for all of the nitrogen in the standing dead foliage to return to the soil.

Phosphorus Allocation

The trend of phosphorus allocation to the various portions of the plants was similar to that of nitrogen allocation. Old-field threeawn allocated more to reproduction (48.2% in 1980 and 27.3% in 1981) than did the other species (Figs. 9 and 10). Also, the aboveground and belowground phosphorus content of old-field threeawn remained relatively proportional while fluctuations occurred between these two fractions throughout the year in the perennial species.

Total phosphorus content in old-field threeawn also emulated nitrogen in that an increase occurred during the growing season until the August sample, then declined (Figs. 11 and 12). The aboveground and belowground portions did essentially the same. Unlike nitrogen, however, total phosphorus content in big bluestem, little bluestem and Indian grass reached its peak in mid or late summer then declined during the fall and winter. Again, as in nitrogen, there was a shift of phosphorus from aboveground to belowground during the fall and winter in these three species. However, the internal translocation was not as efficient as nitrogen. The phosphorus content of Scribner's dichanthelium reached its peak at the end of June, declined during summer and fall, then increased in November with the production of the basal rosette of leaves.

Phosphorus allocation also varied among species and between sample years at the time of flowering (Table 7). All but Indian grass increased the amount of phosphorus allocated aboveground with a concurrent decrease belowground from 1980 to 1981. The annual allocated the greatest amount of phosphorus aboveground for both years while little bluestem and Indian grass the least for 1980 and 1981, respectively. Big bluestem, little bluestem and Indian grass allocated similar amounts of phosphorus aboveground and belowground in 1981. End of growing season phosphorus content also varied among species, however, only big bluestem had a significant difference between sample years, allocating less phosphorus belowground in 1981 than in 1980 (Table 8).

Potassium Allocation

Allocation of potassium to roots, crowns, foliage and sexual reproductive structures was similar to that of nitrogen and phosphorus for all five species (Figs. 13 and 14). However, potassium content in the aboveground and belowground plant components differed (Figs. 15 and 16). Belowground potassium remained relatively stable throughout both years with no apparent remobilization of aboveground potassium to belowground parts. Aboveground potassium increased to an early or mid-summer peak then declined, thus producing the same pattern for the total plant content.

Old-field threeawn, little bluestem and Scribner's dichanthelium had a significant increase in the amount of potassium allocated aboveground and decrease in belowground allocation at the time of flowering from 1980 to 1981 (Table 9). Although there were differences between species within a sample year, the differences were small, especially for 1981. Greater differences among species were found in the end of growing season potassium content (Table 10). Old-field threeawn and Scribner's dichanthelium maintained greater than 68% of their potassium aboveground for both years while the three other species had less than 58% aboveground potassium. Big bluestem and little bluestem had a significant increase in aboveground potassium allocation from 1980 to 1981.

Magnesium Allocation

Of the four elements examined, the allocation of magnesium was the most variable among the species. Magnesium allocation to roots, crowns, foliage and sexual reproduction was similar to each of the other elements (Figs. 17 and 18). Old-field threeawn maintained about equal proportions of magnesium belowground and aboveground. All other species allocated more magnesium belowground than aboveground throughout most of the two years. Peak total magnesium content occurred in late summer for all species in both years except for Scribner's dichanthelium (Figs. 19 and 20). No clear pattern of magnesium remobilization from aboveground to belowground components at the end of the year could be shown except for big bluestem (1980 and 1981) and little bluestem (1981). All species except Indian grass increased their allocation of magnesium aboveground from 1980 to 1981 at the time of flowering (Table 11). Only Indian grass showed a significant decrease in magnesium concentration aboveground and increase belowground at the end of the growing season (Table 12).

DISCUSSION

Phenology

Similar phenological data exist for this and other parts of the tallgrass prairie. However, the species from different geographical locations can exhibit ecotypic differences in phenology (Larsen 1947, McMillan 1959). Early spring activity and flowering were also noted for Scribner's dichanthelium by Ahshapanek (1962). In addition to this study, Weaver and Fitzpatrick (1932), Rice (1950) and McMillan (1959) found that big bluestem, little bluestem and Indian grass initiated growth and flowered much later than Scribner's dichantelium. Even though precipitation patterns varied greatly between the two years for this study, all species flowered at approximately the same time both years. Undoubtedly, a more reliable environmental cue such as photoperiod is responsible for flower initiation (Rice 1950, McMillan 1959, Anderson and Adams 1981). On the other hand, initiation of regrowth in the fall for Scribner's dichanthelium appears to be controlled by available moisture rather than by photoperiod.

Biomass Allocation

It has long been accepted and often verified that annuals and perennials differ in the energy allocation that each devotes to reproduction (Salisbury 1942, Pitelka 1977). Also, reproductive effort in terms of biomass allocation has been shown to be greater in early successional species than in climax species (Abrahamson 1975, Hickman 1975, Roos and Quinn 1977, Soule and Werner 1981). However, there have not always been consistent and corroborative data supporting the theoretical expectations (Gadgil and Solbrig 1972) of decreasing reproductive effort with increasing successional maturity (Werner and Rioux 1977, Werner 1979). Grime (1977) has even questioned the validity of the r- and K-selection theory in plants and has proposed a three-strategy model of plant responses based on the degree of competition, stress and disturbance of the environment. The current study supports greater reproductive effort in annuals and early successional species with one exception. Old-field threeawn, an annual and a member of early successional seral stages in Oklahoma Old-field succession (Booth 1941) consistently allocated greater amounts of biomass to reproduction than big bluestem, little bluestem and Indian grass as expected. However, Scribner's dichanthelium, a perennial species commonly found in climax prairie communities, allocated as much biomass to reproduction as did old-field threeawn.

Nitrogen Allocation

The allocation of carbon and carbohydrate reserves has been considered an important part of productivity in perennial grasslands (White 1973, Redmann and Reekie 1982), however Harper (1977) believed that in some cases the critical resource may be something other than energy (e.g., minerals). Odum (1971) suggested that climax communities will conserve essential nutrients by evolving mechanisms to recycle elements within the system. Undoubtedly, internal cycling of essential plant elements, particularly nitrogen, by the four perennial species of the tallgrass prairie represent such mechanisms. The greater allocation of elements to seeds by old-field threeawn could also be considered a form of internal cycling and conservation.

This study shows that differences exist among species as to where and when plant nitrogen is allocated. Therefore, both temporal and mechanistic differences exist within species of the tallgrass prairie with respect to utilization, redistribution and conservation of nitrogen. Confirmation of the early spring uptake of nitrogen with subsequent remobilization is provided by McKendrick et al. (1975) who found that big bluestem and Indian grass accumulated over 85% of their annual nitrogen requirement by 15 Jun. Also, in other grasses (cereals) 90% of the total nitrogen and phosphorus content of mature plants had been accumulated before the plant reached 25% of its final dry weight (Williams 1955). Power (1977) also found that uptake of nitrogen ceases as the plant approaches maturity.

Nitrogen migration from aboveground to belowground plant parts has been described in several studies of grasses (Weinmann 1940, 1942, Williams 1955, Wetselaar and Farquhar 1980) as well as for woody species (Kramer and Koxlowski 1979, Nilsen and Schlesinger 1981). Clark (1977a) using ^{15}N to study the partitioning of nitrogen in a blue grama grassland found no substantial evidence for leaching or throughfall of nitrogen from aboveground plant parts and concluded that translocation appeared to be the likely method of nitrogen transport from aboveground to belowground. Clark (1977b) also found as much as 46% of the nitrogen in the green herbage was translocated out of the aboveground portion in the fall with a concurrent 39% increase belowground during the same time period. These values for blue grama are quite comparable to the three C_4 perennials of this study. Koelling and Kucera (1965) demonstrated for a Missouri bluestem prairie that transfer or leaching of various constituents - especially nitrogen, phosphorus and potassium - had already occurred before plant materials were deposited in the litter. Tukey (1970) found more inorganic elements such as potassium and magnesium in leachates of plants than organic compounds. Therefore, the flux of nitrogen between aboveground and belowground at the end of the growing season can be interpreted primarily as translocation rather than leaching from above and a concurrent uptake by the roots.

Decomposition

Comparisons of litter decomposition in different species have been carried out extensively using the litter-bag method (Jensen 1974). Most studies have found that litter rich in nitrogen and soluble carbohydrates decomposed more rapidly than nitrogen-poor litter, particularly in the initial stages of decomposition (Witkamp 1966, Williams and Gray 1974). As expected, weight losses in the nitrogen-rich leaves of oldfield threeawn were more rapid than the other species. Scribner's dichanthelium was intermediate in leaf nitrogen content and intermediate in weight loss through decomposition. Risser (1976) found grassland litter in a tallgrass prairie of Oklahoma to turnover every 4.4 years. The turnover rates in this study were probably much slower because of the drought conditions which prevailed during one year of the study.

Other Plant Elements

The elements phosphorus, potassium and magnesium are probably the most widely investigated nutrient elements other than nitrogen. However, most work in the dynamics of these elements has been done in ecosystems other than grasslands (e.g., Likens et al. 1970, Johnson and Risser 1974, Grigal and Ohmann 1980, Nilsen and Schlesinger 1981). Studies of these elements in grasslands have considered primarily the cycling between plant and soil (Sheedy et al. 1973, Woodmansee and Duncan 1980, Callahan and Kucera 1981) with no examination of internal remobilization.

Phosphorus, potassium and magnesium were not conserved and remobilized belowground to the same extent as was nitrogen. In fact, belowground potassium levels did not change appreciably throughout the entire year. Belowground phosphorus levels did increase as aboveground levels decreased, but they were depleted by the beginning of the next growing season. Therefore, redistribution of these elements is likely to be a function of the form in which the element is found and its solubility (Van Goor and Wiersma 1974). Based on studies of a South Dakota prairie, White (1973) attributed the loss of potassium and magnesium in aboveground vegetation to leaching due to their solubility. Tukey (1970) also showed appreciable quantities of inorganic nutrients such as potassium and magnesium lost by leaching or throughfall.

There are many reports that mobile nutrients in leaves decline markedly between maturity and full senescence. The rise and fall pattern of phosphorus, potassium and magnesium concentrations in the aboveground portions of the plant are typical for phloem mobile nutrients (Hill 1980). Nitrogen is also a phloem mobile nutrient. However, most nitrogen in the plant is in the form of organic compounds such as proteins and amino acids, therefore, it would be less likely leached (Mittler 1953, Pate 1976, Storey and Beevers 1977). All of these elements may be remobilized, but from these results, nitrogen is conserved to a much greater extent than the other elements with phosphorus being intermediate and potassium not conserved at all. Magnesium is problematic, however, being classified as a mobile (Price 1970), immobile (Mengel 1965) and moderately mobile element (Bukovac and Wittwer 1957). As mentioned before, the magnesium results in this study were highly variable and difficult to interpret.

These data indicate the physiological adaptive strategies of five grass species that have adapted to an ecosystem subjected not only to limited nutrients, but also grazing, burning and drought (Weaver and Fitzpatrick 1934, Anderson 1982). These five grass species have evolved at least three different adaptive patterns that allow each to conserve limited nitrogen. The annual allocated nitrogen to seeds, Scribner's dichanthelium allocated and stored nitrogen in overwintering leaves and the C_4 perennials conserved nitrogen by allocating it to belowground plant components during the fall and winter. These adaptations appear to respond to and change with existing environmental conditions. Also, different essential plant elements behave very differently in terms of allocation and remobilization.

