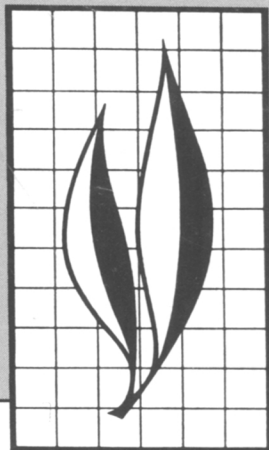


Hilgardia

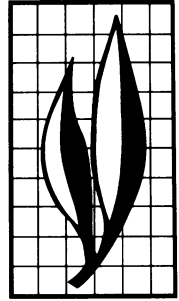
A JOURNAL OF AGRICULTURAL SCIENCE PUBLISHED BY
THE CALIFORNIA AGRICULTURAL EXPERIMENT STATION

Volume 57 • Number 1 • February 1989



Effects of Management on Plant Production and Nutrient Cycling on Two Annual Grassland Sites

**D. Michael Center, Charles E. Vaughn,
and Milton B. Jones**



ABSTRACT

Nutrient (nitrogen, phosphorus, sulfur, potassium, and calcium) dynamics and primary productivity were compared in adjacent sheep-grazed and ungrazed and adjacent subclover-seeded and unseeded annual grassland ecosystems. Above-ground and belowground total plant biomass and nutrient concentrations were measured monthly for two years, and nutrient content of various ecosystem components determined. Nutrient budgets were also developed to compare the effects of the grazing and seeding management practices.

Exclusion of sheep grazing had little effect on the system variables we measured. There were only slight differences between the grazed and ungrazed pastures in aboveground and belowground biomass production and nutrient uptake in either year. There were no substantive between-site differences in nutrient transfers. Subclover growth, accompanied with biennial P and S fertilization, resulted in very large increases in biomass production and much larger flows of all nutrients in both years. The largest nutrient fluxes on all sites were the transfers of mineralized nutrients through the soil available pool to live plants during the growing season. Most of this actively cycling nutrient supply was stored in standing dead material and litter, and was thus retained against leaching between growing seasons. The subsequent fate of these nutrients was then determined by new plant uptake and leaching demands, which showed much annual variation.

THE AUTHORS:

D. Michael Center was Postdoctoral Research Associate, Department of Agronomy and Range Science, University of California, Davis, at the time of this research.

Charles E. Vaughn (corresponding author) is Staff Research Associate, UC Hopland Field Station, 4070 University Road, Hopland, CA 95449.

Milton B. Jones is Agronomist, Department of Agronomy and Range Science, UC Davis, stationed at Hopland.

D. Michael Center, Charles E. Vaughn, and Milton B. Jones

Effects of Management on Plant Production and Nutrient Cycling on Two Annual Grassland Sites¹

INTRODUCTION

California annual grasslands form a vegetation type unique to North America (McNaughton 1968). These grasslands occupy an extensive area in the state's Central Valley, Sierra Nevada foothills, and Pacific Coast (Biswell 1956; Munz and Keck 1949) and represent a valuable range resource.

Plant production on California annual grasslands is almost always limited by N-deficient soils (Jones 1974). Deficiencies of P (Jones 1974) and S (Conrad 1950; Martin 1958) are also widespread. To ameliorate N deficiencies on grazed grasslands, range managers commonly apply N fertilizer or introduce annual legumes—usually subclover (*Trifolium subterraneum*) or rose clover (*Trifolium hirtum*). Fertilizers containing P and/or S often are applied in combination with N or are applied to areas where annual legumes have been introduced. The effects of these improvements on plant production and composition are well documented. Jones (1974) reviewed much of the literature related to fertilization of annual grasslands in California.

Although considerable research has been done on nutrient cycling in perennial range and pasture ecosystems (Charley 1977; Frissel 1977; Gillingham, Syers, and Gregg 1980; Sharpley 1985; Whitehead 1970; Woodmansee et al. 1978), very little work has dealt with the cycling of nutrients in annual grasslands. Jones and Woodmansee (1979) reviewed N, P, and S cycling in annual grasslands. Woodmansee and Duncan (1980) presented N and P dynamics and budgets for 3 years at the San Joaquin Experimental Range in the southern Sierra Nevada foothills, and Katznelson (1977) developed a generalized P budget for the annual grasslands of Israel.

Factors controlling nutrient cycling in annual grassland are generally the same as those in ecosystems dominated by perennial plants. However, vegetation in annual grasslands does not internally store and recycle nutrients from one season to the next; larger amounts of nutrients thus enter and leave the vegetation seasonally than in perennial systems (Jones and Woodmansee 1979).

There is little reported information dealing explicitly with the effects of specific management practices on nutrient dynamics and budgets in agricultural ecosystems (Frissel 1977; Stinner, Odom, and Crossley 1983). We know of no studies of this sort on annual grassland.

In this paper, we report on the results of a 2-year study documenting nutrient dynamics and changes in nutrient budgets resulting from two management practices: the cessation of grazing and the introduction of subclover with periodic P and S fertilization. Budgets were developed for N, P, S, Ca, and K.

¹Approved for publication on August 15, 1988

METHODS

The Study Areas

We conducted the study at the University of California Hopland Field Station in north-coastal California 160 km north of San Francisco. The region has a vegetation complex of annual grassland-oak savanna on upland soils derived from marine sediments; the climate is Mediterranean.

The study was performed in two areas:

Area I, selected to document nutrient dynamics under grazing by sheep, was divided into two adjacent sites—grazed and ungrazed—by the construction of a fence in 1957. Sheep were excluded from one side of the fence. Moderate grazing was allowed on the other side; annual grazing utilization averaged about 40% of herbage peak standing crop from 1958 to 1980 (A.H. Murphy unpublished). The ungrazed site had not been grazed by domestic livestock for 23 years when this study began in 1980. Vegetation on both area I sites was dominated by annual grasses, primarily slender oat (*Avena barbata*) and soft chess (*Bromus mollis*). However, a population of perennial native bunchgrasses, primarily coastrange melic (*Melica imperfecta*) and foxtail barley (*Hordeum jubatum*), had developed on the ungrazed site.

Area II was selected to measure changes in ecosystem nutrient level processes caused by seeding with subclover and periodic fertilization with P and S, a common range improvement practice in this region. This area was also divided into two adjacent sites—seeded and unseeded—separated by a fence. One side was seeded with subclover and fertilized with superphosphate and soil S in 1972; biennial applications of P at about 21 kilograms per hectare (kg/ha) and S at 46 kg/ha continued until 1978. The unseeded

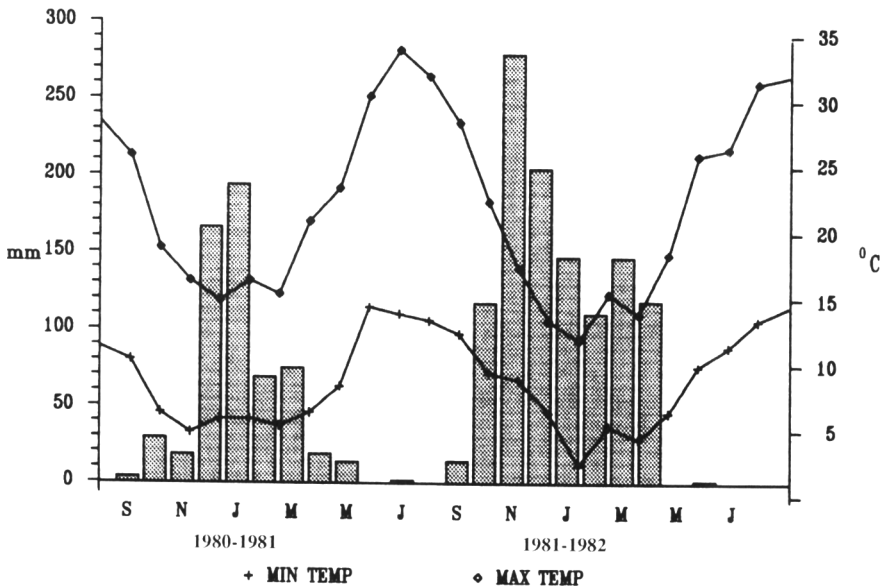


Fig. 1. Monthly rainfall (vertical bars) and mean minimum and maximum temperatures near the study sites at the UC Hopland Field Station for the 1980-81 and 1981-82 growing seasons.

site remained unimproved. Both sites had been grazed moderately by domestic livestock (mostly sheep) since the 1880s. Vegetation on the unseeded site was dominated by annual grasses, primarily soft chess and Mediterranean barley (*Hordeum geniculatum*), but also had a large component of filaree (*Erodium* spp.), a locally common annual forb. The seeded site also had a large component of filaree and annual grasses, mainly soft chess and foxtail fescue (*Vulpia megalura*), but was dominated by subclover. More detailed site descriptions are contained in Vaughn and Murphy (1982) and Vaughn, Center, and Jones (1986). Monthly mean temperatures and rainfall for the two years of the study are shown in figure 1.

The study was conducted during two consecutive annual growth cycles (September through August) from September 1980 through August 1982. We will refer to the annual cycles as the 1981 and 1982 growing seasons.

Sampling Methods

All sites were sufficiently distant from trees to exclude their influence. Four blocks were located at each site. The blocks within each area were selected for similarity in soil, slope, and aspect and were all within 100 m of each other. Each block was subdivided into 12 plots (1.5 m²). We relocated the blocks after the first 12 months of the study using the same selection criteria. Sheep were excluded from all blocks by perimeter fencing.

One plot in each block was randomly sampled each month. Live and dead herbage were clipped to the ground and collected with plant litter by hand in four 30-cm² quadrats in each plot. Material from the four quadrats in each plot was composited to obtain one sample per plot. Two 7.5-cm-diameter by 15-cm-deep soil cores were also taken from each plot, beginning in December 1980. Soil cores were composited, double-plastic-bagged, and frozen for later separation of roots. Soil sampling methods are described in Vaughn, Center, and Jones (1986).

Herbage samples were hand-separated into live and dead material. Dead material was composited with litter. Beginning in February 1981, live herbage was further separated into grasses, legumes, and forbs other than legumes. Roots were separated from soil by hand-washing, flotation, and screening (McKell, Wilson, and Jones 1961). Herbage and root samples were oven-dried to a constant weight at 60°C, weighed, and ground to pass through a 40-mesh screen. Weighed subsamples of the roots were then ashed (6 hr at 550°C), and residue mass determined. Data on root biomass are reported as ash-free values to correct for contamination by mineral soil.

Nutrient Analyses

Nitrogen in plant material was determined in Kjeldahl digests, and P, S, Ca, and K in nitric-perchloric acid digests. Sulfur was determined turbidimetrically (Tabatabai and Bremner 1970), and P was determined by the molybdovanadate reaction (Kitson and Mellow 1944). Calcium was determined by atomic absorption spectrophotometry, and K by flame emission (Varian Techtron 1972). Available soil nutrient analyses have been described previously (Vaughn, Center, and Jones 1986). In addition, we analyzed for soil total N (Bremner and Mulvaney 1982) and S (Arkley 1961), organic P (Tiessen, Stewart, and Bettany 1982), and nonexchangeable, acid-soluble or "reserve" Ca and K (Mokwunye and Melsted 1972).

Values for atmospheric wet and dry nutrient deposition were obtained from a wet/dry precipitation sampling station of the National Atmospheric Deposition Program (NADP) approximately 1 km from each of the study areas. Chemical analysis of precipitation was conducted by Central Analytical Lab in Champaign, Illinois.

As is the case with many long-term ecological studies, the nature and the scale of the manipulations in this study precluded interspersing of the treatments. Therefore, treatments are, in the strictest sense, unreplicated. The blocks in this study are not replicates, but subsamples used to obtain an enhanced estimate of within-site variability. To avoid erroneous application (what Hurlbert [1984] called "pseudoreplication") we did not use statistical inference to test for differences between sites.

RESULTS AND DISCUSSION

Area I

Aboveground live biomass dynamics

Seasonal growth patterns in area I were similar on both sites (fig. 2) and were like those previously described for annual grasslands (George et al. 1985; Pitt and Heady 1978). Differences in seasonal biomass dynamics between the 1981 and 1982 seasons reflect differences in temperature and rainfall patterns in the two years (fig. 1). In 1980, germination occurred in late October, and the first significant growth was measured in the November sample. Growth was slow until late February then very rapid until late March to mid April. In 1981, rains came earlier, and early-season minimum temperatures were higher than in 1980. As a result, significant growth was measured one sampling period earlier (October) and fall growth was more rapid in the 1982 than in the 1981 growing season. Total rainfall and spring rainfall were also higher in 1982. This increased total production and resulted in a season peak one sampling period later in 1982 (May as compared with April). These differences may also reflect the higher soil inorganic N levels at both sites during the second growing season (Vaughn, Center, and Jones 1986), which could well have stimulated more herbage production.

Grasses were dominant on both sites in both years, accounting for a seasonal average of about 85% of the live biomass. The proportion of forbs was also quite similar on both the grazed and ungrazed sites. However, there were more forbs on both sites during the second growing season, representing an average of about 15% of the live herbage as compared with 10% the first year. Legumes made up only a small proportion (1% to 10%) of the monthly live biomass measurements on either site in 1981, and were virtually absent from both sites in 1982.

Estimates of aboveground live annual net production (ANP) are useful in comparing ecosystems. Peak standing crop (PSC) is customarily used for estimating ANP in annual grassland (McNaughton 1968). However, because PSC has been shown to underestimate ANP (Kennedy 1972; Odum 1960; Singh, Lauenroth, and Steinhorst 1975), we calculated ANP in this study by summing all positive monthly increments in live herbage biomass and concomitant positive increments in the standing dead material and litter (standing dead/litter). Positive increments in standing dead/litter concomitant with positive increments in live biomass are included to account for mortality during sampling intervals (Singh, Lauenroth, and Steinhorst 1975). This is still to be considered a minimal estimate, because if increases in the live biomass and the standing dead/litter occurred concomitantly with decomposition of the litter fraction, the latter would not be accounted for in the calculation. We also could not account for losses due to utilization by small herbivores.