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Table 1. Composition and percent aerial cover for herbaceous and woody species at the University of Oklahoma Grassland Research Area. Total cover exceeds 100% due to species overlap.

	PERCENT COVER	
HERBACEOUS SPECIES	1980	1981
Andropogon gerardii	26	30
Schizachyrium scoparium	21	27
Sorghastrum nutans	8	18
Dichanthelium oligosanthes var. *scribnerianum*	8	8
Panicum virgatum	6	7
Aristida oligantha	5	5
Ambrosia psilostachya	5	4
Bouteloua curtipendula var. *curtipendula*	2	4
Psoralea tenuiflora	2	1
Liatris punctata	1	4
Yucca glauca	1	1
Schrankia nuttallii	1	2
Amorpha canescens	1	1
Eurphorbia corrollata	1	1
Baptisia leucophaea	1	1
Baptisia australis	1	1
Bouteloua hirsuta	1	1
Oenothera heterophylla	1	1
Euphorbia spathulata	1	1
Opuntia compressa	1	1
Erigeron tenuis	1	1
Achillea lanulosa	1	1

Table 1. Continued.

Manisuris cylindrica	1	1
Thelesperma filifolium	-	2
Solidago missouriensis	-	1
Ophioglossum engelmannii	-	1
Spiranthes gracilis	-	1
Dalea purpurea	-	1
Oxalis violacea	-	1
Stenosiphon linifolius	-	1
WOODY SPECIES		
Quercus prinoides	17	11
Rhus copallina	8	8
Rhus radicans	5	3
Prunus angustifolia	1	5
Rhus glabra	1	1
Cornus drummondii	1	1
Juniperus virginiana	1	1

Table 2. Dates (1980 and 1981) for phenological stages of development for five Oklahoma tallgrass prairie species.

SPECIES	PHENOLOGICAL STAGE	DATES 1980	 1981
Old-field threeawn	Winter quiescence	1 Jan.- 27 Apr.	1 Jan.-18 Apr.
	Growth initiation	28 Apr.	19 Apr.
	Major flowering	7 Aug.- 24 Aug.	6 Aug.- 19 Aug.
	Fall quiescence	20 Sep.- 31 Dec.	5 Oct.- 31 Dec.
Big bluestem	Winter quiescence	1 Jan.- 8 Apr.	1 Jan.- 31 Mar.
	Growth initiation	9 Apr.	1 Apr.
	Major flowering	13 Sep.- 28 Sep.	3 Sep.- 20 Sep.
	Fall quiescence	12 Nov.- 31 Dec.	22 Nov.- 31 Dec.
Little bluestem	Winter quiescence	1 Jan.- 30 Mar.	1 Jan.- 25 Mar.
	Growth initiation	31 Mar.	26 Mar.
	Major flowering	19 Sep.- 29 Sep.	8 Sep.- 24 Sep.
	Fall quiescence	12 Nov.- 31 Dec.	22 Nov.- 31 Dec.

Table 2. Continued.

SPECIES	PHENOLOGICAL STAGE	DATES 1980	DATES 1981
Indian grass	Winter quiescence	1 Jan.- 8 Apr.	1 Jan.- 31 Mar.
	Growth initiation	9 Apr.	1 Apr.
	Major flowering	18 Sep.- 30 Sep.	8 Sep.- 24 Sep.
	Fall quiescence	12 Nov.- 31 Dec.	22 Nov.- 31 Dec.
Scribner's dichanthelium	Winter quiescence	1 Jan.- 17 Feb.	1 Jan.- 15 Feb.
	Growth initiation	18 Feb.	16 Feb.
	Major flowering	1 May- 23 May	28 Jul.- 16 Sep.
	Summer quiescence	16 Jul.- 2 Nov.	28 Jul.- 16 Sep.
	Fall regrowth initiation	3 Nov.	17 Sep.
	Fall quiescence	21 Nov.- 31 Dec.	3 Dec.- 31 Dec.

Table 3. Percent biomass reproductive effort (weight of inflorescences expressed as a percent of total plant weight). Means with the same letter are not significantly different within a column. An asterisk (*) after the species name indicates a statistically significant difference ($P < 0.05$) between sample years. All statistical analyses were performed using Analysis of Variance and Duncan's Multiple Range Test. Arcsine transformations were performed on all percentages before the analysis.[1]

SPECIES	1980	1981
Old-field threeawn	15.6^{a}	17.9^{a}
Big bluestem*	1.4^{b}	3.2^{b}
Little bluestem	2.7^{b}	4.1^{b}
Indian grass*	2.1^{b}	4.2^{b}
Scribner's dichanthelium	14.9^{a}	18.8^{a}

Table 4. Total (T) nitrogen content (gm^{-2}), and percent of total nitrogen aboveground (A) and belowground (B) when species are in flower. See table 3 for explanation of superscripts.

	1980			1981		
SPECIES	T	A	B	T	A	B
Old-field threeawn*	1.16	69.0^a	31.0^c	1.15	76.0^a	24.0^c
Big bluestem*	1.79	48.6^c	51.4^a	2.07	58.9^b	41.1^b
Little bluestem	1.71	55.6^b	44.4^b	1.82	48.6^c	51.4^a
Indian grass*	1.39	43.2^c	56.8^a	1.69	53.0^c	47.0^a
Scribner's dichanthelium	0.56	67.9^a	32.1^c	0.39	64.0^a	36.0^c

Table 5. End of growing season total (T) nitrogen content (gm^{-2}), and percent of total nitrogen aboveground (A) and belowground (B). See table 3 for explanation of superscripts.

SPECIES	1980 T	1980 A	1980 B	1981 T	1981 A	1981 B
Old-field threeawn	0.44	79.5^a	20.5^c	0.51	78.3^a	21.7^d
Big bluestem*	1.75	33.7^c	66.3^a	2.00	45.6^c	54.4^b
Little bluestem	1.63	35.6^c	64.4^a	1.70	36.4^d	63.6^a
Indian grass*	1.35	37.8^c	62.2^a	1.51	43.7^c	56.3^b
Scribner's dichanthelium	0.89	62.9^b	37.1^b	0.77	61.3^b	38.7^c

Table 6. Nitrogen translocation from aboveground foliage (% export) to belowground roots and crowns (% import).

SPECIES	1980 % EXPORT	 % IMPORT	1981 % EXPORT	 % IMPORT
Big bluestem	50	77	36	85
Little bluestem	47	24	44	61
Indian grass	35	75	37	21

Table 7. Total (T) phosphorus content (gm^{-2}), and percent of total phosphorus aboveground (A) and belowground (B) when species are in flower. See table 3 for explanation of superscripts.

SPECIES	1980 T	1980 A	1980 B	1981 T	1981 A	1981 B
Old-field threeawn*	0.09	75.0^a	25.0^d	0.10	88.3^a	11.7^c
Big bluestem*	0.12	44.8^c	55.2^b	0.13	55.6^c	44.4^a
Little bluestem*	0.12	37.9^d	62.1^a	0.14	52.8^c	47.2^a
Indian grass	0.11	47.2^c	52.8^b	0.10	47.0^c	53.0^a
Scribner's dichanthelium*	0.04	66.7^b	33.3^c	0.04	77.3^b	22.7^b

Table 8. End of growing season total (T) phosphorus content (gm^{-2}), and percent of total phosphorus aboveground (A) and belowground (B). See table 3 for explanation of superscripts.

	1980			1981		
SPECIES	T	A	B	T	A	B
Old-field threeawn	0.03	82.8^{a}	17.2^{d}	0.04	85.7^{a}	14.3^{d}
Big bluestem*	0.08	16.7^{d}	83.3^{a}	0.09	23.3^{d}	76.7^{a}
Little bluestem	0.07	19.1^{d}	80.9^{a}	0.08	22.9^{d}	77.1^{a}
Indian grass	0.07	38.2^{c}	61.8^{b}	0.07	33.8^{c}	66.2^{b}
Scribner's dichanthelium	0.04	59.0^{b}	41.0^{c}	0.03	56.3^{b}	43.7^{c}

Table 9. Total (T) potassium content (gm^{-2}), and percent of total potassium aboveground (A) and belowground (B) when species are in flower. See table 3 for explanation of superscripts.

	1980			1981		
SPECIES	T	A	B	T	A	B
Old-field threeawn*	0.73	64.8^{c}	35.2^{a}	0.92	83.8^{a}	16.2^{b}
Big bluestem	2.28	74.3^{b}	25.7^{b}	2.71	81.0^{a}	19.0^{b}
Little bluestem*	1.33	65.3^{c}	34.7^{a}	1.77	73.8^{b}	26.2^{a}
Indian grass	2.24	83.9^{a}	16.1^{c}	2.53	85.3^{a}	14.7^{b}
Scribner's dichanthelium*	0.46	68.9^{bc}	31.1^{ab}	0.42	77.1^{b}	22.9^{a}

Table 10. End of growing season total (T) potassium content (gm^{-2}), and percent of total potassium aboveground (A) and belowground (B). See table 3 for explanation of superscripts.

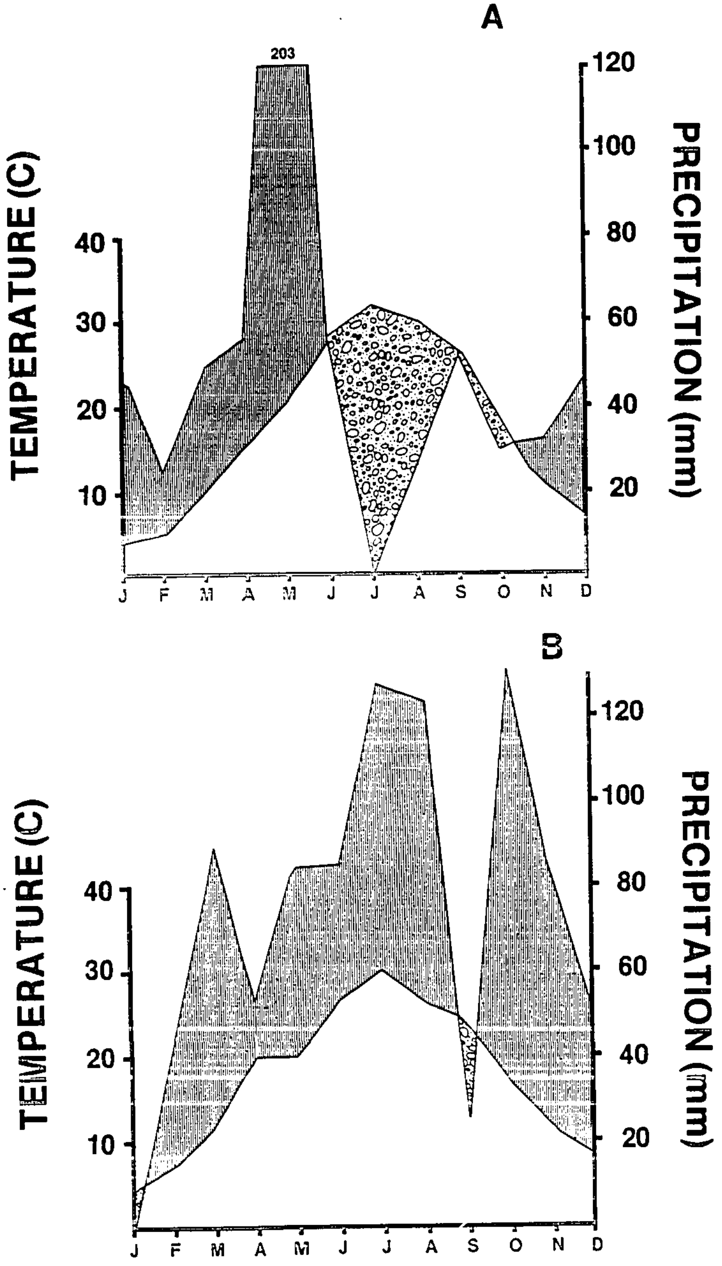
	1980			1981		
SPECIES	T	A	B	T	A	B
Old-field threeawn	0.22	81.7^a	18.3^d	0.25	76.3^a	23.7^c
Big bluestem*	0.97	42.5^c	57.5^b	1.16	57.4^b	42.6^b
Little bluestem*	0.67	26.9^d	73.1^a	0.81	46.9^c	53.1^a
Indian grass	0.52	43.3^c	56.7^b	0.62	40.7^c	59.3^a
Scribner's dichanthelium	0.48	68.3^b	31.7^c	0.42	70.8^a	29.2^c

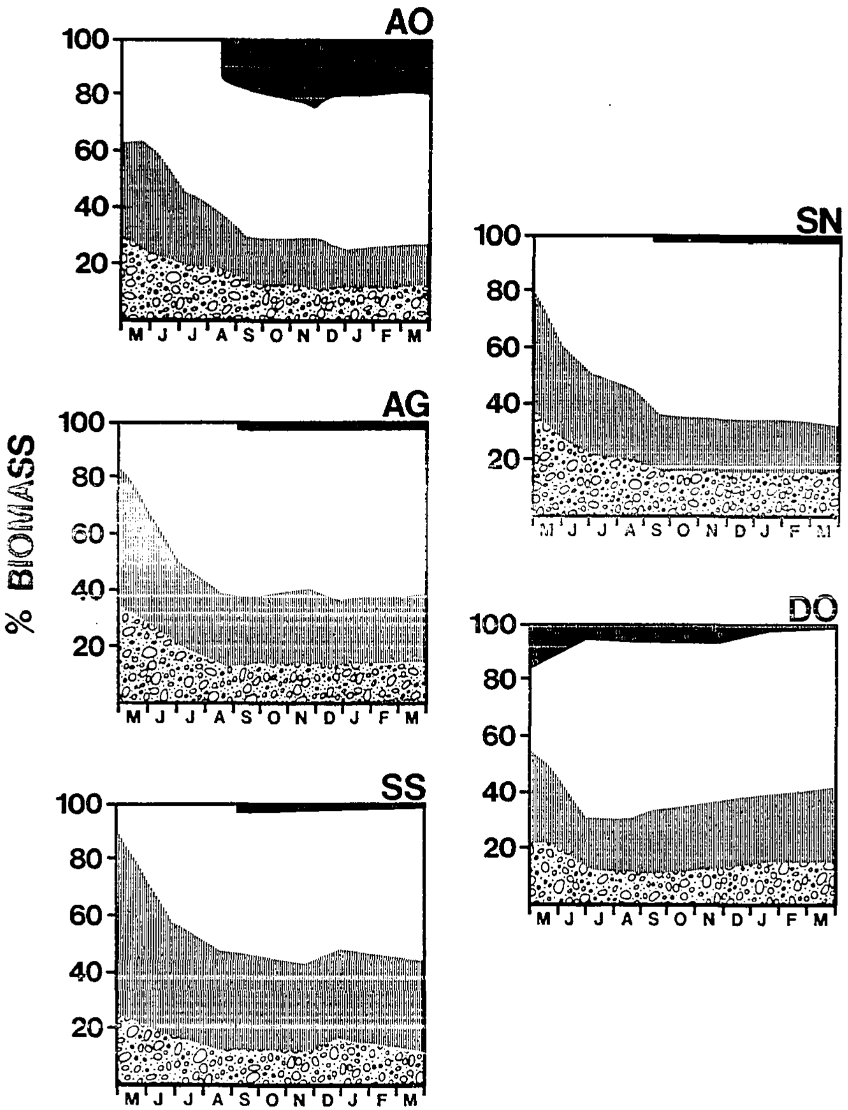
Table 11. Total (T) magnesium content (gm^{-2}), and percent of total magnesium aboveground (A) and belowground (B) when species are in flower. See table 3 for explanation of superscripts.

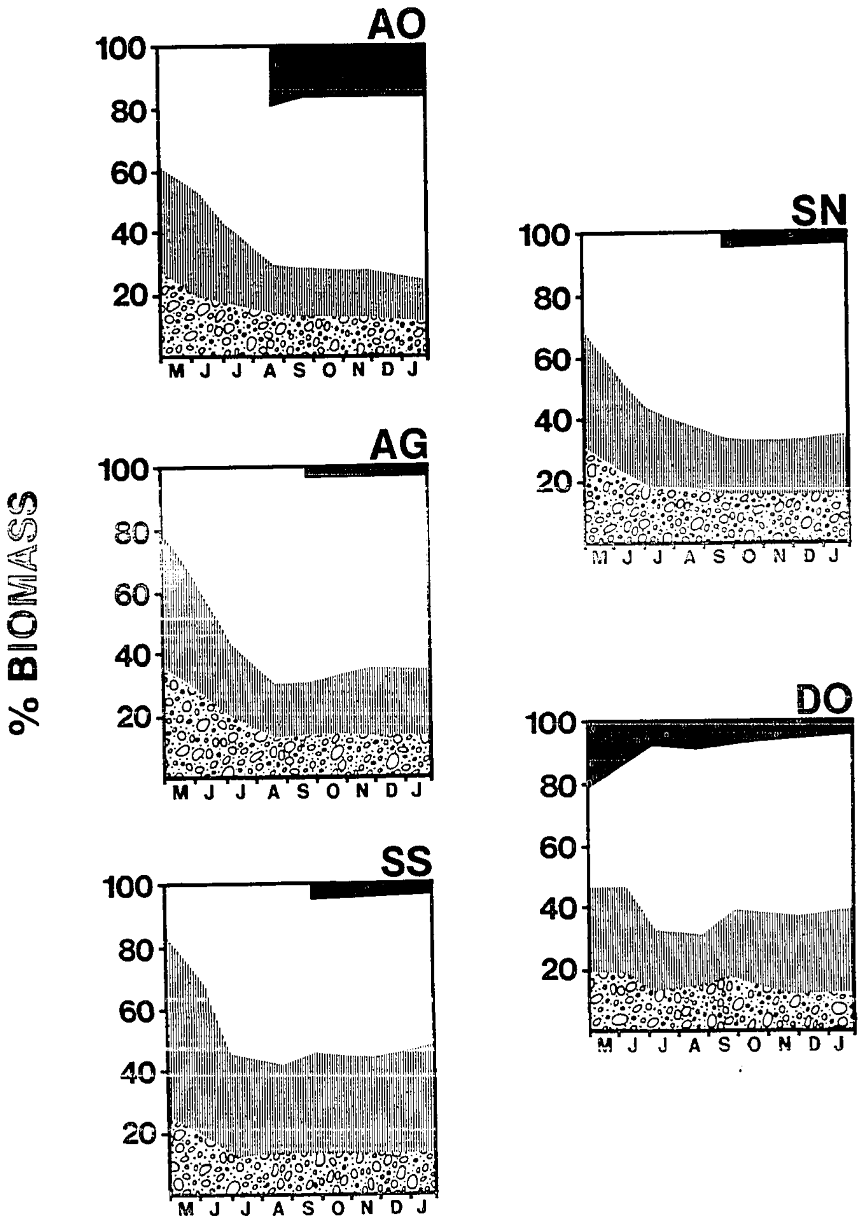
		1980			1981	
SPECIES	T	A	B	T	A	B
Old-field threeawn*	0.26	51.4^a	48.6^c	0.25	67.1^a	32.9^c
Big bluestem*	0.40	46.0^b	54.0^b	0.43	51.2^b	48.8^b
Little bluestem*	0.63	26.8^c	73.2^a	0.51	34.5^c	65.5^a
Indian grass	0.39	41.7^b	58.3^b	0.47	46.7^b	53.3^b
Scribner's dichanthelium*	0.18	39.4^b	60.6^b	0.12	46.8^b	53.2^b

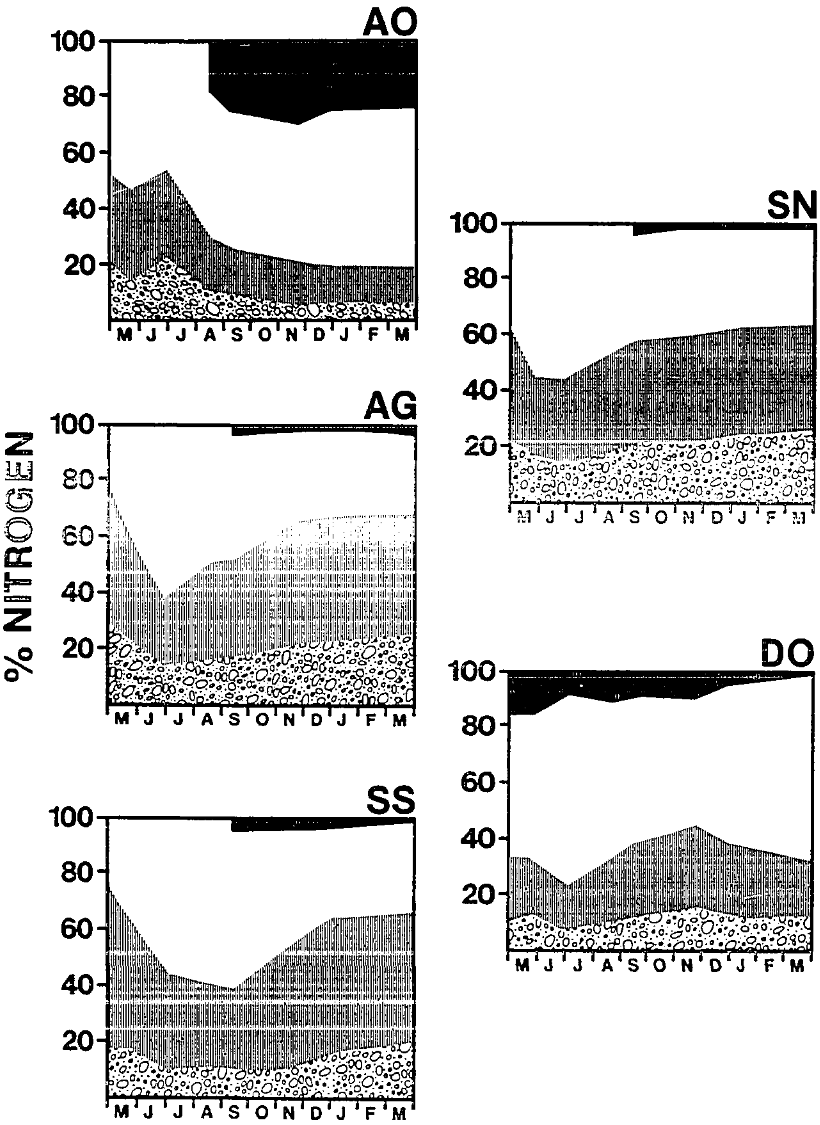
Table 12. End of growing season total (T) magnesium content (gm^{-2}), and percent of total magnesium aboveground (A) and belowground (B). See table 3 for explanation of superscripts.