Annual net production of aboveground biomass was 4,180 and 6,350 kg/ha on the grazed site and 4,670 and 5,360 kg/ha on the ungrazed site during the 1981 and 1982 growing seasons, respectively. Maximum growth rates of the aboveground biomass on the grazed site was 54 kilograms per hectare per day (kg/ha/day) in 1981 and 28 kg/ha/day in 1982. On the ungrazed site, values were 33 and 23 kg/ha/day for 1981

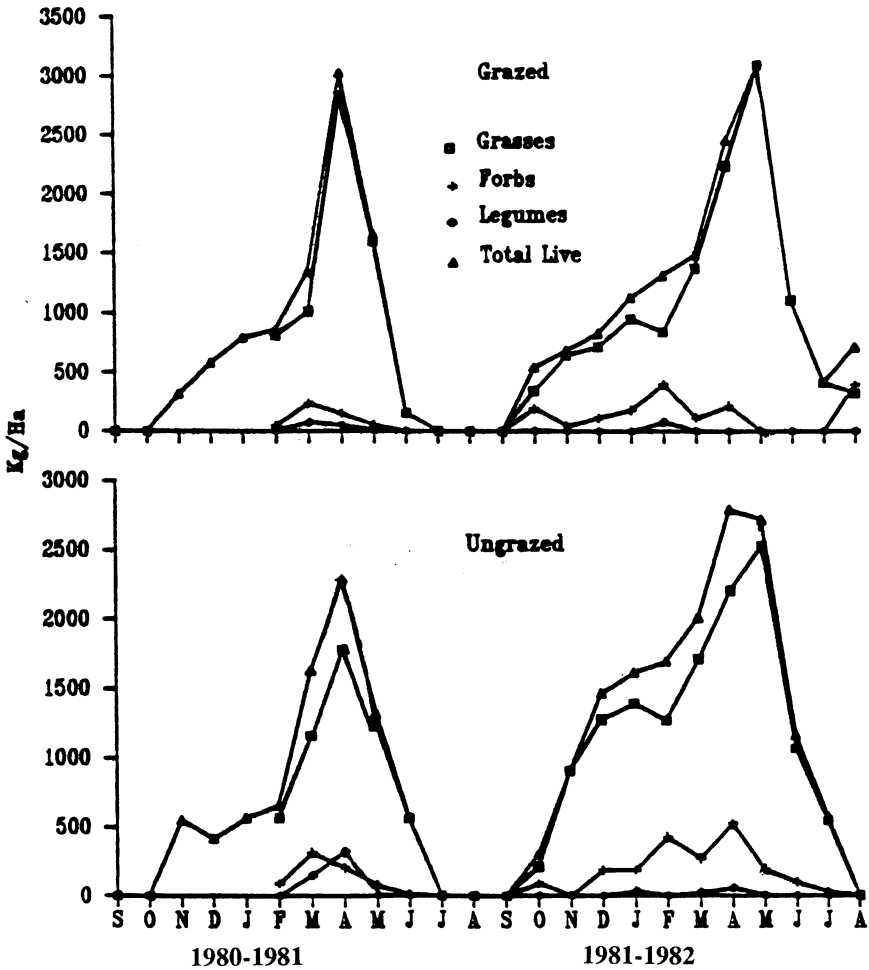


Fig. 2. Aboveground herbage live biomass of grasses, forbs, and legumes on adjacent grazed and ungrazed sites during the 1980-81 and 1981-82 growing seasons.

and 1982, respectively. Growth rates were highest during April of both years on both sites.

Standing dead/litter biomass dynamics

Patterns were basically similar for both sites in both years of the study (fig. 3). Litter declined as moisture became available, probably reflecting decomposition by soil microorganisms. This decline continued until the inputs to standing dead material from live plants exceeded litter decomposition in the late winter and early spring. Even though decomposition was rapid, a net accumulation of standing dead/litter began. Conditions for decomposition became less favorable as soil moisture decreased later in the spring. As live plants died and shattered, inputs of standing dead increased, resulting in increases in standing dead/litter from late spring (April 1981 and March 1982) until

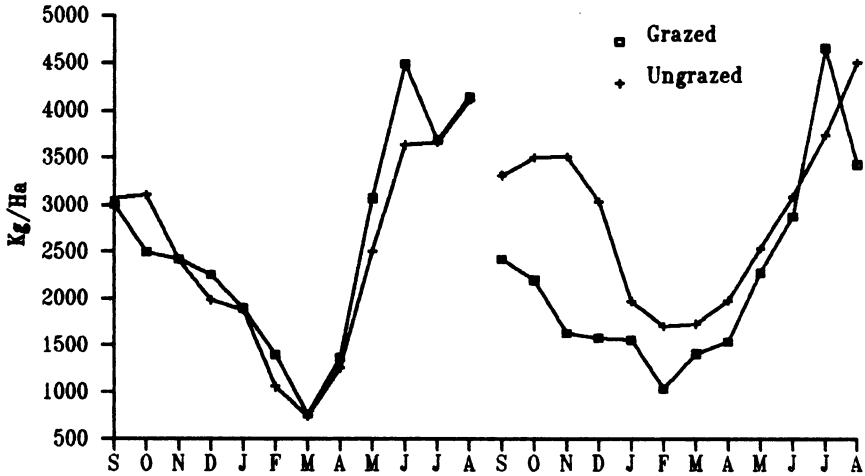


Fig. 3. Aboveground herbage standing dead/litter biomass on adjacent grazed and ungrazed sites, 1980-81 and 1981-82 growing seasons.

nearly all vegetation was dead in early summer. Presumably, biological decomposition is very low during the dry summer months in Mediterranean ecosystems (Saville 1977; Schlesinger and Hasey 1981), and any decreases in standing dead/litter during the dry season were due to shattering, utilization by small herbivores, or loss during sampling.

Grazing was heavier before enclosure of these sites in 1981 than it was in 1980 (A.H. Murphy unpublished). This probably accounted for the larger difference in standing dead/litter between grazed and ungrazed sites at the beginning of the second year. There were very small differences in standing dead/litter at the end of either growing season between sites protected from grazing for 23 or 24 years and sites protected for 1 year. This result indicates a rapid stabilization in the amount of standing dead/litter after the removal of grazing.

Belowground biomass dynamics

Belowground biomass was not sampled until December 1980. Sampling variability was high in both years. Standard deviations on the grazed site averaged 37% and ranged from 8% to 64% of the mean, and on the ungrazed site averaged 28% and ranged from 4% to 70%.

Seasonal patterns of belowground biomass (15-cm depth) differed markedly between growing seasons at both sites (fig. 4). Belowground biomass changed relatively little during the portion of the 1981 season sampled, although we measured positive growth on both sites. In the 1982 season, belowground biomass remained low until November and December, when it began to increase and continued to accumulate until late summer.

These patterns of belowground-biomass accumulation differ from those reported by Saville (1977) for an annual grassland site near our study site. Saville reported an increase in belowground biomass from a minimum value at the start of the growing season to a maximum in April, then a decline through the summer. This difference may partly be due to the sampling variability we encountered, but it probably also reflects the longer growing season and the higher proportion of late-season annual grasses and summer annual forbs in our 1982 samples (fig. 2).

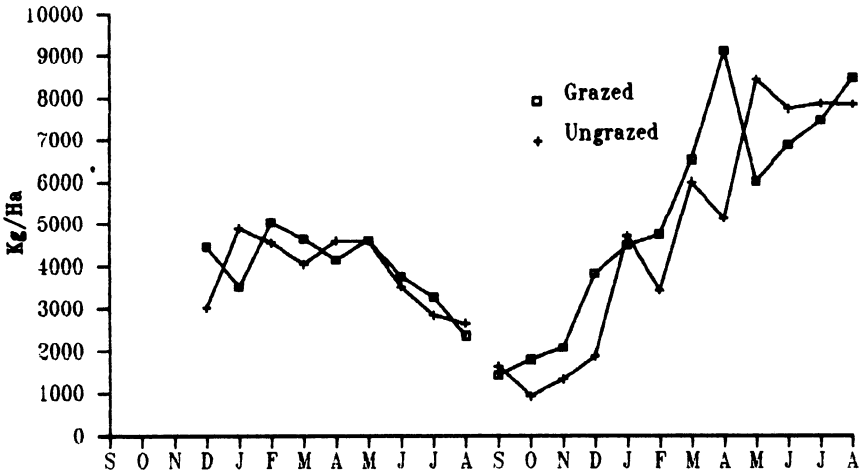


Fig. 4. Belowground plant biomass on adjacent grazed and ungrazed sites, 1980-81 and 1981-82 growing seasons.

We estimated belowground ANP by summing all positive monthly increments in root biomass, assuming that the positive increments would come from live root growth. However, we did not sample belowground biomass in the first three months of the 1981 growing season (fig. 4). Using data from Saville (1977), we assumed that 20% of the root mass measured that December was live roots, and we estimated this fraction to be the positive increment in live root growth from September to December when measuring 1981 belowground ANP. We consider this to be a minimal estimate, because root mortality and any subsequent positive increments between sampling intervals would not be included; early-season plant death can be significant on annual pastures (Pendleton et al. 1983).

Root ANP was 2,890 and 10,090 kg/ha on the grazed site and 3,050 and 9,740 kg/ha on the ungrazed site for the 1981 and 1982 growing seasons, respectively. While these values appear high, particularly for the second year, we are aware of no root ANP data from annual grassland sites against which to compare the results. Previous studies from Hopland Field Station, however, have reported live, ash-free, root mass at PSC ranging from 2,880 to 4,900 kg/ha on annual and perennial grassland sites, respectively (Saville 1977), to a corrected value of about 3,700 kg/ha on another annual grassland site (McKell, Jones, and Perrier 1962). Assuming that 60% of the belowground biomass at PSC was live roots (Saville 1977), then comparable live-root PSC values in our study were 2,490 and 3,600 kg/ha on the grazed site and 2,760 and 3,080 kg/ha on the ungrazed site for the 1981 and 1982 growing seasons, respectively. The similarity of these values suggests that our belowground biomass measurements were valid.

That portion of total ANP (root ANP plus live top ANP) accounted for by roots varied considerably between years. Root:shoot ANP ratios were 0.7 and 1.6 on the grazed site and 0.7 and 1.8 on the ungrazed site in the 1981 and 1982 growing seasons, respectively. This large between-year variation reflects several factors. As mentioned, the first-year root ANP values must be considered minimal estimates. The large component of late-season annual grasses and summer annual forbs (fig. 2) in the second year no doubt contributed to the higher ratios as well. Probably most importantly, the second growing season was longer, wetter, and generally milder during both the fall and spring. These conditions favor both dead root decomposition and high rates of root growth (Saville 1977). They certainly resulted in more dynamic turnovers in be-

lowground biomass and larger temporal fluctuations in root accumulation, and were reflected in the much larger net production measurements. Despite the large differences, the ratios are well within the range of values reported by Savelle (1977) in his comprehensive study. He reported that seasonal root:shoot ratios, calculated as accumulated net production, varied between 0.6 and 1.9.

Mineral concentration dynamics in live herbage

Seasonal patterns of live herbage concentrations of N, P, K, and S were generally similar within each species group and year on both sites (fig. 5). Highest concentrations of these nutrients occurred at the beginning of the season, shortly after germination when biomass was low. These levels were followed by general decline to a minimum concentration just before senescence and death. This decline in concentration was probably due to a diluting of nutrients in the rapidly growing plants and does not reflect a decrease in the absolute amount of nutrients in the live plants (Freney, Spencer, and Jones 1978). The slight increase in late-season concentrations of most nutrients on the grazed site in 1982 was probably due to a shift in the species composition of the grass group toward late-season annual grasses. Because of the later rains in 1982, prairie threeawn (*Aristida oligantha*) and medusahead (*Taeniatherum asperum*) were more abundant that year than in 1981.

Seasonal patterns of N, P, S, and K concentrations in forbs and grasses were generally similar. However, the levels in forbs were lower early in the season and then increased very rapidly until they were equivalent to the concentrations in grasses. Woodmansee and Duncan (1980) reported similar later season peaks in P concentrations in filaree. The concentrations of N, P, S, and K declined in both forbs and grasses as they matured and reached senescence. Death was one to three sampling dates earlier for forbs than for the grasses. Late-season increases in concentrations of these nutrients in forbs in 1982 were due to the presence of the forb turkey mullein (*Eremocarpus setigerus*) in the samples.

Amounts of legumes sufficient for chemical analysis were harvested infrequently on these sites. Therefore, data are insufficient to discuss seasonal patterns of mineral concentrations in legumes or to discern differences between sites or years. As would be expected, when they were present, concentrations of N in the legumes were usually higher than in the grasses and forbs for the corresponding site and sampling date. Calcium concentrations also were usually higher in legumes than in forbs or grasses, while P, S, and K concentrations were generally similar. These data agree well with seasonal patterns of concentrations of N and P reported by Woodmansee and Duncan (1980) and of N, P, and S reported by Jones (1974).

Dynamics of Ca concentrations differed markedly from those of the other nutrients studied on both sites (fig. 5). In grasses, concentrations were highest just after germination, when biomass was low, but remained constant or declined only slightly as biomass increased. These patterns were similar on both sites. However, for reasons that are not clear, Ca concentration dynamics in forbs were different between sites. On the ungrazed site, they were at a minimum early in the season, increased until PSC, and then declined until plant death. On the grazed site, Ca concentrations were more irregular, declining from post-germination values then increasing to a maximum near PSC. These data suggest that Ca was not diluted in plant tops as biomass increased as were the other nutrients studied. Biddulph (1959) observed that in most plant species, once Ca is deposited, little can be remobilized to other plant parts. Loneragan and Snowball (1969) also found that several annual rangeland species were luxury consumers of Ca. High concentrations of Ca in older leaves may then account for the seasonal pattern of Ca dynamics observed in the present study.

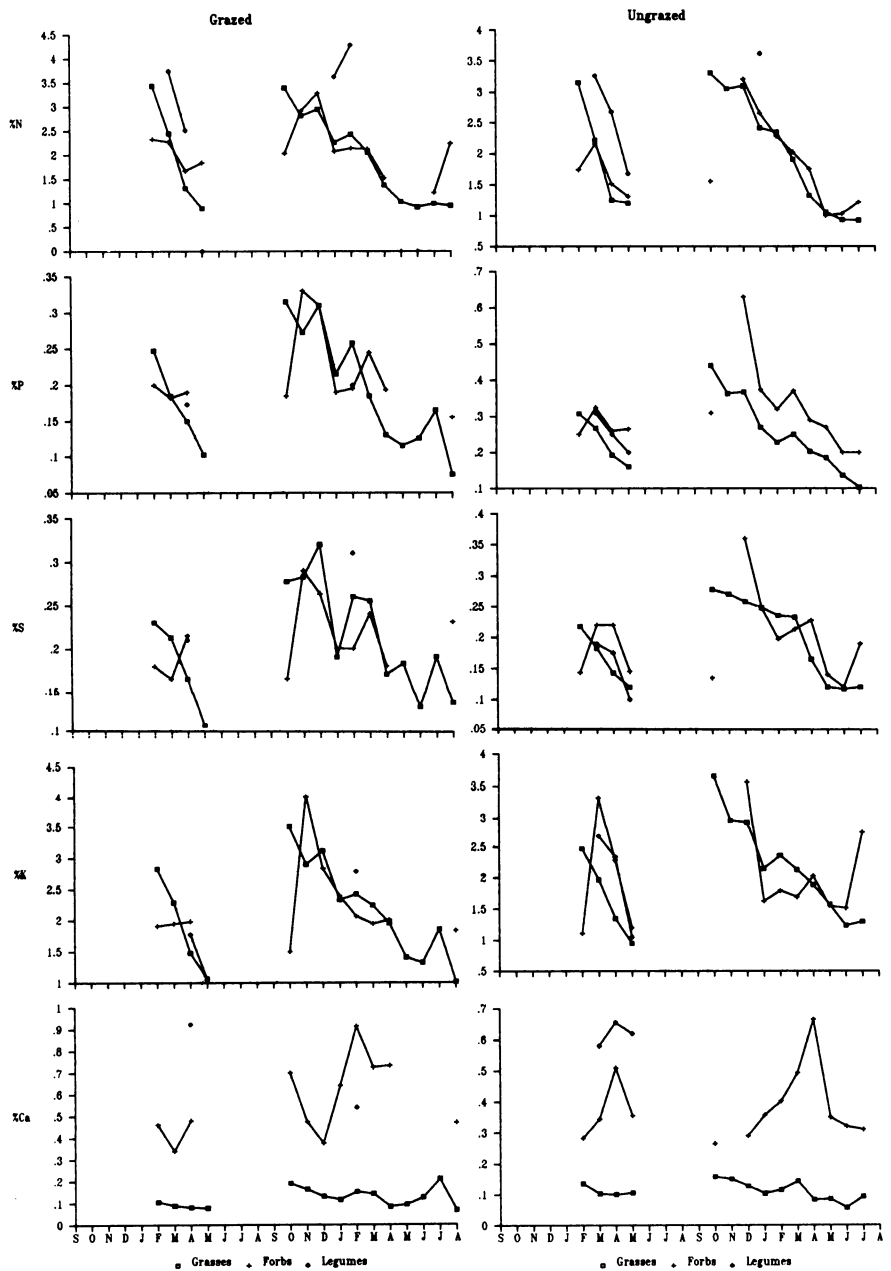


Fig. 5. Concentrations of N, P, S, K, and Ca in aboveground herbage live biomass of grasses, forbs, and legumes on adjacent grazed and ungrazed sites, 1980-81 and 1981-82 growing seasons.

Mineral concentration dynamics in standing dead/litter

The concentrations of N, P, and S in standing dead/litter fluctuated similarly on both sites in both years (fig. 6). These three nutrients decreased slightly after the first rainfall, then increased in mid-winter to late winter, and declined generally through the summer. This pattern agrees with those of N and P fluctuation observed by Woodmansee and Duncan (1980). They reported an increase in microbial activity during late winter due to warmer temperatures. They postulated that this increased activity could cause an apparent rise in N and P concentrations in the litter due to the immobilization of N and P mineralized from the litter substrate.

Another factor contributing to the increases in N, P, and S concentrations is that young plant parts or whole plants high in these nutrients were beginning to die more rapidly because of crowding and shading (Brougham 1958; Donald 1963) and aging (Robson 1973). This process would contribute material high in these nutrients to the standing dead part of the standing dead/litter component. Our data suggest this mechanism was probably more important than microbial activity in this study. Increases in concentration of N, P, and S began anywhere from November to January in both years on both sites. These increases appeared to be independent of temperature, because temperatures were low in 1981 from December until late February and again from December through early March of 1982 (fig. 1). Lower temperatures would not be expected to stimulate microbial activity. The late-season concentration declines probably reflect some decomposition, but they were largely due to the very low nutrient levels in the dying herbage (fig. 5) that was being transferred to litter.

Potassium concentrations in litter began to decline rapidly with the first rains to minimum levels in early winter of both years at both sites. Concentrations remained low until spring, when they began to increase again. There were only small differences in K concentrations in litter between sites at any sampling date in either year. Potassium did not decrease in late summer as N, P, and S did, probably because loss of K from litter appears to be largely due to leaching. This has been demonstrated in other ecosystems (Cromack and Monk 1975; Van Hook 1971).

Calcium concentrations in litter varied the least seasonally of all elements studied. Except in the grazed site in 1982, concentrations of Ca changed very little through the season. The tendency of Ca to not leach readily and to remain in litter (Stinner et al. 1984) and the fairly constant level in live plant tissue through the season combined to create seasonally stable concentrations of the element in litter. The reasons for the decreases in Ca concentrations during December and January on the grazed site in the second year are unclear. They resulted primarily from declines in only two blocks, and thus may largely reflect sampling variability.

Mineral concentration dynamics belowground

Both concentrations and seasonal variation in concentrations of all nutrients studied in the belowground plant biomass were small compared with those in aboveground vegetation (fig. 7). Using data from Savelle (1977), we estimated belowground biomass to range from a low of 40% overall dead roots in April to 100% dead roots in October. This high percentage of dead material would tend to dampen changes in overall concentration due to changes in concentration of minerals in the live root component.

Concentrations of N, P, and S in belowground biomass were between levels measured in aboveground live material and litter, while concentrations of Ca were slightly higher belowground. Concentrations of K were much lower in belowground biomass than in either aboveground component.

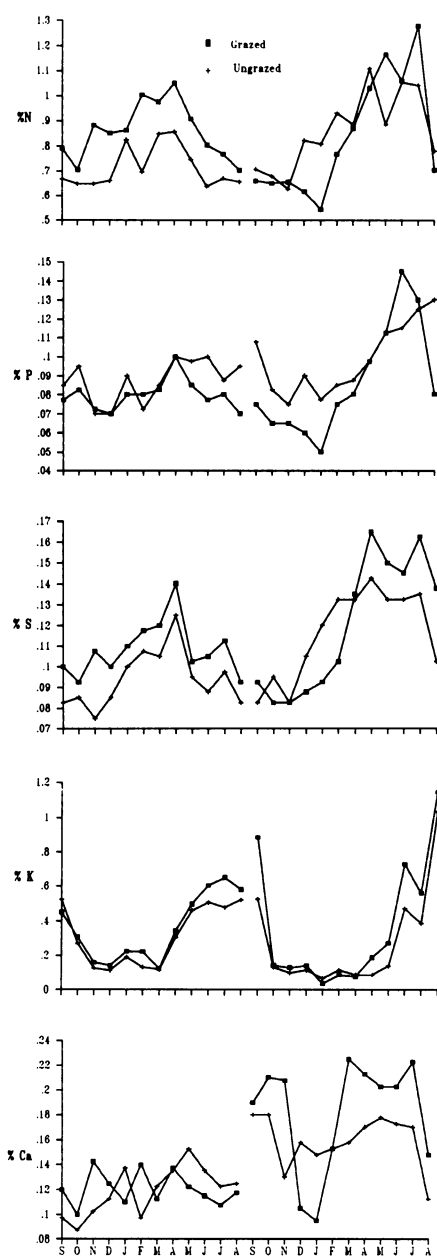


Fig. 6. Concentrations of N, P, S, K, and Ca in aboveground herbage standing dead/litter biomass on adjacent grazed and ungrazed sites, 1980-81 and 1981-82 growing seasons.

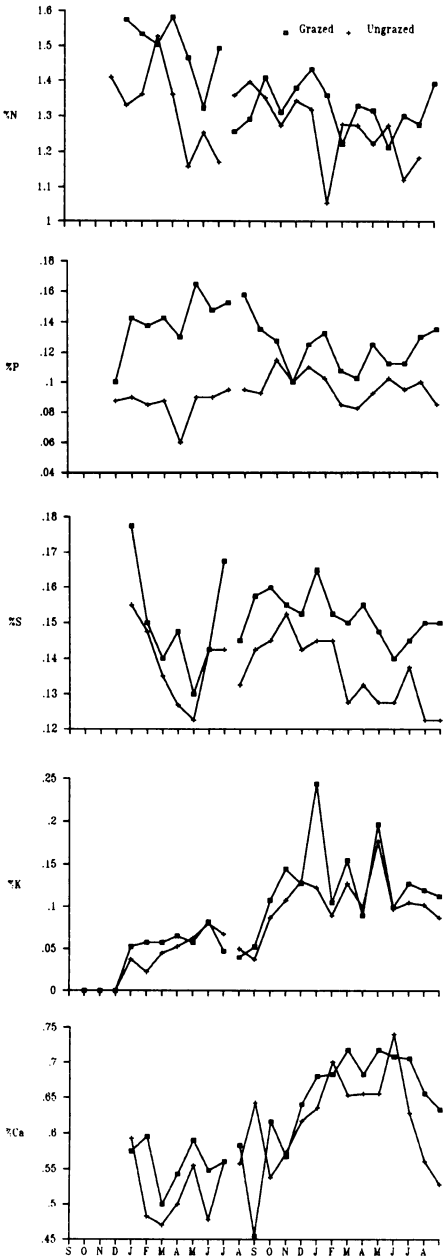


Fig. 7. Concentrations of N, P, S, K, and Ca in belowground plant biomass on adjacent grazed and ungrazed sites, 1980-81 and 1981-82 growing seasons.

Aboveground live herbage nutrient uptake

Herbage nutrient uptake patterns were all quite similar (fig. 8) and closely followed seasonal aboveground live biomass dynamics (fig. 2). While the high levels observed in early-season nutrient concentrations generally declined through the growing season, the standing crop of nutrients continued to increase as biomass did. The rapid late-season declines in herbage nutrient content reflected seed dispersal and subsequent senescence of the annual vegetation.

Most of the N, P, K, and S accumulation on both sites was by grasses, reflecting the larger grass component in the live herbage. However, when compared with the other nutrients, a much higher proportion of aboveground Ca accumulated in forbs and legumes. This difference was due to the higher concentration of Ca in the forbs and legumes than in grasses (fig. 5), and was well illustrated at peak standing crop in 1981. Forbs and legumes accounted for only 6% and 17% of the live herbage biomass at that date on the grazed and ungrazed sites, respectively. However, they represented 34% and 53% of the live-herbage Ca content of the respective sites.

The live herbage uptake of individual nutrients was generally similar between sites. An exception was the larger standing crop of P in forbs and grasses on the ungrazed site in the second year. This finding probably reflects the higher levels of available soil P on the ungrazed than the grazed site (Vaughn, Center, and Jones 1986). There was also a large increase in nutrient uptake by forbs on the grazed site late in the second year. This increase no doubt reflects the presence of summer annual forbs.

Nutrient uptake by individual herbage groups was also quite similar between sites. In the first year, however, the standing crop of all nutrients in forbs and legumes was higher on the ungrazed site and probably reflected the higher biomass of those herbage groups (fig. 2).

Nutrient budgets

Construction. We based most of the information for the nutrient budgets on parameters directly measured during this study. If data were lacking, estimates were obtained first from studies conducted on similar sites at Hopland Field Station and then from the literature. If no reasonable estimate was available, we either estimated the missing parameter values by mass balance or assigned no value.

Annual net uptake of a given nutrient by live tops was measured by summing the positive monthly uptake increments for each species group plus concomitant positive uptake increments in litter. A similar procedure has been used in crops and old field vegetation by Stinner, Odum, and Crossley (1983), and in a forested ecosystem by Whittaker et al. (1979). We measured annual net nutrient uptake for live roots as for live tops, disregarding litter increments, on the assumption that positive increments would result only from live root uptake. Much of the nutrient uptake by annual plants is accrued in undecomposed litter and dead roots at the end of an annual growth cycle. We measured these annual net changes in nutrient content for litter and dead roots as that difference in nutrient standing crop between the end (August) and beginning (September) of each growing season. We estimated the missing September root mass for the first growing season to be 80% of the December measurement. This estimate was based on the assumption that all roots were dead in September, that all increases in belowground biomass in the first 3 months came from live roots, and that 20% of the December root mass was live (Saville 1977).

Since all aboveground vegetation in the annual grassland ecosystem dies each year, all nutrients flowing through aboveground plant parts (annual net uptake) were assumed to be transferred from the live roots and to the standing dead/litter component

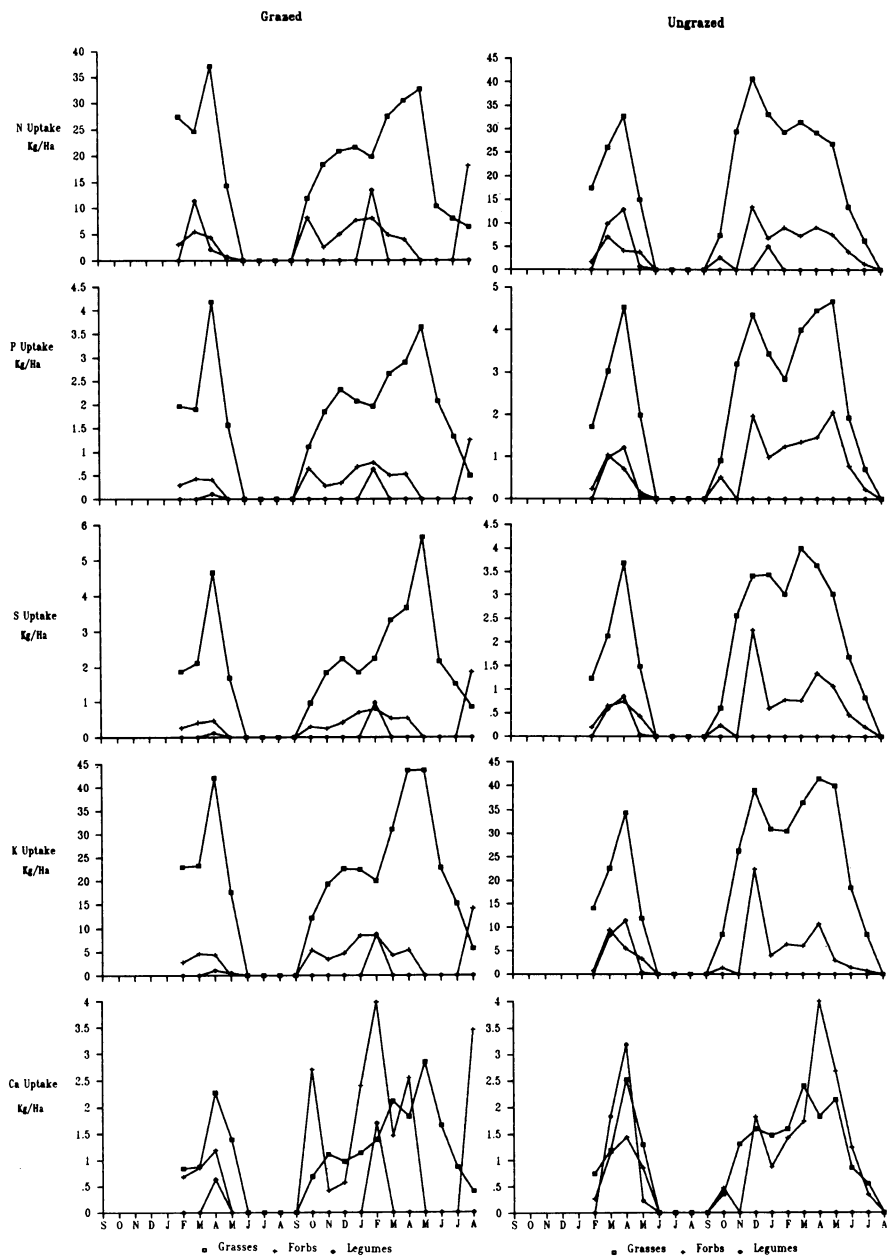


Fig. 8. Uptake of N, P, S, K, and Ca in aboveground herbage live biomass of grasses, forbs, and legumes on adjacent grazed and ungrazed sites, 1980-81 and 1981-82 growing seasons.

each year. Nutrient flows from litter to soil microflora and fauna (decomposers) were estimated by subtracting the annual net change in standing crop of each nutrient in litter from the flow of nutrients into litter. Losses of plant material due to small herbivores were assumed to be small and were not considered here. The transfer of nutrients from live to dead roots was measured as the annual net root uptake, again the sum of all positive monthly uptake increments for that growing season. We estimated flows from dead roots to soil decomposers as the difference between the annual net root uptake and the annual net change measured in dead root nutrient standing crop. All flows from litter and dead roots to the soil decomposer component were assumed to be transferred to the soil available pool. Nutrient transfers from the soil available pool to live roots were estimated as the sum of the live top and live root annual net uptake amounts. For the N budgets, the contribution of dinitrogen fixation to live roots, if any, was subtracted from this total.