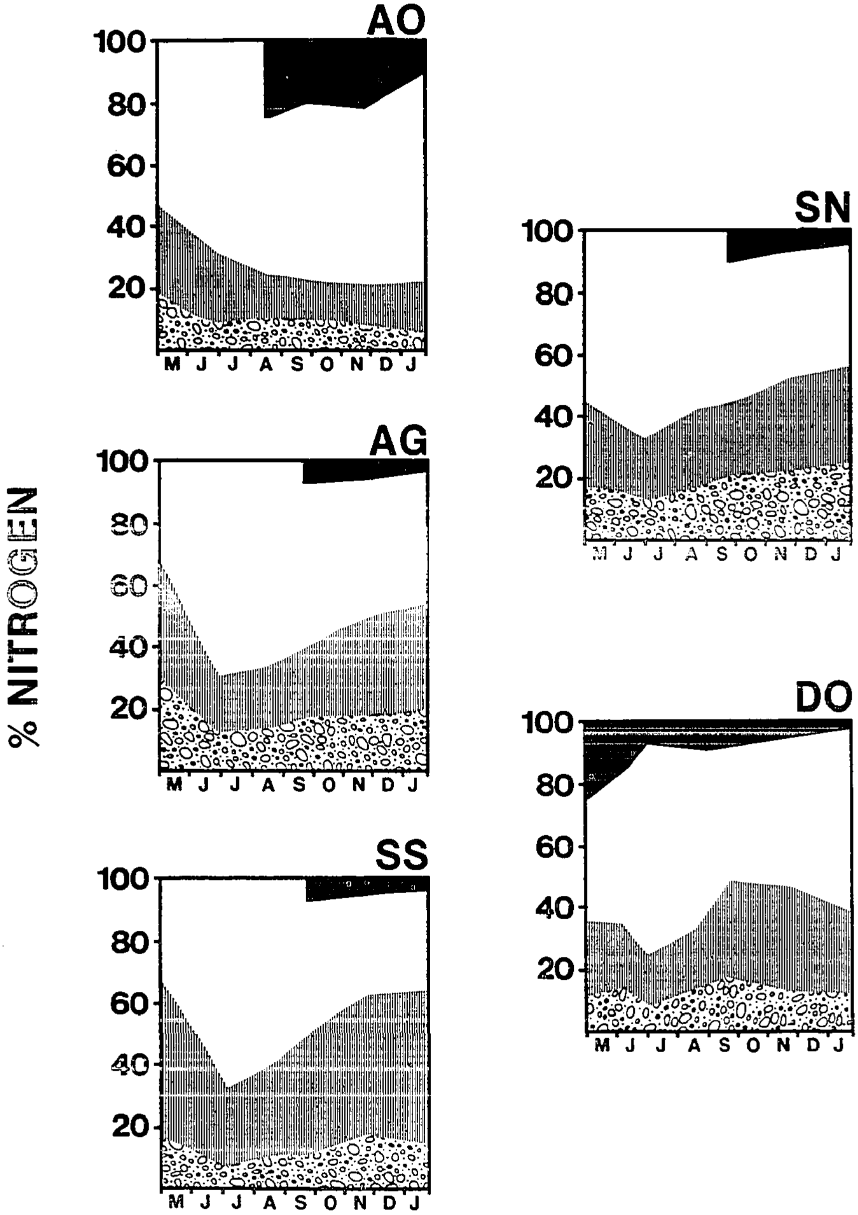
	1980			1981		
SPECIES	T	A	B	T	A	B
Old-field threeawn	0.09	68.9^{a}	31.1^{d}	0.09	65.9^{a}	34.1^{d}
Big bluestem	0.36	33.9^{c}	66.1^{b}	0.37	27.9^{c}	72.1^{b}
Little bluestem	0.48	16.0^{d}	84.0^{a}	0.36	13.6^{d}	86.4^{a}
Indian grass*	0.23	31.6^{c}	68.4^{b}	0.31	23.5^{c}	76.5^{b}
Scribner's dichanthelium	0.21	53.6^{b}	46.4^{c}	0.17	53.8^{b}	46.2^{c}

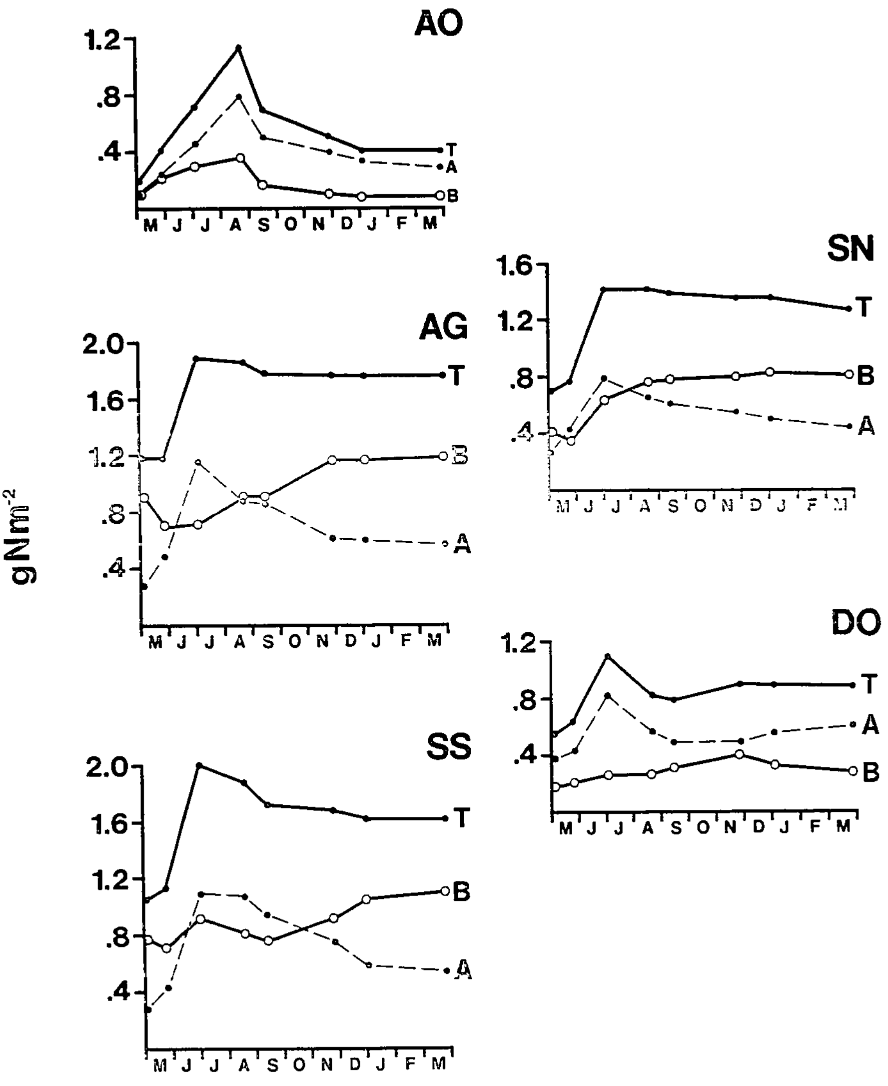

A
203
TEMPERATURE (C)
40
30
20
10
PRECIPITATION (mm)
120
100
80
60
40
20
J
F
M
A
M
J
J
A
S
O
N
D
B
TEMPERATURE (C)
40
30
20
10
PRECIPITATION (mm)
120
100
80
60
40
20
J
F
M
A
M
J
J
A
S
O
N
D

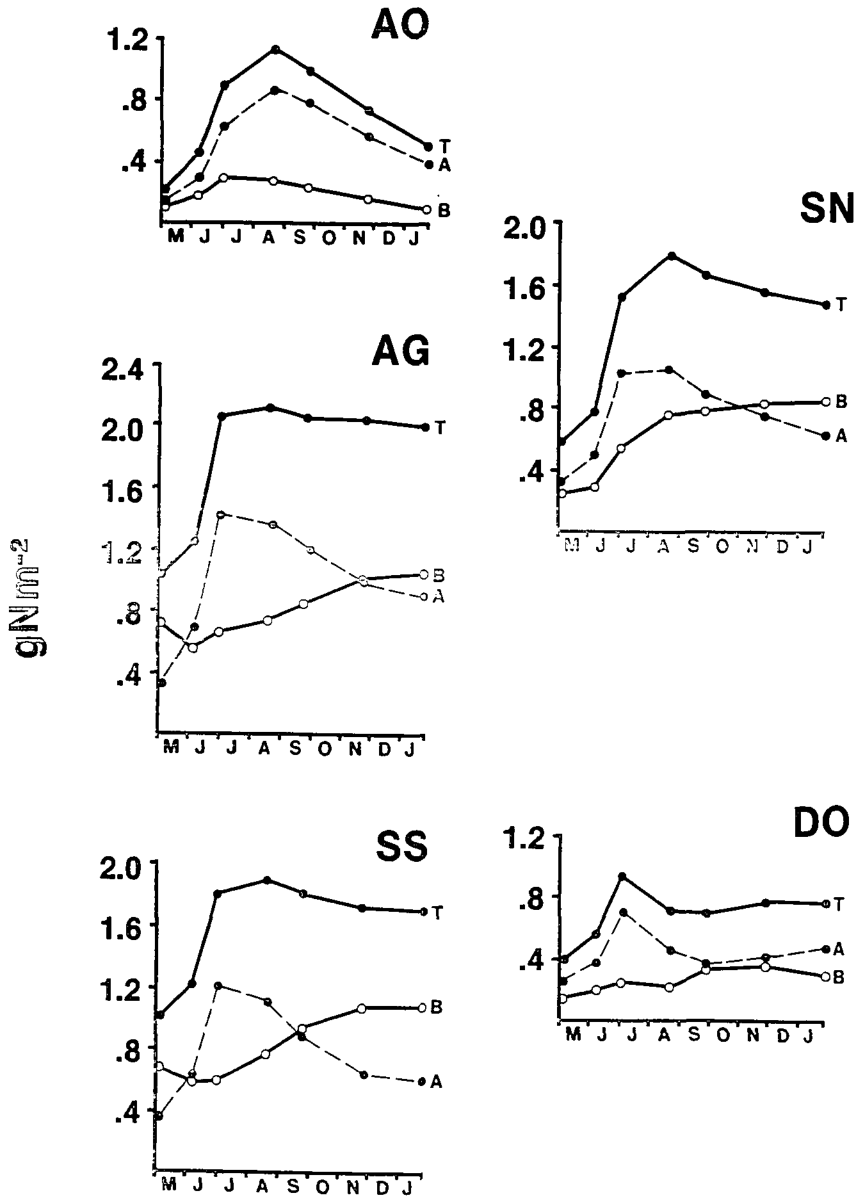

% BIOMASS
AO
AG
SS
SN
DO
100
80
60
40
20
M J J A S O N D J F M


% BIOMASS
AO
100
80
60
40
20
M J J A S O N D J
SN
100
80
60
40
20
M J J A S O N D J
AG
100
80
60
40
20
M J J A S O N D J
DO
100
80
60
40
20
M J J A S O N D J
SS
100
80
60
40
20
M J J A S O N D J

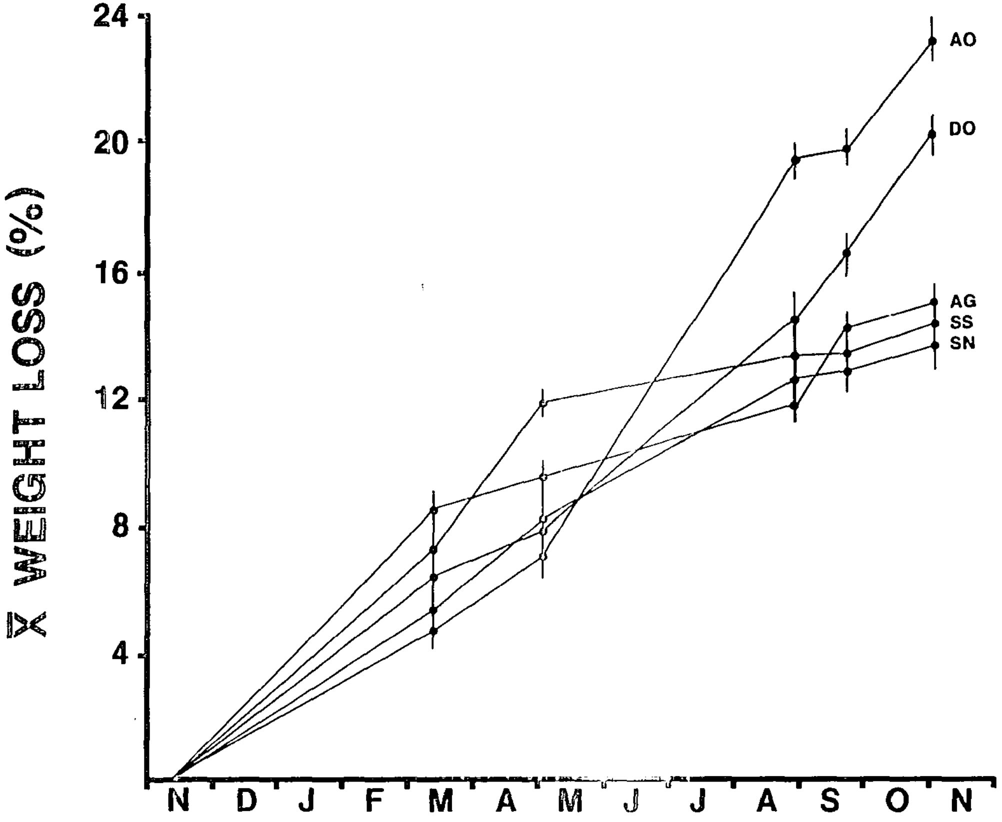

AO
AG
SS
SN
DO
% NITROGEN
100
80
60
40
20
M J J A S O N D J F M

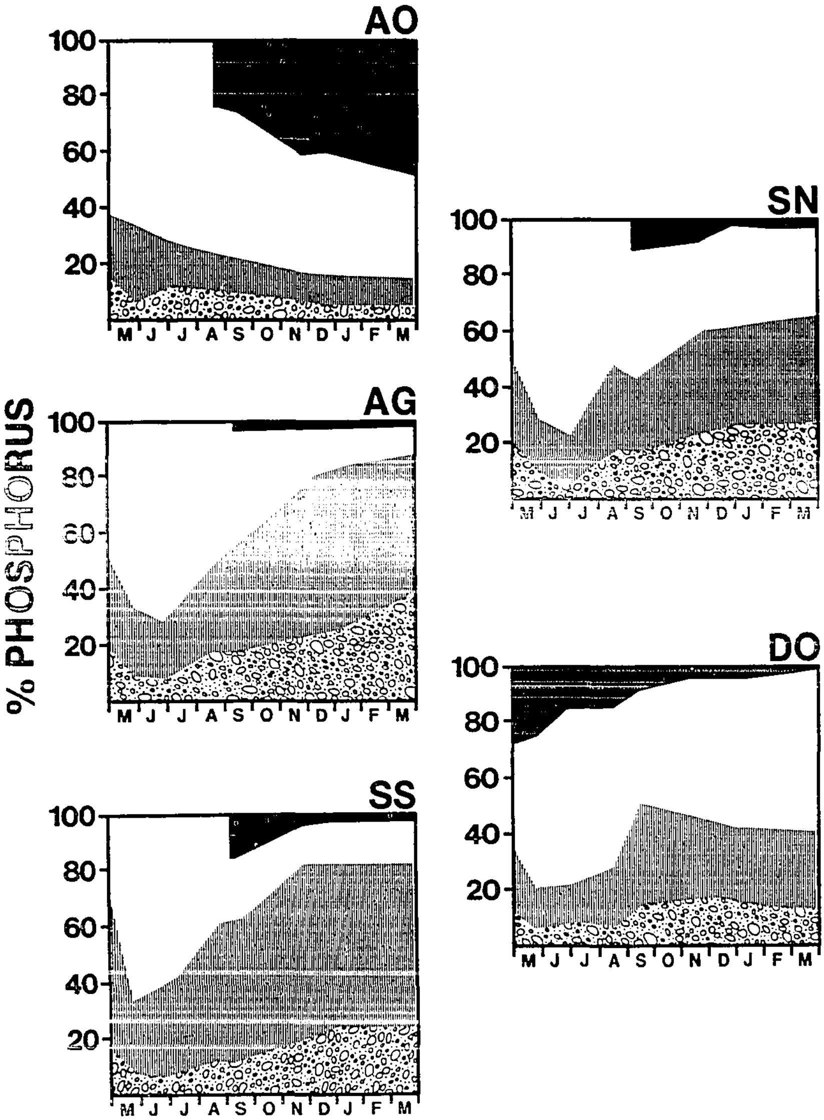

% NITROGEN
AO
AG
SS
SN
DO
100
80
60
40
20
M J J A S O N D J

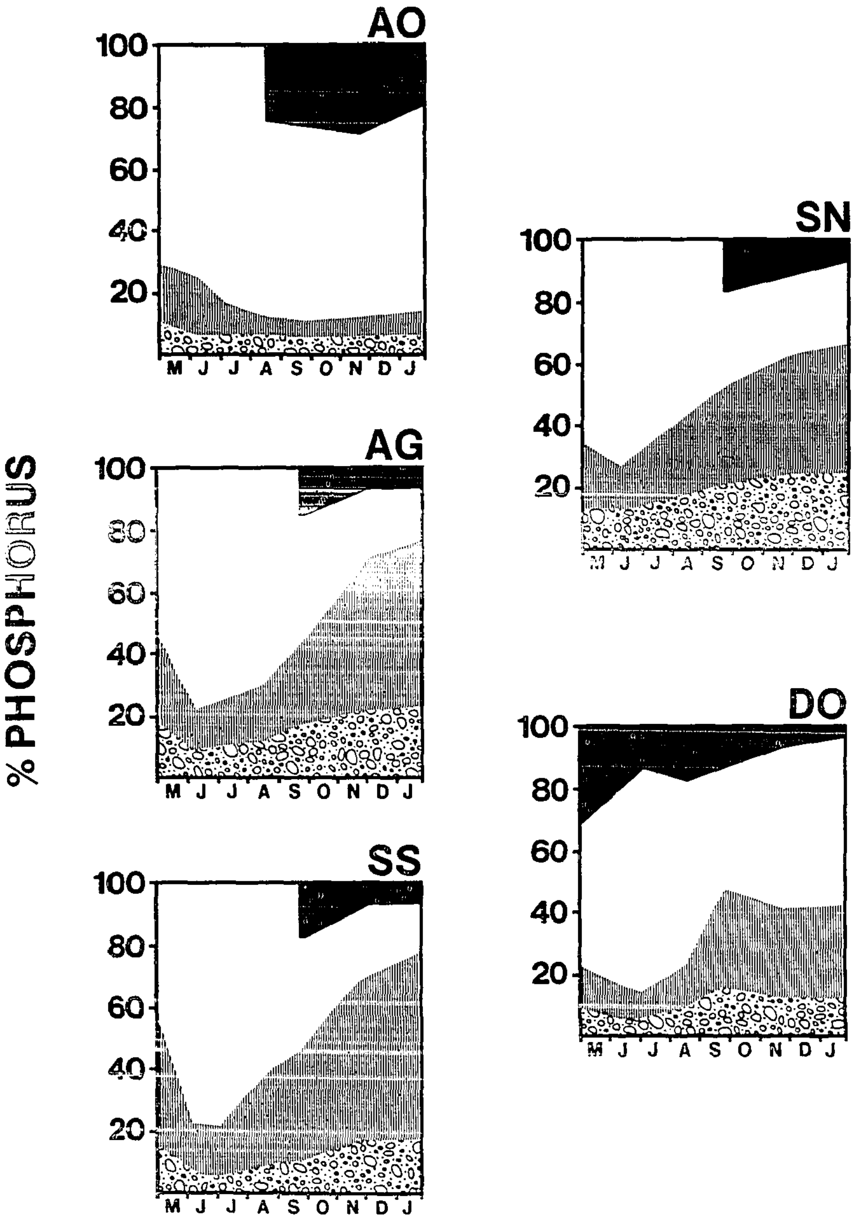

gNm^{-2}
AO
1.2
.8
.4
M J J A S O N D J F M
T
A
B
AG
2.0
1.6
1.2
.8
.4
M J J A S O N D J F M
T
B
A
SS
2.0
1.6
1.2
.8
.4
M J J A S O N D J F M
T
B
A
SN
1.6
1.2
.8
.4
M J J A S O N D J F M
T
B
A
DO
1.2
.8
.4
M J J A S O N D J F M
T
A
B