We used data from studies at Hopland (Phillips et al. 1983; Shock, Williams, Jones, Center, and Phillips 1984 and unpublished) to calculate the ratio of root N concentration to shoot N concentration and the percentage of N derived from N_2 fixation in legumes. A root:shoot N concentration ratio of 1.33 was calculated. From this, we estimated that 81% of legume shoot N and 64% of legume root N were derived from N_2 fixation. It was assumed that no N was transferred from living legume roots to the soil and that all transfer was from dead legume roots (Simpson 1965 and 1976).

Volatilization of ammonia from the soil was not measured. However, net losses from the system due to volatilization were assumed to be small in this study, because Denmead et al. (1976) found that the plant canopy recaptured a large part of the volatilized ammonia in similar ungrazed grasslands. We also assumed that denitrification was small, because N losses from denitrification on annual ryegrass plots in Oregon were less than 1 kg/ha/yr (Myrold 1988). Atmospheric nutrient deposition values were calculated from data provided by the NADP.

We did not measure leaching and runoff on the study sites. Estimates of N and S leaching were obtained from lysimeter studies done at Hopland (Jones, Delwiche, and Williams 1977; Jones, Martin, and Williams 1968; Jones, Street, and Williams 1974; and Shock, Jones, Williams, and Center 1984). Because of the disturbed nature of the soil profile in lysimeters and the effects of soil disturbance in enhancing nutrient transformations (Reisenauer 1975), we consider these estimates to be maximal values for leaching. Losses of P due to leaching and runoff were assumed to be zero (Jones and Woodmansee 1979). We have no reliable estimates for leaching and runoff losses of K and Ca from annual grassland ecosystems. However, stream-water chemistry from a Hopland Field Station watershed near our study sites indicated that, while K output was probably negligible, the system losses of Ca may have been significant (R.H. Burgy unpublished).

We partitioned belowground biomass between live and dead roots using data from research conducted at Hopland near our study site (Savelle 1977). Our analytical methods for determining organic N, P, and S were not sufficiently sensitive to measure annual nutrient flows between decomposers and soil organic matter. We therefore estimated these transfers by mass balance. Levels of available nutrients in the soil were measured monthly during this study and have been reported elsewhere (Vaughn, Center, and Jones 1986). All soil values presented in the budgets were measured at live herbage PSC, corrected for bulk density, and represent amounts in the upper 15 cm of soil depth. Available soil P, or the amount of P in solution, was measured with a water extract (Bingham 1949). Labile inorganic P was estimated using the relationship: $0.55 (\text{Bray P}) + 6.1 = \text{labile inorganic P}$. This relationship has been reported for grassland soils by Sharpley et al. (1984). We assumed labile inorganic P to be in equilibrium with available soil P. We assumed similar equilibria to exist between soil cation "reserve" and exchangeable, or readily available, fractions.

For economy, we have illustrated only the first-year budgets on the grazed site (fig. 9 to 13). The remaining budgets are summarized for area I in tables 1 to 5, and for area II in tables 6 to 10. Boxes in the budget diagrams represent internal ecosystem nutrient budget components. "Clouds" indicate external inputs or outputs. Numbers in the boxes represent values (kg/ha) at live aboveground biomass PSC and are given only as a point-in-time reference. Biomass PSC did not necessarily coincide with PSC of the various nutrients. Circled numbers in the litter and dead root component boxes are the annual net changes (+/-) in nutrient standing crop. Arrows represent annual nutrient transfers between components (kg/ha/yr).

Nitrogen budget. The amounts of N in various system components at PSC, and the amount of annual transfer between components, are summarized in table 1. Figure 9 shows the N budget for the first growing season on the grazed site. Although budgets were generally similar between sites in each year, they were substantially different between years.

In 1981, N_2 fixed by legumes accounted for 13% of annual N transfer to live roots on both area I sites. Most of the remainder of annual net N uptake had to have come from mineralization processes, because atmospheric inputs were very small in both years (1 kg/ha). Very little legume N was measured on either site during the second growing season, so virtually all of the plant-available N in both systems came from mineralization.

Table 1. NITROGEN BUDGETS FOR 1981 AND 1982 GROWING SEASONS AT ADJACENT GRAZED AND UNGRAZED ANNUAL GRASSLAND SITES, HOPLAND FIELD STATION

Item	1981		1982	
	Grazed	Ungrazed	Grazed	Ungrazed
<i>Distribution*</i>	<i>kg/ha</i>			
Live tops:				
Grasses	37	33	33	29
Forbs	3	3	0	9
Legumes	1	9	0	0
Litter†	15 (+4)	11 (+9)	26 (+9)	24 (+11)
Live roots	37	37	44	39
Dead roots‡	24 (-25)	25 (+2)	29 (+97)	26 (+70)
Total plant biomass	117	118	132	127
Soil organic	4,500	4,070	4,500	4,070
Soil available	44	30	20	23
<i>Transfers</i>	<i>kg/ha/y</i>			
Live tops to litter	57	53	80	52
Litter to decomposers	53	47	71	41
Live roots to				
dead roots	36	34	147	135
Dead roots to				
decomposers	61	32	50	65
Decomposers to				
available	114	79	121	106
Atmosphere to available	1	1	1	1
Available to live roots	81	76	224	186
N_2 to live roots	12	11	3	1
Available to leaching	20	20	25	25

* Nitrogen distribution (kg/ha) is at herbage peak standing crop.

† Numbers in parentheses are annual net changes (+/-) in N standing crop in litter and dead roots.

‡ Nitrogen transfers (kg/ha/yr) are annual flows.

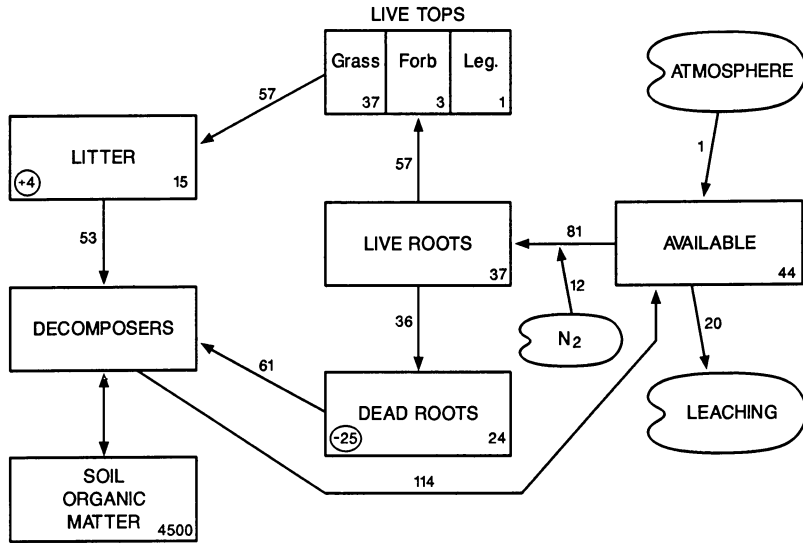


Fig. 9. Nitrogen budget for the 1980-81 growing season for a grazed site. Boxes represent internal ecosystem components in kg N/ha at peak standing crop; "clouds" represent either external inputs or outputs; and arrows represent annual N transfers in kg N/ha/yr.

The total amount of system N transfer, represented by the annual flow from the soil available pool to live roots plus any N₂ fixation, increased substantially in 1982. The higher production due to a warmer, wetter fall and longer rainy season accounted for most of this increase. However, the N inputs from N₂ fixation in 1981 became available as roots and litter from the previous year were mineralized, constituting a low level of N fertilization in 1982 (Woodmansee and Duncan 1980). This was no doubt a contributing factor to the higher plant-available inorganic N levels observed during most of the second growing season (Vaughn, Center, and Jones 1986).

Nitrogen uptake by plants and subsequent transfer to litter and dead roots represented the largest part of the N transfer within both sites in both years. Annual net uptake accounted for 93 and 87 kg/ha of N in the first year on the grazed and ungrazed sites, respectively, and 227 and 187 kg/ha on the respective sites in the second growing season. Of this total plant N accumulation, allocation to plant tops represented 61%, 61%, 35%, and 28% for these respective sites and years. These root:shoot ratios for annual net N uptake are generally similar to those we observed for biomass distribution. The larger fraction of root N in the second growing season was apparently due to the much higher root mass that year, because root N concentrations were very similar between years (fig. 7).

Soil organic N substrates can be separated into several fractions defined by their turnover rates (Molina et al. 1983; Parton et al. 1987; Paul and Juma 1981). Over the short period of a single growing season, soil N dynamics are largely influenced by a relatively small, labile pool of live microbes, microbial products, and soil organic matter, with a short turnover time (1 to 5 years). This pool is augmented by flows from plant litter decay and a slower soil organic N fraction with an intermediate turnover time (20 to 40 years). The very large resistant N component that has the longest turnover time (200 to 1,500 years) has little effect on short-term N cycling.

During the first growing season on the grazed plot (fig. 9), N transfer to the soil available pool exceeded outflow, with an apparent net gain of 14 kg/ha. This gain resulted primarily from the annual drawdown of 25 kg/ha in the dead root standing crop of N, which we measured as an annual net loss of N in the root component. With the three other N budgets for area I, however, estimated transfers to the available pool were not sufficient to satisfy the outflows represented by transfers to live roots and leaching. We assume that there was a net drawdown from the more labile soil organic N reserves to meet these requirements. The annual net changes in litter and dead root N content during the second season, totaling increases of 106 and 81 kg/ha of N on the grazed and ungrazed sites, respectively, represent a large accretion of potentially mineralizable N. This pool of N conceivably served as a future source of partial recharge for the system N deficits.

Judging from mass balance and the limited apparent N inputs, it appears that our lysimeter-derived estimates of N leaching losses were probably too high for these sites. There were apparent annual system N deficits of 8 kg/ha on the ungrazed site in the first year, and 21 and 23 kg/ha in the second year on the grazed and ungrazed sites, respectively. Woodmansee and Duncan (1980) suggested that, under ordinary circumstances, N leaching from annual grassland sites in a 55-cm average rainfall zone was nil. It is obvious that stable, productive grasslands could not sustain annual net N losses on the order of 10 to 20 kg/ha in the long term.

Phosphorus and sulfur budgets. Budgets for P and S were similar to those for N in many ways. Except for those aspects of the budgets that were different, our discussion will be brief. Figures 10 and 11 illustrate the P and S budgets for the grazed site during the 1981 growing season. The remaining P and S budgets for area I appear in tables 2 and 3.

There were no measured inputs or assumed losses of P to or from the systems through fixation, atmospheric deposition, or leaching as occurred with N. The immediately available pool of soil P was very small, and apparently well buffered by the dynamic labile inorganic P. This latter P source is replenished to some extent by slightly soluble P minerals and adsorbing surfaces, but apparently largely through P mineralization in the short term (Katznelson 1977). The mineralization of P in litter and dead roots supplied from about 53% to 100% of the plant P requirements in area I, which indicates the importance of mineralization processes in soil P turnover.

Total net annual P uptake by live plants in the first year was 7.4 and 9.5 kg/ha on the grazed and ungrazed sites, respectively, and in the second year 20.4 and 20.3 kg/ha. System P flows through live roots, then, were about one-tenth the levels of N, and annual plant P uptake was twice as high in the second growing season as it was in the first. The allocation of P to plant tops represented 65% and 72% of net annual P uptake during the first year on the grazed and ungrazed sites, respectively, and 34% and 48% during the second growing season. Nutrient accumulation in herbage was generally higher for P than for N because of higher relative P concentrations in the tops than in roots.

The transfer of P from decomposers to the soil available pool was more than sufficient to meet plant P requirements during the first year on the grazed site. As with N, this condition was largely due to the annual net decrease in the standing crop of P in dead roots. Estimated P transfers to the soil available pool were not sufficient to meet measured plant demands with the remaining area I budgets, however, and we assume again that those needs were met by a drawdown from the more labile organic and inorganic soil P reserves (Parton, Stewart, and Cole 1988). These apparent declines could be entirely offset by the mineralizable P accumulation in litter and dead roots because, unlike the case with N, there were no losses of P from the system over the two growing seasons considered. In general, the P cycle was more stable than the N cycle and appeared to be relatively more closed.

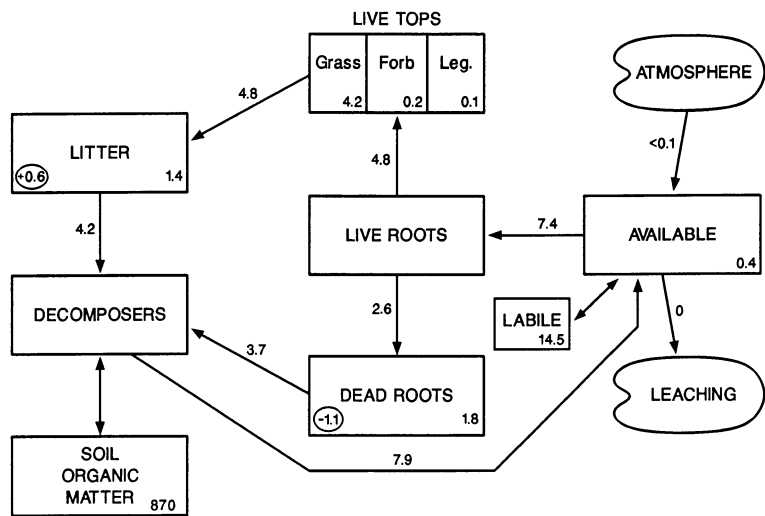


Fig. 10. Phosphorus budget for the 1980-81 growing season for a grazed site. Boxes represent internal ecosystem components in kg P/ha at peak standing crop; "clouds" represent either external inputs or outputs; and arrows represent annual P transfers in kg P/ha/yr.