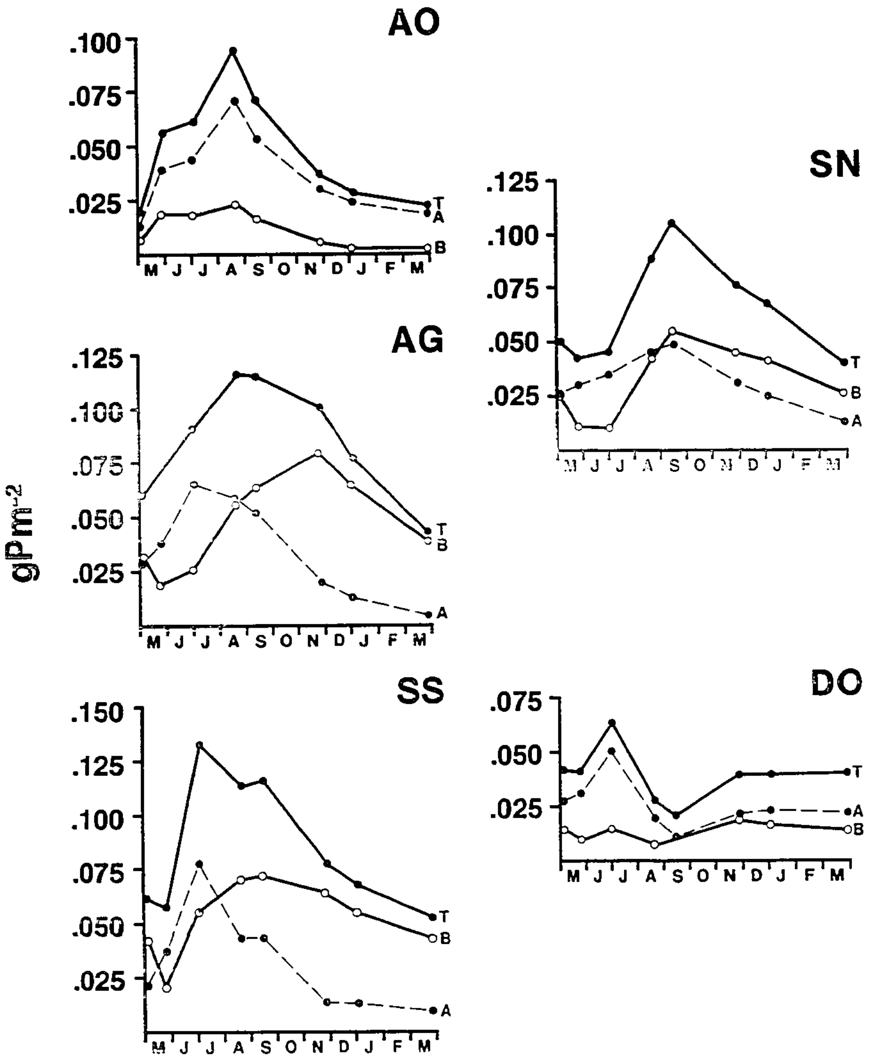


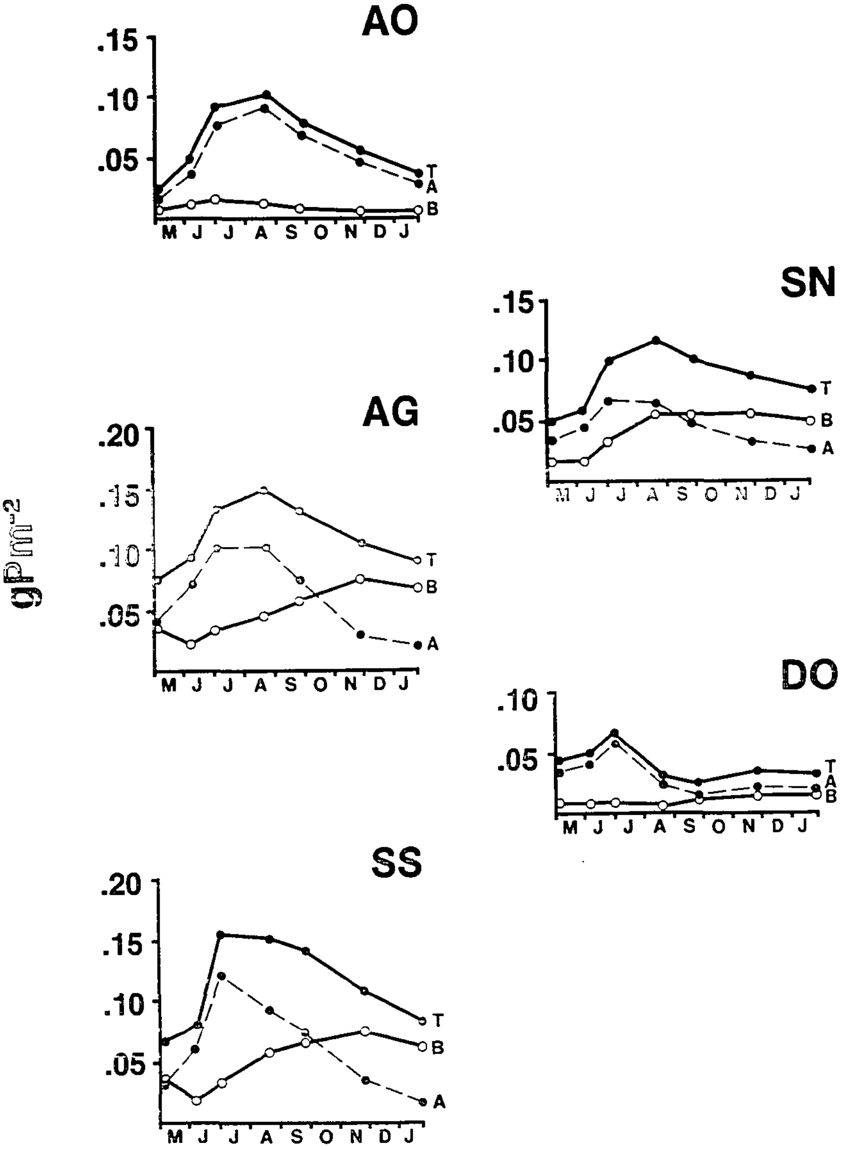
AO
1.2
.8
.4
M J J A S O N D J
T
A
B
SN
2.0
1.6
1.2
.8
.4
M J J A S O N D J
T
B
A
AG
2.4
2.0
1.6
1.2
.8
.4
M J J A S O N D J
T
B
A
g N m^-2
SS
2.0
1.6
1.2
.8
.4
M J J A S O N D J
T
B
A
DO
1.2
.8
.4
M J J A S O N D J
T
A
B