Table 2. PHOSPHORUS BUDGETS FOR 1981 AND 1982 GROWING SEASONS AT ADJACENT GRAZED AND UNGRAZED ANNUAL GRASSLAND SITES, HOPLAND FIELD STATION

Item	1981		1982	
	Grazed	Ungrazed	Grazed	Ungrazed
<i>Distribution*</i>				
<i>kg/ha</i>				
Live tops:				
Grasses	4.2	4.5	3.6	4.5
Forbs	0.2	0.5	0	1.5
Legumes	0.1	0.8	0	0
Litter:	1.4 (+0.6)	1.2 (+1.2)	2.5 (+1.1)	2.0 (+2.4)
Live roots	2.7	2.7	3.1	3.7
Dead roots [†]	1.8 (-1.1)	1.8 (+0.4)	2.0 (+7.6)	2.5 (+7.1)
Total plant biomass	10.4	11.6	11.2	14.2
Soil organic	870	840	870	840
Soil available	0.4	0.5	0.2	0.1
Soil labile inorganic	14.5	15.4	14.7	10.4
<i>Transfers</i>				
<i>kg/ha/yr</i>				
Live tops to litter	4.8	6.8	7.0	9.7
Litter to decomposers	4.2	5.6	5.9	7.3
Live roots to dead roots	2.6	2.7	13.4	10.6
Dead roots to decomposers	3.7	2.3	5.8	3.5
Decomposers to available	7.9	7.9	11.7	10.8
Atmosphere to available	<0.1	<0.1	<0.1	<0.1
Available to live roots	7.4	9.5	20.4	20.3
Available to leaching	0	0	0	0

* Phosphorus distribution (kg/ha) is at herbage peak standing crop.
† Numbers in parentheses are annual net changes (+/-) in P standing crop in litter and dead roots.
‡ Phosphorus transfers (kg/ha/yr) are annual flows.

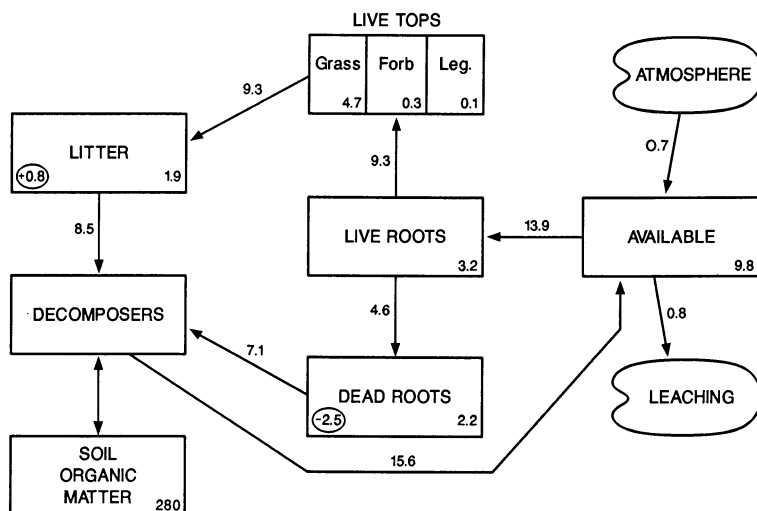


Fig. 11. Sulfur budget for the 1980-81 growing season for a grazed site. Boxes represent internal ecosystem components in kg S/ha at peak standing crop; "clouds" represent either external inputs or outputs; and arrows represent annual S transfers in kg S/ha/yr.

Table 3. SULFUR BUDGETS FOR 1981 AND 1982 GROWING SEASONS AT ADJACENT GRAZED AND UNGRAZED ANNUAL GRASSLAND SITES, HOPLAND FIELD STATION

Item	1981		1982	
	Grazed	Ungrazed	Grazed	Ungrazed
<i>Distribution*</i>	<i>kg/ha</i>			
Live tops:				
Grasses	4.7	3.7	5.7	3.4
Forbs	0.3	0.5	0	1.3
Legumes	0.1	0.6	0	0
Litter†	1.9 (+0.8)	1.6 (+0.8)	3.3 (+2.5)	3.0 (+2.0)
Live roots	3.2	3.4	5.0	3.9
Dead roots‡	2.2 (-2.5)	2.3 (+0.1)	3.4 (+10.4)	2.6 (+7.2)
Total plant biomass	12.4	12.1	17.4	14.2
Soil organic	280	280	280	280
Soil available	9.8	7.8	8.0	8.0
<i>Transfers§</i>	<i>kg/ha/yr</i>			
Live tops to litter	9.3	5.3	9.8	7.6
Litter to decomposers	8.5	4.5	7.3	5.6
Live roots to dead roots	4.6	5.0	15.4	13.1
Dead roots to decomposers	7.1	4.9	5.0	5.9
Decomposers to available	15.6	9.4	12.3	11.5
Atmosphere to available	0.7	0.7	1.6	1.6
Available to live roots	13.9	10.3	25.2	20.7
Available to leaching	0.8	0.8	1.6	1.6

* Sulfur distribution (kg/ha) is at herbage peak standing crop.

† Numbers in parentheses are annual net changes (+/-) in S standing crop in litter and dead roots.

‡ Sulfur transfers (kg/ha/yr) are annual flows.

Net annual plant S uptake was 13.9 and 10.3 kg/ha on the grazed and ungrazed sites, respectively, in the first year and 25.2 and 20.7 kg/ha the second year. Sulfur levels in the systems were quite similar to levels of P, with transfers through live roots being about one-ninth those of N. Sulfur allocation to plant tops represented 67% and 51% of total plant S uptake on the grazed and ungrazed sites, respectively, during the first growing season and 39% and 37% in the second season. This distribution was generally similar to that observed for net annual P uptake. It reflects similar relative concentrations of P and S in the tops and roots.

Our observations regarding the adequacy of litter and dead root mineralization to meet net annual plant S uptake were similar to those for N and P. Only on the grazed site during the first year was this process apparently sufficient to meet plant S demands. For the remaining budgets, we assume that S needs required some temporary drawdown from labile S reserves in the soil (Parton, Stewart, and Cole 1988) and that these deficits could be eventually recharged from the large standing crop of S in the current year's accumulation of litter and dead roots.

While system levels of S and P were similar, the cycling of S was more open than that of P. As with N, there were also external inputs to and losses from the S systems. Atmospheric deposition of S was not large in comparison with previously reported amounts (Jones and Woodmansee 1979), but these inputs still represented an average of about 6% of the net annual plant S uptake for both sites in both years. Our estimates of S leaching losses were equivalent to the measured inputs and suggest that these lysimeter-derived data were probably valid.

Potassium and calcium budgets. Budgets for K (fig. 12, table 4) and Ca (fig. 13, table 5) are less complete than those for N, P, and S. Because of the lack of suitable separation techniques (Mokwunye and Melsted 1972), the soil organic cation component was not measured. In addition, we had no way to account directly for primary soil mineral weathering, which can be an important process releasing K and Ca for plant growth in Mediterranean ecosystems (Marion 1982). One new system component we did measure for the cation budgets was the acid-soluble, nonexchangeable soil cation fraction. This is considered a soil "reserve" source to replace the exchangeable cations depleted by plant uptake (Metson 1974).

Even at the lowest seasonal levels (Vaughn, Center, and Jones 1986), available pools of K and Ca were more than adequate to supply all of these nutrients accumulated in the plants (tables 4 and 5). This finding suggests that mineralization from litter and roots during the growing season may not have been as important a process in supplying K and Ca as it was for N, P, and S. It certainly indicates that K and Ca were much less limiting to plant growth than the other nutrients on these study sites.

The cations demonstrated patterns of net mineralization and total annual plant uptake very similar to those for N, P, and S. Apparent annual deficits were presumably balanced by large nutrient accruals in the litter and dead root components at the end of the growing season. This was particularly true for Ca. Except for the first year on the grazed site, much of this annual nutrient accumulation for N, P, and S was in dead roots. The same was true for Ca, because little or none of the element was stored in the standing dead/litter component (table 5). Potassium, however, was accumulated primarily in the litter on the area I sites (table 4).

The flux of K through live roots exceeded that of Ca. System transfers of both K and Ca surpassed those of P and S but were generally less than those of N, at least through the common components we were able to quantify. The proportion of total K uptake by live herbage ranged from 76% to 95% in area I. This finding probably reflects the tendency of K to accumulate in plant tops in excess of need (Stinner et al. 1984). Certainly it was also due to the very low concentrations of K in the roots on the area I sites (fig. 7). Shoot uptake as a proportion of total plant uptake was much lower for Ca than for the other nutrients, accounting for just 10% to 31% over both sites and years. This

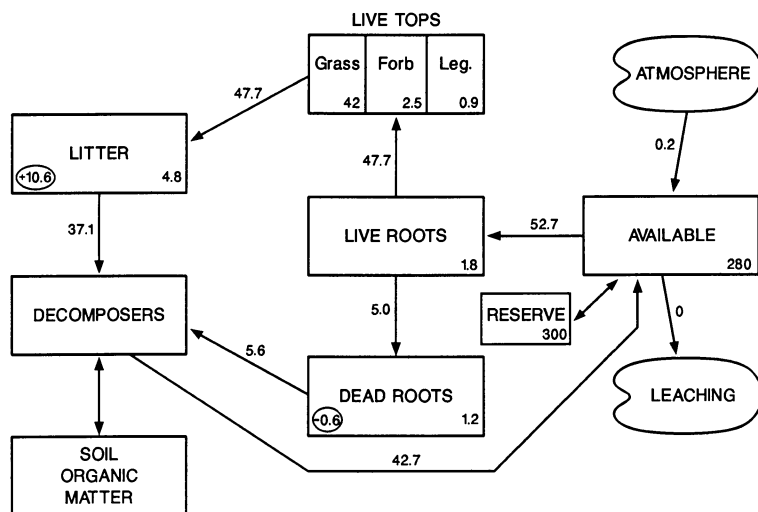


Fig. 12. Potassium budget for the 1980-81 growing season for a grazed site. Boxes represent internal ecosystem components in kg K/ha at peak standing crop; "clouds" represent either external inputs or outputs; and arrows represent annual K transfers in kg K/ha/yr.

Table 4. POTASSIUM BUDGETS FOR 1981 AND 1982 GROWING SEASONS AT ADJACENT GRAZED AND UNGRAZED ANNUAL GRASSLAND SITES, HOPLAND FIELD STATION

Item	1981		1982	
	Grazed	Ungrazed	Grazed	Ungrazed
<i>Distribution*</i>	<i>kg/ha</i>			
Live tops:				
Grasses	42.0	34.4	43.7	41.6
Forbs	2.5	3.8	0	10.7
Legumes	0.9	7.6	0	0
Litter†	4.8 (+10.6)	3.9 (+5.3)	6.4 (+17.6)	1.8 (+29.1)
Live roots	1.8	1.8	3.6	5.4
Dead roots‡	1.2 (-0.6)	1.2 (+0.1)	2.4 (+8.0)	3.6 (+5.4)
Total plant biomass	53.2	52.7	56.1	63.1
Soil "reserve"	300	360	300	360
Soil available	280	270	190	170
<i>Transfers</i>	<i>kg/ha/yr</i>			
Live tops to litter	47.7	55.2	80.9	81.0
Litter to decomposers	37.1	49.9	63.3	51.9
Live roots to dead roots	2.9	2.8	26.1	8.0
Dead roots to decomposers	3.5	2.7	18.1	2.6
Decomposers to available	40.6	52.6	81.4	54.5
Atmosphere to available	0.2	0.2	0.3	0.3
Available to live roots	50.6	58.0	107.0	89.0
Available to leaching	0	0	0	0

* Potassium distribution (kg/ha) is at herbage peak standing crop.

† Numbers in parentheses are annual net changes (+/-) in K standing crop in litter and dead roots.

‡ Potassium transfers (kg/ha/yr) are annual flows.

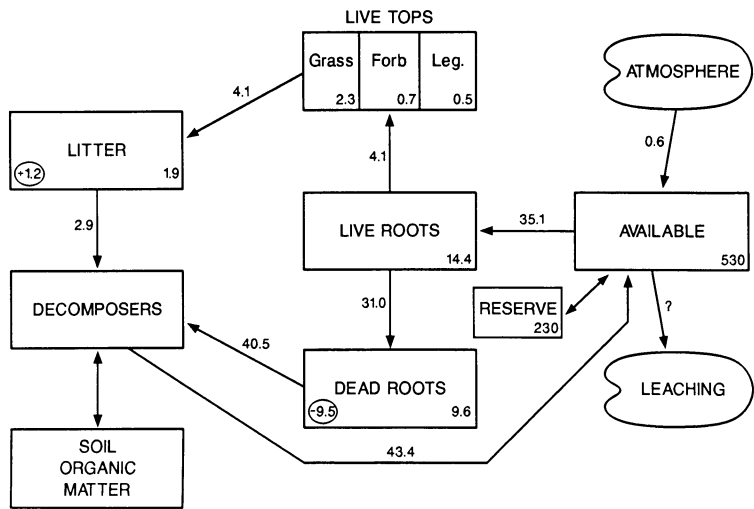


Fig. 13. Calcium budget for the 1980-81 growing season for a grazed site. Boxes represent internal ecosystem components in kg Ca/ha at peak standing crop; "clouds" represent either external inputs or outputs; and arrows represent annual Ca transfers in kg Ca/ha/yr.

Table 5. CALCIUM BUDGETS FOR 1981 AND 1982 GROWING SEASONS AT ADJACENT GRAZED AND UNGRAZED ANNUAL GRASSLAND SITES, HOPLAND FIELD STATION

Item	1981		1982	
	Grazed	Ungrazed	Grazed	Ungrazed
<i>Distribution*</i>				
<i>kg/ha</i>				
Live tops:				
Grasses	2.3	2.5	2.8	1.8
Forbs	0.7	0.7	0	4.0
Legumes	0.5	2.1	0	0
Litter:	1.9 (+1.2)	1.9 (+1.6)	4.6 (+0.8)	3.6 (-0.9)
Live roots	14.4	15.0	25.2	20.4
Dead roots [†]	<u>9.6</u> (-9.5)	<u>10.0</u> (+2.9)	<u>16.8</u> (+44.6)	<u>13.6</u> (+32.4)
Total plant biomass	29.4	32.2	49.4	43.4
Soil "reserve"	230	230	230	230
Soil available	530	440	810	540
<i>Transfers</i>				
<i>kg/ha/yr</i>				
Live tops to litter	4.1	7.1	15.8	8.2
Litter to decomposers	2.9	5.5	15.0	9.1
Live roots to dead roots	10.3	16.0	67.3	73.1
Dead roots to decomposers	19.8	13.1	22.7	40.7
Decomposers to available	22.7	18.6	37.7	49.8
Atmosphere to available	0.6	0.6	0.7	0.7
Available to live roots	14.4	23.1	83.1	81.3
Available to leaching	?	?	?	?

* Calcium distribution (kg/ha) is at herbage peak standing crop.
† Numbers in parentheses are annual net changes (+/-) in Ca standing crop in litter and dead roots.
‡ Calcium transfers (kg/ha/yr) are annual flows.

result reflects the relatively higher concentrations of Ca in the roots (fig. 7), which has also been observed in forested ecosystems (Pastor and Bockheim 1984) and may be due to the greater relative immobility of this element.

Area II

The patterns of biomass dynamics and nutrient cycling in area II were fundamentally similar to those in area I. For brevity, we will limit our discussion to those results that differed substantially in the two study areas.