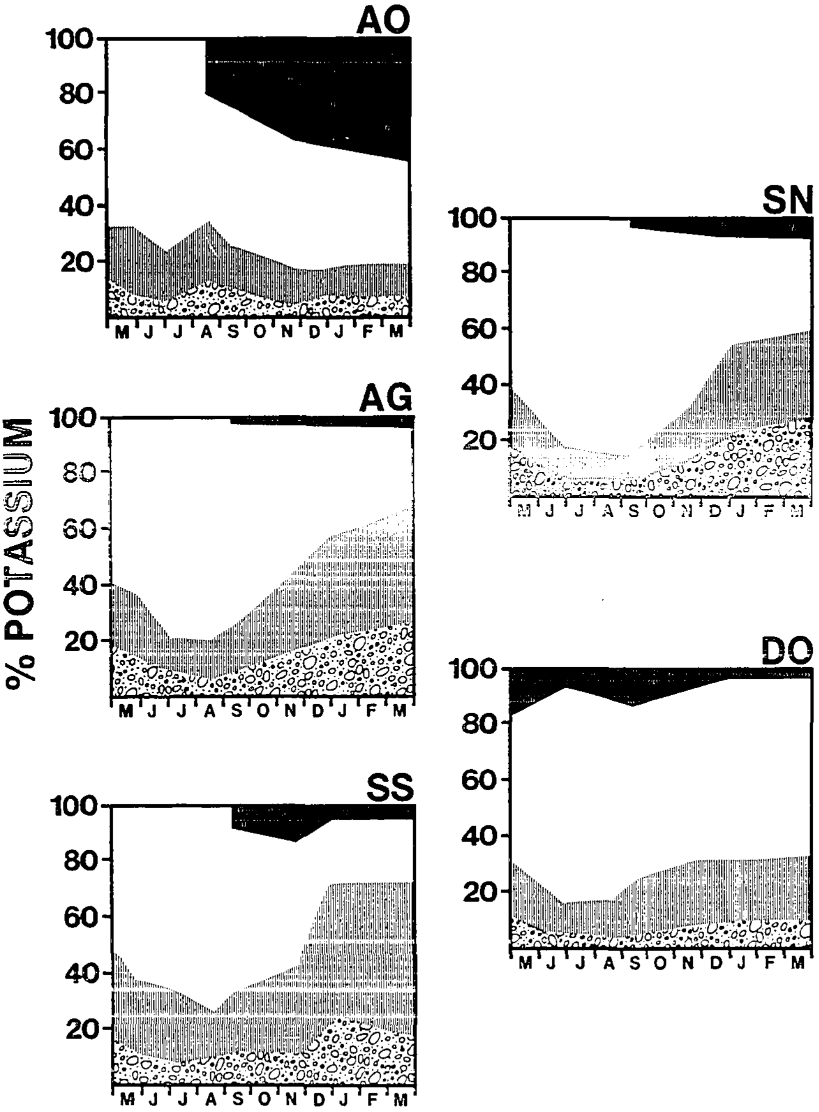

X̄ WEIGHT LOSS (%)
4
8
12
16
20
24
N
D
J
F
M
A
M
J
J
A
S
O
N
AO
DO
AG
SS
SN

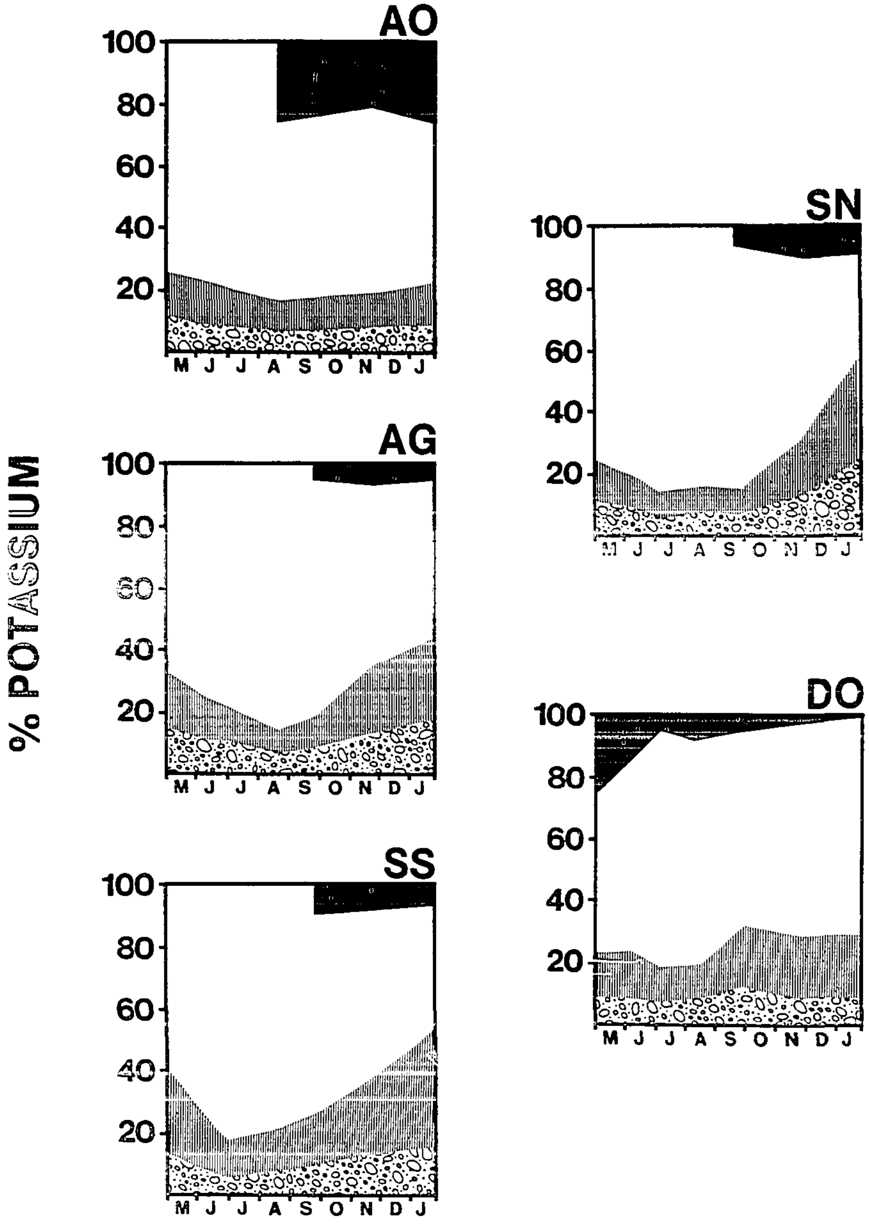

% PHOSPHORUS
AO
SN
AG
DO
SS
100
80
60
40
20
M J J A S O N D J F M

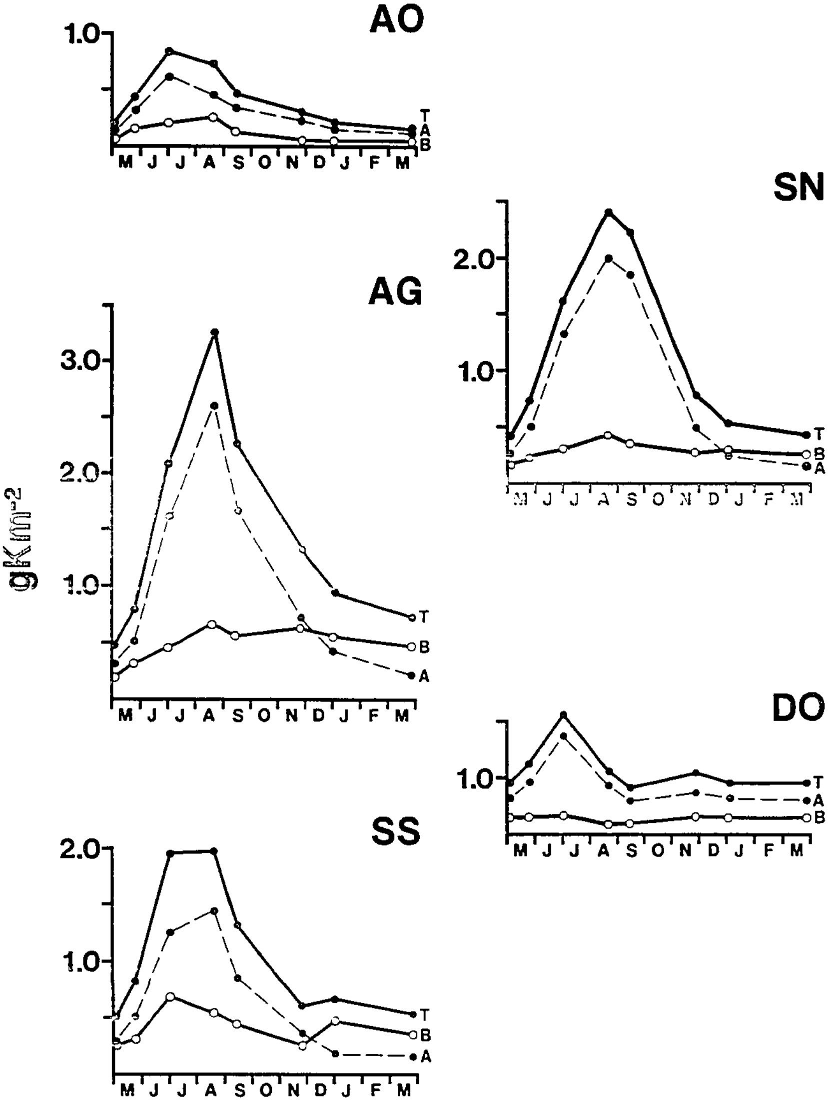

% PHOSPHORUS
AO
100
80
60
40
20
M J J A S O N D J
SN
100
80
60
40
20
M J J A S O N D J
AG
100
80
60
40
20
M J J A S O N D J
DO
100
80
60
40
20
M J J A S O N D J
SS
100
80
60
40
20
M J J A S O N D J

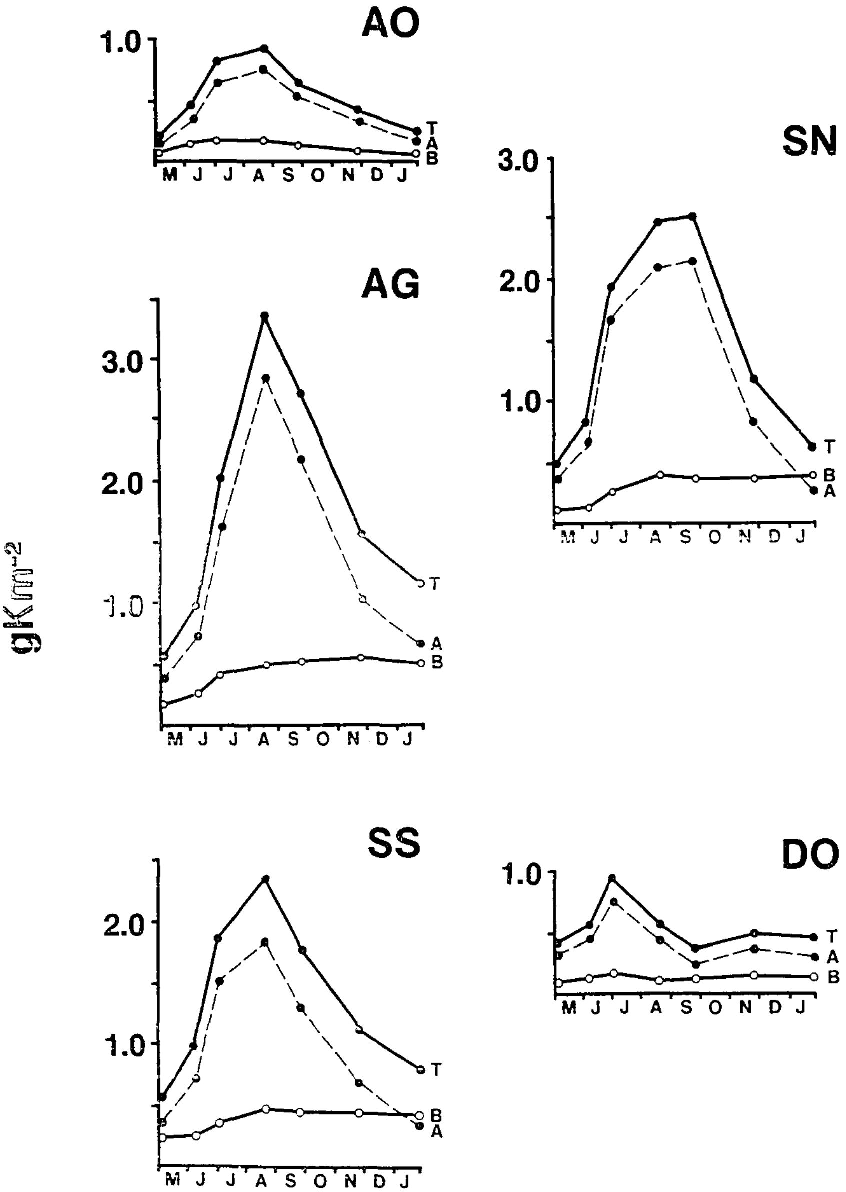

AO
.100
.075
.050
.025
T
A
B
M J J A S O N D J F M
SN
.125
.100
.075
.050
.025
T
B
A
M J J A S O N D J F M
AG
.125
.100
.075
.050
.025
T
B
A
M J J A S O N D J F M
gPm-2
SS
.150
.125
.100
.075
.050
.025
T
B
A
M J J A S O N D J F M
DO
.075
.050
.025
T
A
B
M J J A S O N D J F M

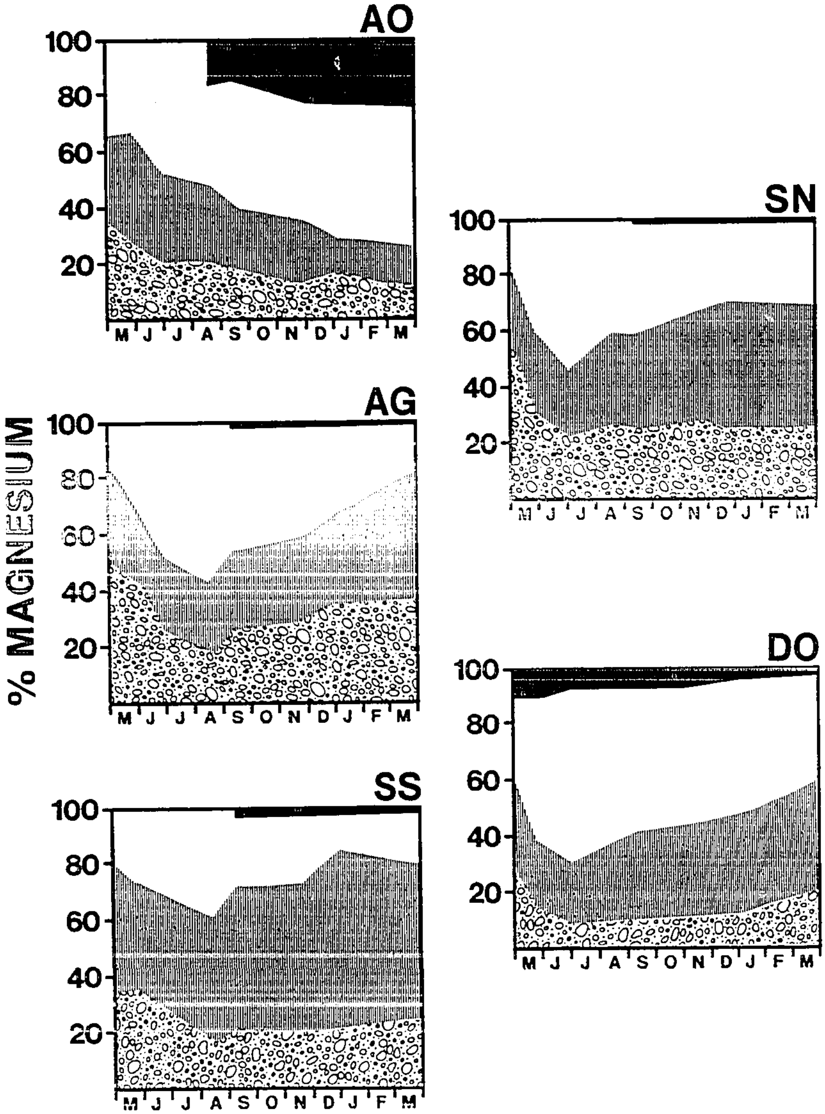

gPm⁻²
AO
.15
.10
.05
T
A
B
M J J A S O N D J
SN
.15
.10
.05
T
B
A
M J J A S O N D J
AG
.20
.15
.10
.05
T
B
A
M J J A S O N D J
DO
.10
.05
T
A
B
M J J A S O N D J
SS
.20
.15
.10
.05
T
B
A
M J J A S O N D J