Aboveground live biomass dynamics

Total biomass accumulation patterns on both area II sites in both years were similar to those observed in area I (fig. 14). However, forbs and legumes accounted for a larger fraction of the total aboveground biomass on the area II sites. These two components represented an average of about 40% and 66% of the live herbage on the unseeded and seeded sites, respectively, over both growing seasons. As would be expected, legumes constituted a greater portion of live herbage on the seeded sites, representing a seasonal average of 27% and 38% in the first and second years, respectively.

Estimates of annual net production for 1981 were 6,320 and 3,720 kg/ha for the seeded and unseeded sites, respectively. In 1982, ANP was 8,250 and 3,650 kg/ha on the respective sites. Maximum growth rates in 1981 were 91 (in April) and 59 (in March) kg/ha/day for the seeded and unseeded sites, respectively; in 1982, they were 47 (in March) and 26 (in April) kg/ha/day on the respective sites. The increased productivity on the seeded site was certainly due to the inputs represented in P and S fertilizers and sub-clover seeding. These additions had resulted in an average herbage biomass increase of 2,000 kg/ha at peak standing crop when comparing pre-fertilization (1960-1972) and post-fertilization (1973-1979) periods (Vaughn and Murphy 1982).

Standing dead/litter biomass dynamics

The dynamics of standing dead/litter were similar for both area II sites in both years (fig. 15), and they were somewhat different from the patterns observed on the area I sites. The standing dead/litter component was smaller in area II at the beginning of each study year, no doubt reflecting heavier grazing in that area than in area I during both years before site enclosure (A.H. Murphy unpublished). It remained relatively constant through the growing season. Litter began to accumulate earlier in both years on the area I sites (fig. 3). There was only a rapid accumulation in area II when plants began to senesce and die late in the spring (May 1981 and June 1982), with greater accretions on the seeded site in both years.

We observed a considerable amount of young plant mortality in area II during the winter and spring, especially on the seeded site. The fact that the mass of standing dead/litter did not accumulate appreciably during this period suggests that decomposition rates were probably equal to inputs from plant mortality. It would appear that high-quality litter on the area II sites with their large component of leafier forbs and legumes (fig. 14) enhanced decomposition and/or mineralization rates. Savelle (1977) reported that foliar material decomposed more rapidly than did more lignified grass culms. Schlesinger and Hasey (1981) reported similar findings regarding the effects of lignin on decomposition. They also suggested that in P-deficient environments, the P content of litter is important in determining decomposition rates. Litter nutrient content, particularly on the seeded site with much higher relative N, P, and S levels (fig. 18), may also have contributed to the apparent greater rates of decomposition.

Belowground biomass dynamics

Figure 16 illustrates the patterns of belowground biomass accumulation for the area II sites. As with area I, sampling variability was high. On the seeded site, standard deviations averaged 24% of the mean and ranged from 4% to 52%. The average was 29% on the unseeded site, and the range 3% to 52%.

Except for the unseeded site in the first growing season, which showed little fluctuation, the patterns of belowground biomass accumulation in area II were generally similar to those observed with live aboveground biomass. Belowground biomass increased from minimum values at the start of the growing season to a late-spring maximum accumulation near live herbage PSC. Biomass then declined through the summer. These patterns were similar to others observed at Hopland (Saville 1977) and were probably representative for annual grasslands. Higher summer root biomass in the second year in area II reflects greater aboveground productivity during that growing season than in the first. We did not sample any late-season grasses or summer annual forbs on these sites.

Belowground biomass ANP values were 8,040 and 14,420 kg/ha on the seeded site and 3,150 and 8,500 kg/ha on the unseeded site during the 1981 and 1982 growing seasons, respectively. As we observed in area I, roots accounted for a larger part of the total plant ANP in the second year. Root:shoot ANP ratios were 1.3 and 0.9 in the first year on the seeded and unseeded sites, respectively, and 1.7 and 2.3 in the second year. The between-year differences probably reflect the same factors as in area I. Again, the ratios were generally within the range of values reported by Saville (1977).

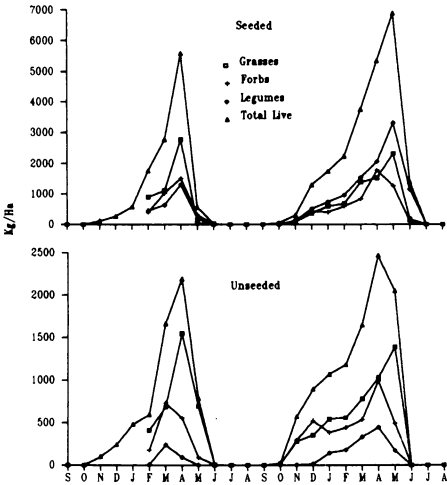


Fig. 14. Aboveground herbage live biomass of grasses, forbs, and legumes on adjacent subclover-seeded and unseeded sites, 1980-81 and 1981-82 growing seasons.

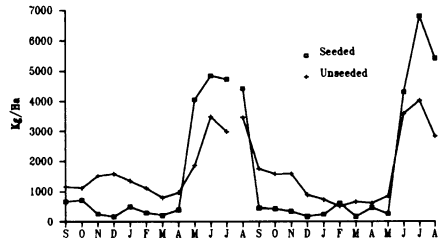


Fig. 15. Aboveground herbage standing dead/litter biomass on adjacent subclover-seeded and unseeded sites, 1980-81 and 1981-82 growing seasons.

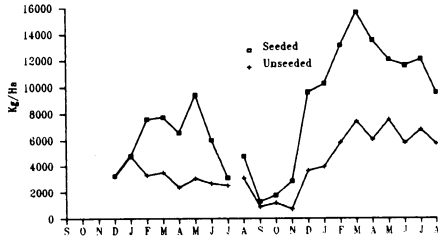


Fig. 16. Belowground plant biomass on adjacent subclover-seeded and unseeded sites, 1980-81 and 1981-82 growing seasons.

Mineral concentration dynamics in live herbage

Seasonal dynamics of live herbage nutrient concentrations (fig. 17) were similar to those discussed for area I. Actual concentrations, particularly of N and P, were somewhat higher on the area II sites, however. Higher P levels were probably due to greater availability of soil P seasonally in area II (Vaughn, Center, and Jones 1986), most notably on the seeded site, which had a history of P fertilization. The higher herbage N concentrations in area II were almost certainly due to the much larger legume component, because they do not reflect greater soil N levels (tables 1 and 6).

Concentrations of N, P, and S in composite total forage samples tended to be slightly higher on the seeded than on the unseeded site. These trends occurred in both years, and were no doubt the result of prior fertilization and much larger legume content (fig. 14) on the seeded site. Concentrations of Ca in grass and forbs were similar on both sites but were higher in legumes on the seeded site. While it is possible that subclover has a higher functional requirement for Ca than do the unseeded native legumes (Longeragan and Snowball 1969), the higher levels may also reflect additions of Ca in the superphosphate fertilizers (about 20% Ca) and/or higher levels of available soil Ca (table 10). Potassium levels fluctuated similarly on both sites in both years.

Mineral concentration dynamics in standing dead/litter

As with live herbage, concentrations of all nutrients in the litter component (fig. 18) followed the same general patterns as in area I. Except for higher Ca levels, litter nutrient concentrations on the unseeded site were generally similar to those on area I sites. The higher Ca was probably due to the larger proportion of Ca-rich forbs and legumes on the unseeded site (fig. 14). Concentrations of N, P, S, and Ca in litter were higher in both years on the seeded than any other site and reflect the higher concentrations of these nutrients in all live herbage groups (fig. 17). Litter K concentrations and seasonal fluctuations were similar in both years on all sites.

There were pronounced increases in litter N, P, S, and Ca concentrations on the seeded site beginning in February of the second year. Schlesinger and Hasey (1981) noted similar increases in N and P concentrations during the decomposition of some chaparral shrub foliage. The increases they observed were probably the result of decay and subsequent immobilization in the litter-microbe residue, and they occurred as litter mass decreased. In our study, however, the increases in litter nutrient concentrations accompanied a 260% increase (370 kg/ha) in litter mass during February (fig. 15), and probably reflect the death of young, nutrient-rich plant parts and whole plants as well as immobilization. The higher litter mass and nutrient levels coincided with the initiation of maximum live biomass accumulation (fig. 14), suggesting that the decomposition and mineralization of the current year's litter was an important process in regulating growth on this site.

Mineral concentration dynamics belowground

Over both years, fluctuations in root nutrient levels in area II were inconsistent and showed no regular patterns (fig. 19). The concentrations of nutrients in roots relative to live herbage and litter were much the same as in area I, with two major exceptions. Litter concentrations of all nutrients on the seeded site exceeded those in the roots in the spring of the second growing season, presumably because of the nutrient-rich additions from recently dead herbage. Additionally, K concentrations in roots from both area II sites exceeded those in litter for most of the 2-year study and were much higher than root concentrations in area I. All roots were washed in the same manner during

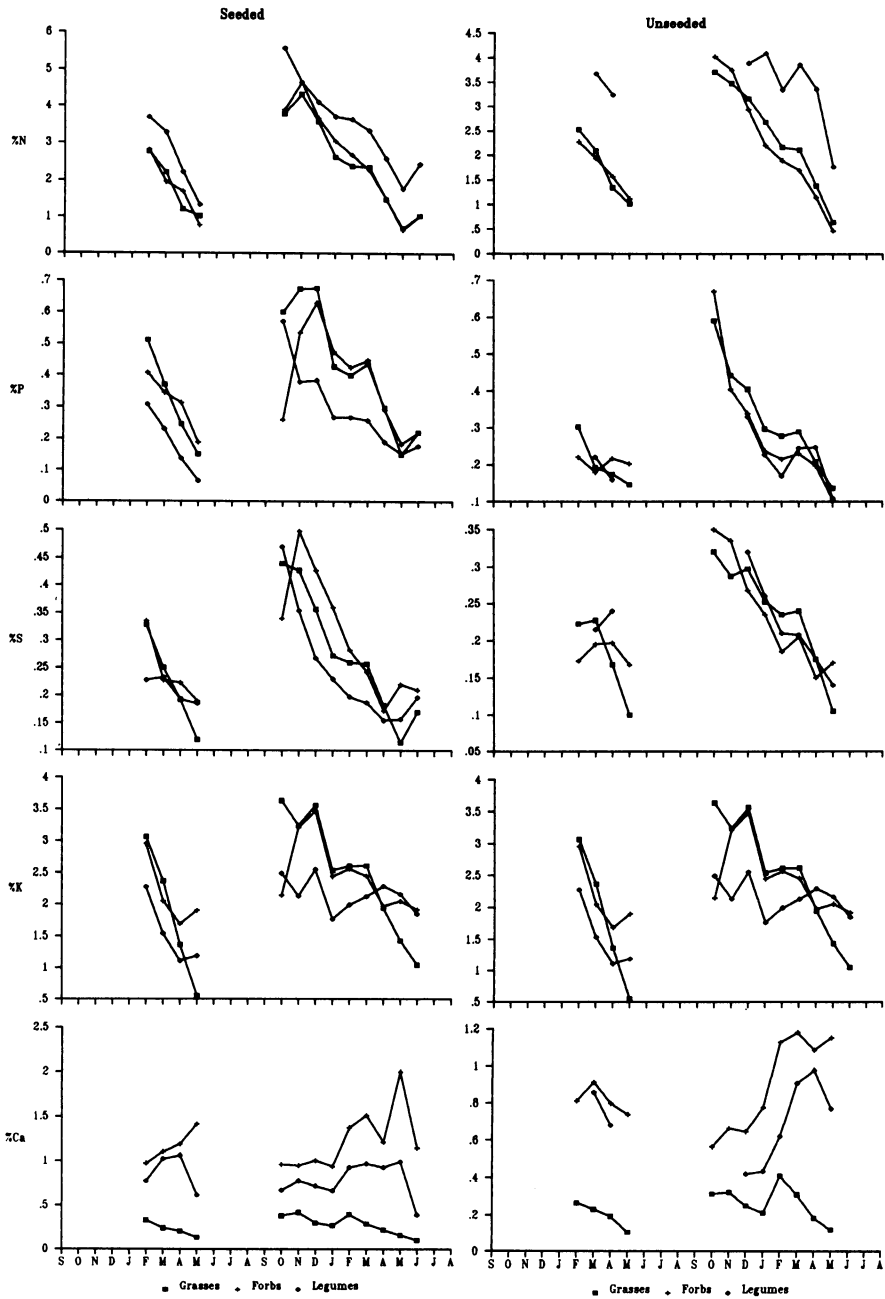


Fig. 17. Concentrations of N, P, S, K, and Ca in aboveground herbage live biomass of grasses, forbs, and legumes on adjacent subclover-seeded and unseeded sites, 1980-81 and 1981-82 growing seasons.

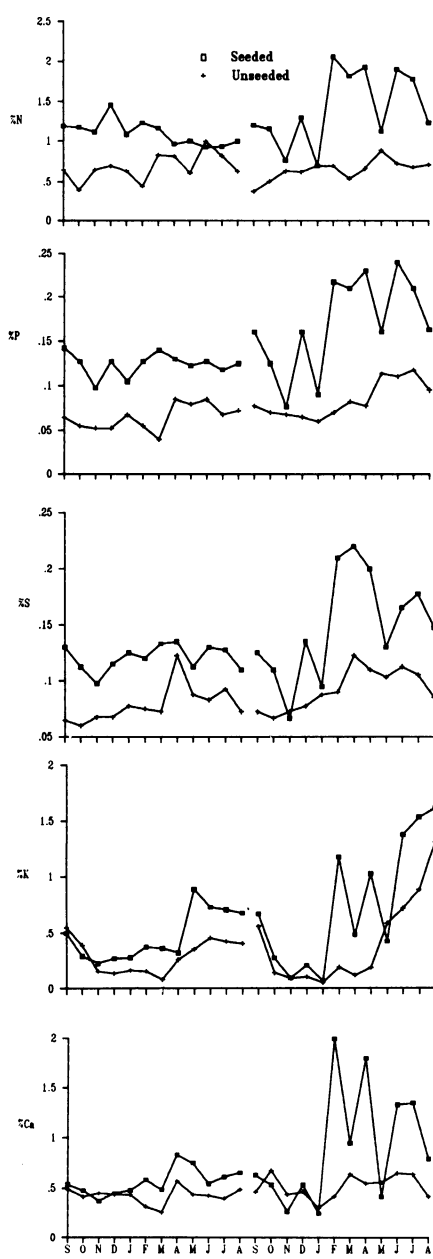


Fig. 18. Concentrations of N, P, S, K, and Ca in aboveground herbage standing dead/litter biomass on adjacent subclover-seeded and unseeded sites, 1980-81 and 1981-82 growing seasons.

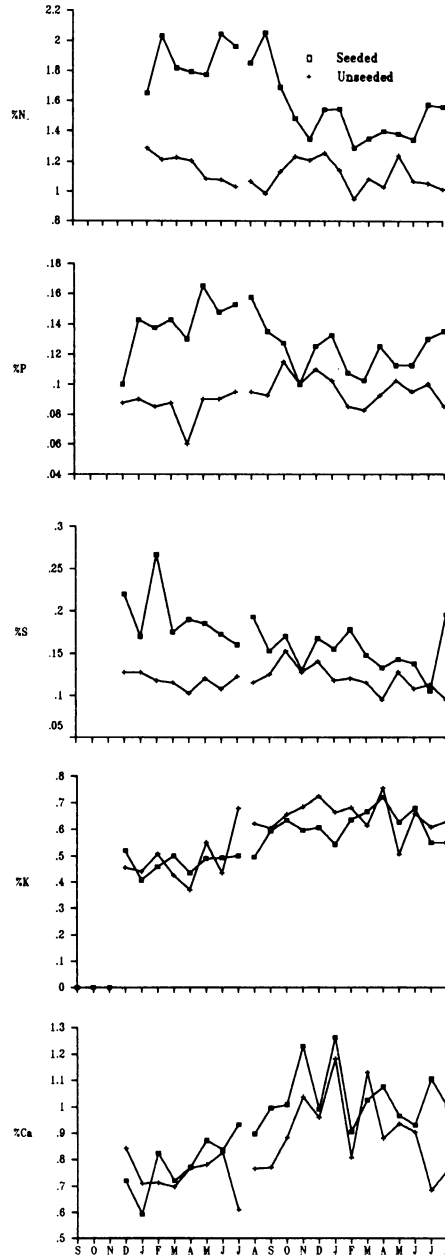


Fig. 19. Concentrations of N, P, S, K, and Ca in belowground plant biomass on adjacent subclover-seeded and unseeded sites, 1980-81 and 1981-82 growing seasons.

separation from soil, so the leaching of soluble constituents such as K should have been similar for all samples. It is unlikely, then, that sample preparation could account for these differences. Our measurements also showed similar seasonal soil K availability in both areas (Vaughn, Center, and Jones 1986), so the reasons for the differences are not clear. They may reflect the different plant species on the two areas and their relative tendencies to concentrate K in roots. It is also possible that the neutral, normal ammonium acetate used to extract K in our study is a poor index of K availability in these soils (Knudsen, Petersen, and Pratt 1982). The much larger nonexchangeable "reserve" component in area II than area I soils (tables 4 and 9) may provide a better indication of relative K release rates.

There were no differences in root cation concentrations between the area II sites, although both had higher Ca levels than either site in area I (fig. 7). The differences in Ca between areas probably reflect the differences in relative available and "reserve" soil levels. They also could reflect the larger component of legumes and forbs in area II, which have higher relative Ca concentrations in their roots (Loneragan and Snowball 1969).

Concentrations of N and P in roots were higher at the seeded than at any other site in both years. Root S levels were also highest on the seeded site in the first year but were similar to those in area I in the second growing season. Greater concentrations of N in the roots probably resulted from the much larger legume component on the seeded site (fig. 14) and may also reflect the effects of P and S fertilizers in enhancing N_2 fixation (Jones and Woodmansee 1979). Fertilizers also had the apparent effect of increasing P and S concentrations in the roots; declines in P and S, as well as N, from the first to the second growing season were probably due to the difference in time (2 vs. 3 years) after 1978 fertilizer application.

Aboveground live herbage nutrient uptake

As we found in area I, nutrient uptake dynamics on both area II sites closely followed the patterns of live herbage biomass accumulation (fig. 20). The distribution of nutrients within herbage groups on the unseeded site was also similar to that in area I: there was more N, P, S, and K in the grasses and more Ca in the forbs in both years. On the seeded site, however, there was more N, S, and K uptake by legumes in the second growing season, reflecting the larger legume component that year (fig. 14).

Uptake of all nutrients by all herbage groups was much higher on the seeded than the unseeded site in both years. The higher nutrient contents were primarily due to greater live herbage biomass on the seeded site, because herbage nutrient concentrations (fig. 17) were not consistently higher. The increases in both herbage biomass and nutrient content on the seeded site certainly reflect fertilizer responses.

Nutrient budgets

Nutrient transfer dynamics between system components in area II were generally similar to those described for area I. For economy, we will emphasize only the distinguishing aspects (tables 6 to 10).

Nitrogen budget. Dinitrogen fixation generally accounted for larger amounts of system N in area II (table 6) than area I, no doubt reflecting the larger legume component in the live herbage (fig. 14). For apparently similar reasons, there was more fixed N_2 on the seeded than on the unseeded site and in the second than in the first growing season. Fixed N_2 accounted for 27% of total plant N uptake (including available soil N) on the seeded site in 1981 and 40% in 1982; it accounted for 7% and 21% on the unseeded site in the respective years.

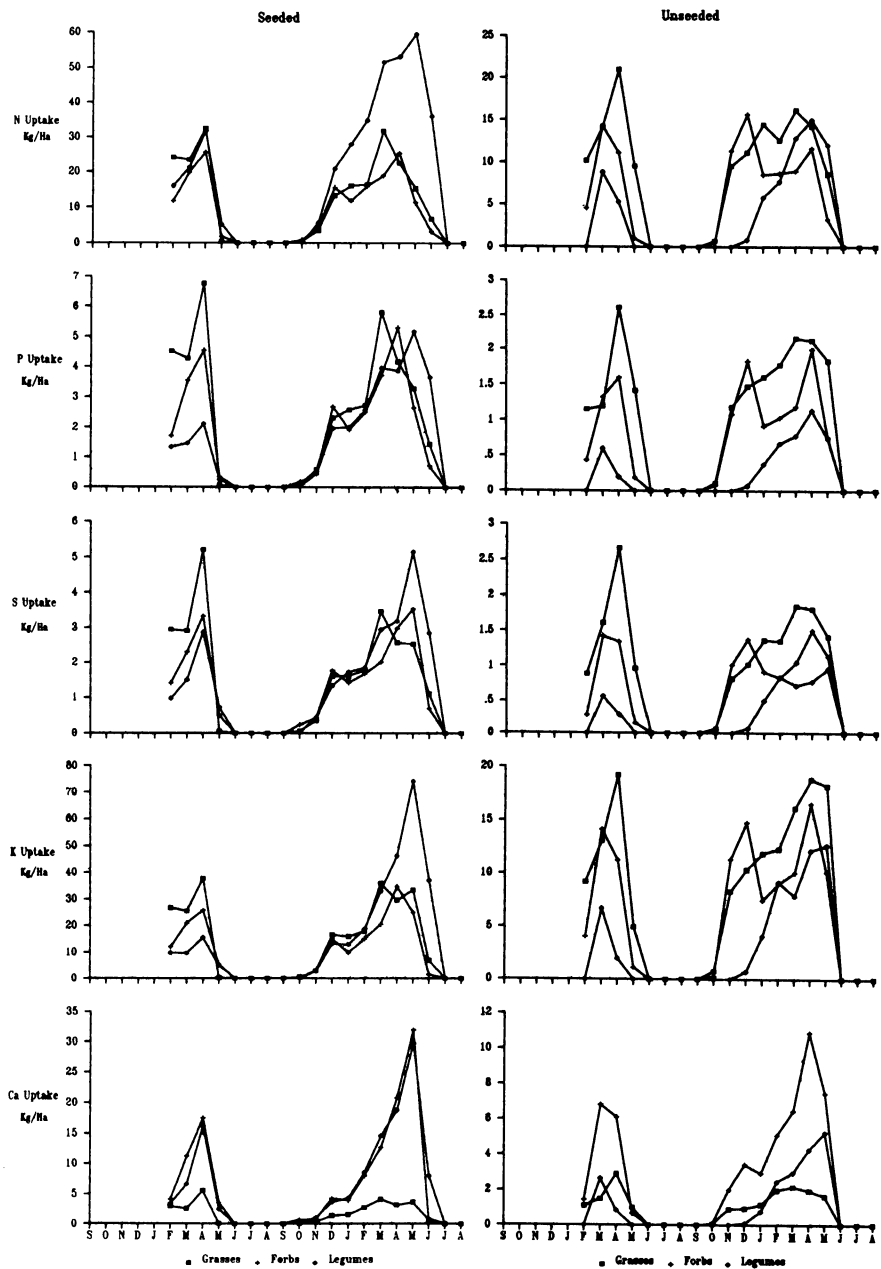


Fig. 20. Uptake of N, P, S, K, and Ca in aboveground herbage live biomass of grasses, forbs, and legumes on adjacent subclover-seeded and unseeded sites, 1980-81 and 1981-82 growing seasons.

Table 6. NITROGEN BUDGETS FOR 1981 AND 1982 GROWING SEASONS AT ADJACENT SUB-CLOVER SEEDED AND UNSEEDED ANNUAL GRASSLAND SITES, HOPLAND FIELD STATION

Item	1981		1982	
	Seeded	Unseeded	Seeded	Unseeded
<i>Distribution*</i>	<i>kg/ha</i>			
Live tops:				
Grasses	33	21	15	14
Forbs	26	8	8	12
Legumes	28	3	59	15
Litter:	4 (+37)	7 (+17)	11 (+70)	5 (+7)
Live roots	70	16	100	37
Dead roots†	47 (+56)	10 (-2)	67 (+128)	25 (+48)
Total plant biomass	208	65	260	108
Soil organic	4,040	3,650	4,040	3,650
Soil available	23	21	15	29
<i>Transfers</i>	<i>kg/ha/yr</i>			
Live tops to litter	90	44	120	52
Litter to decomposers	53	27	50	45
Live roots to				
dead roots	172	38	266	120
Dead roots to				
decomposers	116	40	138	72
Decomposers to				
available	169	67	188	117
Atmosphere to available	1	1	1	1
Available to live roots	190	76	233	136
N ₂ to live roots	72	6	153	36
Available to leaching	36	20	44	25

* Nitrogen distribution (kg/ha) is at herbage peak standing crop.

† Numbers in parentheses are annual net changes (+/-) in N standing crop in litter and dead roots.

‡ Nitrogen transfers (kg/ha/yr) are annual flows.

Annual net N uptake by plants was 262 and 82 kg/ha/yr during the first growing season on the seeded and unseeded sites, respectively. During the second season, it was 386 and 172 kg/ha/yr on the respective sites. Allocation of this total N uptake to plant tops represented 34%, 54%, 31%, and 30% for these respective sites and years. These root:shoot ratios for annual net N uptake on the unseeded site were similar to those observed for annual net biomass production. On the seeded site, however, the ratios for annual net N uptake were considerably higher than for biomass production, indicating higher seasonal N levels in roots relative to tops. This finding no doubt reflects the large subclover component and roots and nodules with relatively higher N concentrations (Phillips, Center, and Jones 1983).

Transfers to the soil available pool during the growing season from mineralization by soil decomposers and from atmospheric deposition were insufficient to meet the apparent leaching and plant uptake demands. Again, we assume that this N requirement was met by temporary drawdowns from the more labile soil organic N reserves. However, except for the unseeded site in 1981, the annual accumulation of potentially mineralizable N in litter and dead roots at the end of the growing season was more than sufficient to balance this deficit. Considering this large litter and dead root storage component, the seeded site had annual positive N balances of 37 and 110 kg/ha/yr at the end of the first and second growing seasons, respectively. The unseeded site had balances of -13 and +12 kg/ha/yr at the end of the respective annual cycles.

Table 7. PHOSPHORUS BUDGETS FOR 1981 AND 1982 GROWING SEASONS AT ADJACENT SUBCLOVER SEEDED AND UNSEEDED ANNUAL GRASSLAND SITES, HOPLAND FIELD STATION

Item	1981		1982	
	Seeded	Unseeded	Seeded	Unseeded
<i>Distribution*</i>	<i>kg/ha</i>			
Live tops:				
Grasses	6.3	2.6	3.3	2.1
Forbs	4.6	1.2	2.0	2.0
Legumes	1.9	0.1	5.2	1.1
Litter [†]	0.5 (+4.6)	0.7 (+1.3)	1.6 (+8.0)	0.5 (+1.3)
Live roots	5.1	1.9	8.2	3.4
Dead roots [‡]	<u>3.4</u> (+4.9)	<u>1.2</u> (+0.7)	<u>5.4</u> (+11.2)	<u>2.2</u> (+4.0)
Total plant biomass	21.8	7.7	25.7	11.3
Soil organic	640	650	640	650
Soil available	1.0	0.4	1.2	0.2
Soil labile inorganic	25.2	16.3	28.5	19.8
<i>Transfers[§]</i>	<i>kg/ha/yr</i>			
Live tops to litter	13.7	4.8	17.1	6.2
Litter to decomposers	9.1	3.5	9.1	4.9
Live roots to dead roots	15.5	4.1	20.7	9.4
Dead roots to decomposers	10.6	3.4	9.5	5.4
Decomposers to available	19.7	6.9	18.6	10.3
Atmosphere to available	<0.1	<0.1	<0.1	<0.1
Available to live roots	29.2	8.9	37.8	15.6
Available to leaching	0	0	0	0

* Phosphorus distribution (kg/ha) is at herbage peak standing crop.

[†] Numbers in parentheses are annual net changes (+/-) in P standing crop in litter and dead roots.

[‡] Phosphorus transfers (kg/ha/yr) are annual flows.

In the second year on the unseeded site, inputs from N_2 fixation were sufficient to balance the N cycle over the two growing seasons measured. Dinitrogen fixation inputs exceeded leaching outputs on the seeded site to the extent that there were large net gains in system N in both years. We assume that some of this additional N was leached (table 6; Jones, Delwiche, and Williams 1977) but that much of it would eventually be accumulated in organic matter. Barrow (1969) observed that Australian sub-clover pastures fertilized with P and S accumulated N at the rate of about 38 kg/ha/yr during establishment periods of 3 to 40 years. Our data on organic N (table 6; Vaughn, Center, and Jones 1986) suggest that N was accumulated on the seeded site at the rate of about 50 kg/ha/yr over the first 8 years of establishment (1972-80). Nitrogen accumulation rates of this order on the seeded site during our two-year study are certainly conceivable given the measured positive system N balances. However, the Kjeldahl determination of total soil N is not sensitive enough to detect these changes in such a short period.