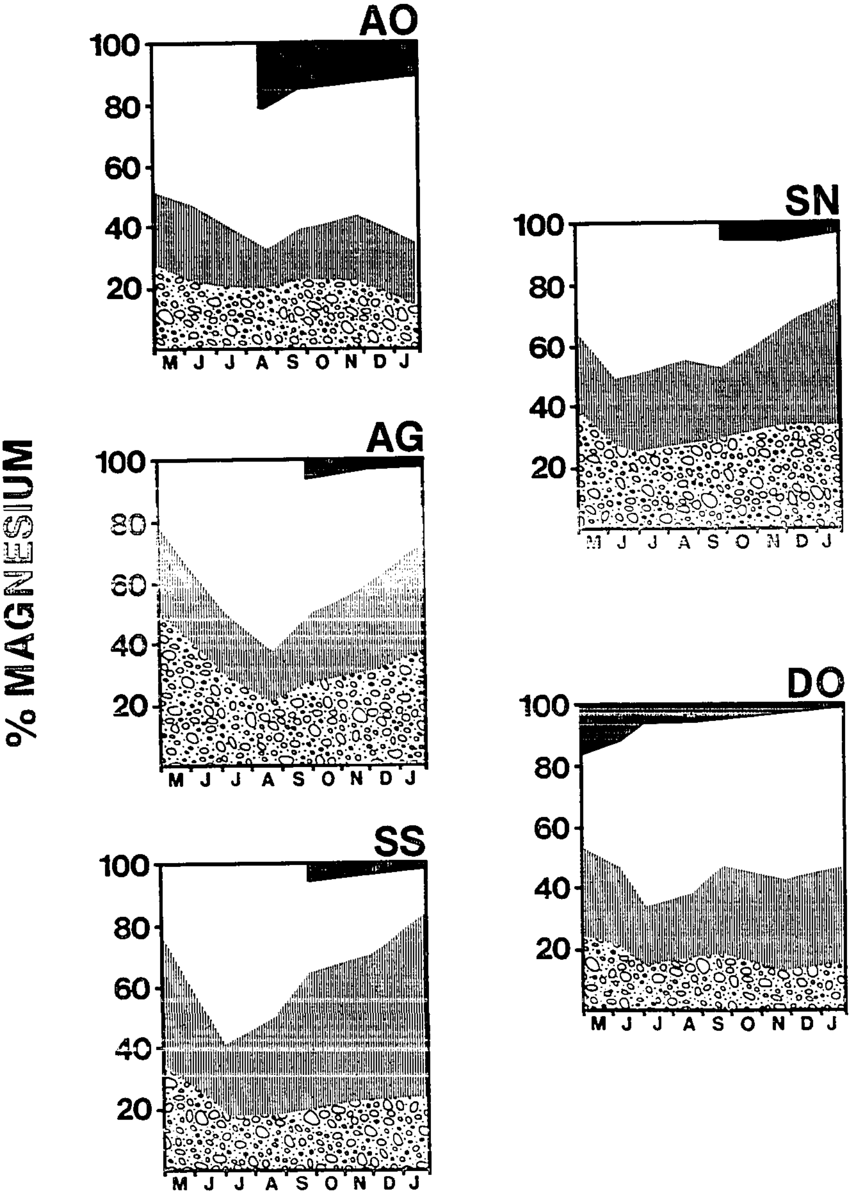

% POTASSIUM
AO
SN
AG
DO
SS
100
80
60
40
20
M J J A S O N D J F M

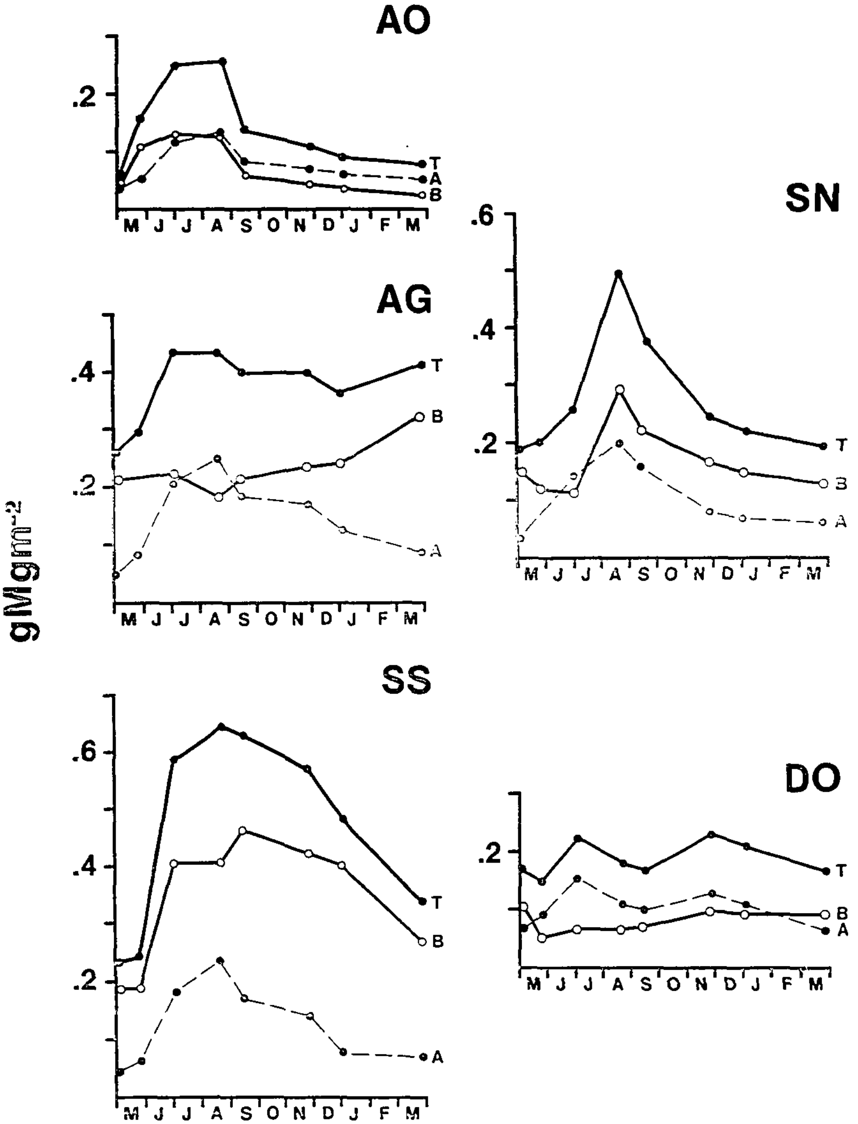

% POTASSIUM
AO
100
80
60
40
20
M J J A S O N D J
AG
100
80
60
40
20
M J J A S O N D J
SS
100
80
60
40
20
M J J A S O N D J
SN
100
80
60
40
20
M J J A S O N D J
DO
100
80
60
40
20
M J J A S O N D J

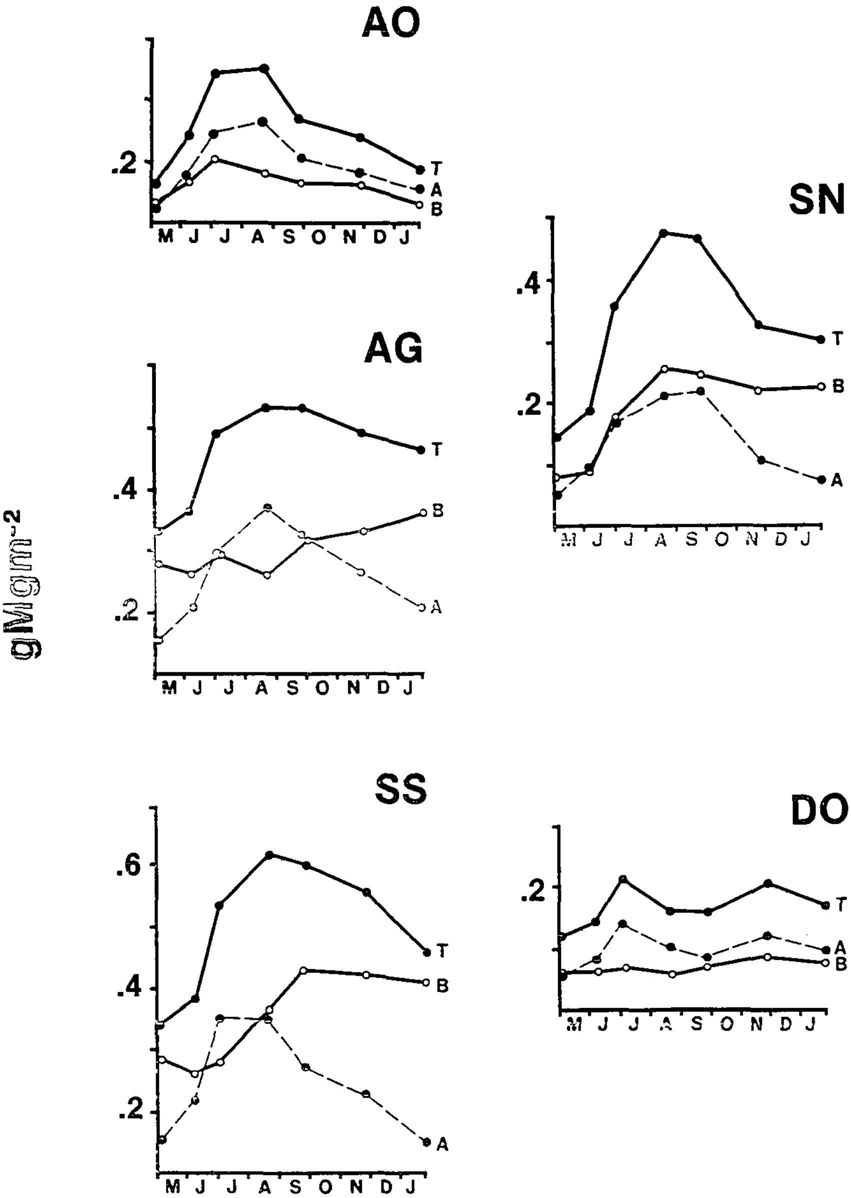

gKm^{-2}
AO
1.0
T
A
B
M J J A S O N D J F M
AG
3.0
2.0
1.0
T
B
A
M J J A S O N D J F M
SS
2.0
1.0
T
B
A
M J J A S O N D J F M
SN
2.0
1.0
T
B
A
M J J A S O N D J F M
DO
1.0
T
A
B
M J J A S O N D J F M


gKm-2
AO
1.0
T
A
B
M J J A S O N D J
SN
3.0
2.0
1.0
T
B
A
M J J A S O N D J
AG
3.0
2.0
1.0
T
A
B
M J J A S O N D J
SS
2.0
1.0
T
B
A
M J J A S O N D J
DO
1.0
T
A
B
M J J A S O N D J


% MAGNESIUM
AO
SN
AG
DO
SS
100
80
60
40
20
M J J A S O N D J F M


% MAGNESIUM
AO
SN
AG
DO
SS
100
80
60
40
20
M J J A S O N D J


AO
AG
SS
SN
DO
gMgm⁻²
.2
.4
.6
T
A
B
M J J A S O N D J F M


gMgm-2
AO
.2
T
A
B
M J J A S O N D J
SN
.4
.2
T
B
A
M J J A S O N D J
AG
.4
.2
T
B
A
M J J A S O N D J
SS
.6
.4
.2
T
B
A
M J J A S O N D J
DO
.2
T
A
B
M J J A S O N D J