Phosphorus and sulfur budgets. Annual net plant uptake values for both P (table 7) and S (table 8) on the unseeded site were very similar to those observed on the area I sites. Plant P uptake was 8.9 and 15.6 kg/ha/yr during the first and second growing seasons, respectively; S uptake was 9.6 and 19.1 kg/ha/yr during the respective seasons. On the seeded site, net P uptake was 29.2 and 37.8 kg/ha/yr during the first and second years, respectively, which represented net uptake increases of 3.3 and 2.4 times

Table 8. SULFUR BUDGETS FOR 1981 AND 1982 GROWING SEASONS AT ADJACENT SUB-CLOVER SEEDED AND UNSEEDED ANNUAL GRASSLAND SITES, HOPLAND FIELD STATION

Item	1981		1982	
	Seeded	Unseeded	Seeded	Unseeded
<i>Distribution*</i>	<i>kg/ha</i>			
Live tops:				
Grasses	5.2	2.7	2.5	1.8
Forbs	3.3	1.0	2.7	1.5
Legumes	2.6	0.2	5.2	0.8
Litter†	0.6 (+4.1)	1.1 (+1.8)	1.3 (+8.0)	0.7 (+1.1)
Live roots	7.5	2.2	10.3	3.5
Dead roots‡	5.0 (+3.5)	1.5 (+0.4)	6.2 (+16.7)	2.3 (+4.3)
Total plant biomass	24.2	8.7	28.9	10.6
Soil organic	360	270	360	270
Soil available	11.3	9.3	7.9	8.6
<i>Transfers</i>	<i>kg/ha/yr</i>			
Live tops to litter	11.5	4.6	12.5	5.0
Litter to decomposers	7.4	2.8	4.5	3.9
Live roots to dead roots	19.6	5.0	31.8	14.1
Dead roots to decomposers	16.1	4.6	15.1	9.8
Decomposers to available	23.5	7.4	19.6	13.7
Atmosphere to available	0.7	0.7	1.6	1.6
Available to live roots	31.1	9.6	44.3	19.1
Available to leaching	1.6	0.8	1.6	0.8

* Sulfur distribution (kg/ha) is at herbage peak standing crop.

† Numbers in parentheses are annual net changes (+/-) in S standing crop in litter and dead roots.

‡ Sulfur transfers (kg/ha/yr) are annual flows.

the uptake measured on the unseeded site in the respective years. Sulfur net uptake on the seeded site was 31.1 (a 3.2-fold increase) and 44.3 kg/ha/yr (a 2.3-fold increase) during 1981 and 1982, respectively. Larger relative between-site differences in the first growing season probably reflected the more recent fertilizer additions in 1978. The larger P and S transfers on the seeded site were no doubt due to the previous applications of P and S fertilizers. Phosphorus additions apparently stimulated the growth of subclover, which has a higher P requirement than many annual forbs and grasses (Ozanne, Keay, and Biddiscombe 1969). Applied S may act directly to increase plant production and S uptake by ameliorating S deficiencies (Jones 1974). It also stimulates rhizobial activity, increasing legume production and N_2 fixation and, therefore, mineralizable N for plant growth (Jones and Woodmansee 1979).

Relative flows of P, S, and N through live roots in area II were very similar to those observed in area I: system P flows were about one-tenth those of N, and S flows were about one-ninth. Allocation of total plant P uptake to plant tops was 47% and 54% in the first year on the seeded and unseeded sites, respectively, and 45% and 40% on the respective sites in the second year. The allocation of P to herbage was generally higher than that of N in area II, reflecting higher relative seasonal P concentrations in tops than in roots. Allocation of S to plant tops was similar to that of N, at 37%, 48%, 28%, and 26% of the total annual net S uptake for the respective sites and years.

The apparent mineralization of litter and dead roots during the growing season did not account for sufficient P or S to balance measured plant uptake of these nutrients in either year in area II. We assume that these P and S requirements were met by tempo-

Table 9. POTASSIUM BUDGETS FOR 1981 AND 1982 GROWING SEASONS AT ADJACENT SUBCLOVER SEEDED AND UNSEEDED ANNUAL GRASSLAND SITES, HOPLAND FIELD STATION

Item	1981		1982	
	Seeded	Unseeded	Seeded	Unseeded
<i>Distribution*</i>	<i>kg/ha</i>			
Live tops:				
Grasses	38	19	34	19
Forbs	26	9	25	17
Legumes	14	1	74	12
Litter†	1 (+19)	2 (+6)	4 (+86)	1 (+26)
Live roots	17	9	46	23
Dead roots‡	12 (+10)	6 (+8)	30 (+45)	15 (+30)
Total plant biomass	108	46	213	87
Soil "reserve"	1,000	680	1,000	680
Soil available	300	250	190	230
<i>Transfers</i>	<i>kg/ha/yr</i>			
Live tops to litter	80	40	155	57
Litter to decomposers	61	34	69	31
Live roots to dead roots	51	25	111	46
Dead roots to decomposers	41	17	66	16
Decomposers to available	102	51	135	47
Atmosphere to available	0.2	0.2	0.3	0.3
Available to live roots	131	65	266	103
Available to leaching	0	0	0	0

* Potassium distribution (kg/ha) is at herbage peak standing crop.

† Numbers in parentheses are annual net changes (+/-) in K standing crop in litter and dead roots.

‡ Potassium transfers (kg/ha/yr) are annual flows.

rary inputs from the more labile soil reserves, which were then largely balanced by P and S storage in litter and dead roots at the end of both years. It is also conceivable that dissolution of residual P and S fertilizers on the seeded site represented some external nutrient inputs, particularly in the first year.

We assume that a small amount of the fertilizer-derived S was leached (table 8; Jones, Martin, and Williams 1968), but that most of it accumulated in organic matter. Our soil S measurements (table 8; Vaughn, Center, and Jones 1986) indicated that, while inorganic S levels had increased very little, about 90 kg/ha of organic S had accrued on the seeded site. This amount is about equivalent to all of the fertilizer-S inputs during the first 8 years of pasture establishment.

The fate of fertilizer-P inputs appeared to be just the opposite. There was no measurable accumulation of P in the organic matter, but the inorganic labile and available pools were consistently higher on the seeded than unseeded site (table 7). Total inorganic P analyses (Vaughn, Center, and Jones 1986) indicated that large amounts of inorganic P, about 200 kg/ha, had accumulated on the seeded site. This amount slightly exceeds the approximately 185 kg/ha of fertilizer P that had previously been applied, but it is certainly within reasonable analytical limits. Barrow (1969) and Sharpley (1986) both suggested that little fertilizer P is converted to organic P in the short term, so it is likely that the detection and quantification of organic P accumulation on the seeded site would require longer term studies.

Potassium and calcium budgets. The same limitations discussed for the cation budgets in area I also apply to area II (tables 9 and 10). Available soil levels of K and

Table 10. CALCIUM BUDGETS FOR 1981 AND 1982 GROWING SEASONS AT ADJACENT SUB-CLOVER SEEDED AND UNSEEDED ANNUAL GRASSLAND SITES, HOPLAND FIELD STATION

Item	1981		1982	
	Seeded	Unseeded	Seeded	Unseeded
<i>Distribution*</i>	<i>kg/ha</i>			
Live tops:				
Grasses	5	3	4	2
Forbs	18	5	24	11
Legumes	14	1	30	4
Litter:	4 (+26)	4 (+8)	4 (+41)	3 (+4)
Live roots	31	11	70	32
Dead roots:	20 (+24)	7 (+3)	47 (+83)	21 (+36)
Total plant biomass	92	31	179	73
Soil "reserve"	600	410	600	410
Soil available	1,430	1,110	1,420	960
<i>Transfers</i>	<i>kg/ha/yr</i>			
Live tops to litter	40	12	67	19
Litter to decomposers	14	4	26	15
Live roots to dead roots	75	28	198	97
Dead roots to decomposers	51	25	115	61
Decomposers to available	65	29	141	76
Atmosphere to available	0.6	0.6	0.7	0.7
Available to live roots	115	40	265	116
Available to leaching	?	?	?	?

* Calcium distribution (kg/ha) is at herbage peak standing crop.

† Numbers in parentheses are annual net changes (+/-) in Ca standing crop in litter and dead roots.

‡ Calcium transfers (kg/ha/yr) are annual flows.

Ca were usually more than sufficient to supply the annual plant net uptake demands for these nutrients. The one exception was the K budget on the seeded site in the second growing season. In this case, the available pool was buffered by a very large inorganic reserve component.

There were larger transfers of both cations on the seeded than on any other site, no doubt reflecting greater utilization of available system nutrients by the much larger plant biomass (fig. 14). The larger Ca flows on the seeded site probably also reflected its larger component of Ca-rich legumes and forbs.

Relative system transfers of K and Ca were generally similar in both sites in area II. Nutrient fluxes through live roots followed the order of $N > Ca = K > S > P$. The higher flows of Ca relative to those in area I sites probably were due to greater soil Ca availability and the larger forb and legume component. The proportion of net annual plant Ca uptake in live herbage ranged from 16% to 34% in area II. These figures are quite low compared with those for the other nutrients measured but are similar to those discussed for Ca in area I. They likely reflect higher Ca concentrations in roots and the relative immobility of Ca. Shoot uptake of K in area II accounted for between 55% and 62% of total net plant K uptake. These ratios are much lower than the comparable ratios in area I, due primarily to the much higher concentrations of K in roots on both area II sites.

Area II cation budgets were very similar to those reported for N, P, and S. Annual net plant K and Ca uptake demands caused temporary system deficits, which were balanced by nutrient storage in litter and dead roots at the end of both growing seasons. A much

larger amount of this K storage was in dead roots in area II than in area I, no doubt because of the higher concentrations of K in the roots. Very little Ca was accumulated in litter on any except the seeded site. This reflected both the larger mass and higher levels of Ca in the litter on the subclover-seeded grassland.

CONCLUSIONS

Although exclusion of grazing in area I did cause some changes in plant species composition, it resulted in little between-site difference in the other system variables we measured. There were no appreciable between-site differences in aboveground or belowground biomass annual net production or nutrient uptake in either year of the study, nor were there substantive differences in nutrient concentration dynamics. Between-year differences in biomass production and nutrient flows, reflecting primarily variation in temperature and rainfall, were generally greater than the between-site differences. These findings indicate that moderate grazing had little short-term (23 years) impact on productivity and nutrient cycling in this area.

In area II, 8 years of subclover growth and biennial fertilization with P and S resulted in large increases in biomass production and in amounts of system nutrient flows. Biomass production in both years of this study was greatly increased by these practices, reflected in large part by the much greater legume component. Dinitrogen fixation by these legumes resulted in system N inputs that exceeded the external inputs of P and S from fertilization. Most of the nutrient input was apparently accumulated in the soil—N and S primarily in the organic and P in the inorganic fraction. Increased biomass production and the changes in botanical composition on the seeded site also resulted in larger system K and Ca flows.

Herbage biomass annual net production far exceeded peak standing crop in both years on all sites because of the large measured contributions from recent dead herbage to the litter component. This finding suggested rapid turnover rates of plant material during the growing season, and was reflected also in belowground ANP and net annual nutrient uptake. High turnover rates suggest a close association between nutrient release, in this case the decomposition and mineralization of dead plant parts, and plant nutrient uptake (Gray 1983). This was obviously a dynamic process, and much of the plant-available supply of N, P, S, K, and Ca must have been remineralized and transferred through the systems more than once in a single growing season.

In addition to their role as biologically active substrates for mineralization, the litter and dead roots were very important storage components of the nutrient budgets on these annual grassland sites. Nutrient transfers through the soil available supplies to live plants during the growing season represented the largest flows in the budgets. Most of this nutrient pool remained stored in standing dead/litter as well as dead roots, and was retained against leaching between growing seasons. The subsequent fate of these nutrients would then be determined by new plant uptake and leaching demands, which showed a great deal of annual variation. If mineralization should exceed nutrient requirements, then net gains might be used in recharging the system soil storage compartments.

The nutrient cycles varied in their degrees of openness. Nitrogen had an open cycle, with inputs from N_2 fixation and atmospheric deposition and losses from leaching possibly representing a large portion of the total amount of N cycling through the system in any year. The P cycle was relatively closed, with no assumed loss of P from the cycle due to leaching and negligible inputs from natural sources. The S, K, and Ca cycles were open, but possible losses and inputs from natural sources represented a smaller portion of the total budget than in the N cycle.

ACKNOWLEDGMENTS

We would like to acknowledge the invaluable aid of Ms. Elaine Rose and Ms. Monica Turner with the field work, Mr. Brown San Diego with sample preparation, and Mr. Al Murphy for suggestions and administrative support.

LITERATURE CITED

- Arkley, T. H.
1961. Sulfur compounds of soil systems. Ph.D. thesis, Univ. Calif., Berkeley.
- Barrow, N. J.
1969. The accumulation of soil organic matter under pasture and its effect on soil properties. *Aust. J. Exp. Agric. Anim. Husb.* 9:437-44.
- Biddulph, O.
1959. Translocation of inorganic solutes. *In Plant Physiology*, vol. 2, ed. F.C. Steward, 553-603. New York: Academic Press.
- Bingham, F. T.
1949. Soil tests for phosphate. *Calif. Agric.* 3(8):11,14.
- Biswell, H. K.
1956. Ecology of California grasslands. *J. Range Manage.* 9:19-24.
- Bremner, J. M., and C. S. Mulvaney
1982. Nitrogen-total. *In Methods of soil analysis*, part 2. 2d ed, ed. A.L. Page, *Agronomy* 9:595-624. Madison, Wisconsin: American Society of Agronomy.
- Brougham, R. W.
1958. Leaf development in swards of white clover (*Trifolium repens* L.). *N. Z. J. Agric. Res.* 1:707-18.
- Charley, J. L.
1977. Mineral cycling in rangeland ecosystems. *In Rangeland plant physiology*. Science Series Number 4, ed. R.E. Sosebee, 215-56. Denver: Range Sci. Dept., Soc. Range Manage.
- Conrad, J. P.
1950. Sulfur fertilization in California and some related factors. *Soil Sci.* 70:43-54.
- Cromack, K. Jr., and C. D. Monk
1975. Litter production, decomposition, and nutrient cycling in a mixed hardwood watershed and a white pine watershed. *In Environmental chemistry and cycling processes*, eds. D.S. Adriano and I.L. Bresbin, 605-21. Washington, D.C.: U.S. Dept. of Energy.
- Denmead, O. T., J. R. Freney, and J. R. Simpson
1976. A closed ammonia cycle within a plant canopy. *J. Agric. Sci.* 42:162-71.
- Donald, C. M.
1963. Competition among crop and pasture plants. *Adv. Agron.* 15:1-118.
- Freney, J. R., K. Spencer, and M. B. Jones
1978. The diagnosis of sulphur deficiency in wheat. *Aust. J. Agric. Res.* 29:727-38.
- Frissel, M. J. (ed.)
1977. Cycling of nutrients in agricultural ecosystems. *Agro-Ecosystems* 4:1-354.
- George, M., J. Clawson, J. Menke, and J. Bartolome
1985. Annual grassland forage productivity. *Rangelands* 7:17-19.
- Gillingham, A. G., J. K. Syers, and P. E. H. Gregg
1980. Phosphorus uptake and return in grazed steephill pastures. II. Above-ground components of the phosphorus cycle. *N. Z. J. Agric. Res.* 23:323-30.

- Gray, J. T.
1983. Nutrient use by evergreen and deciduous shrubs in southern California. I. Community nutrient cycling and nutrient-use efficiency. *J. Ecology* 71:21-41.
- Hurlbert, S. H.
1984. Pseudoreplication and the design of ecological field experiments. *Ecol. Mono.* 54:187-211.
- Jones, M. B.
1974. Fertilization of annual grasslands of California and Oregon. *In* Forage fertilization, ed. D.A. Mays, 255-75. Madison, Wis.: Am. Soc. Agron.
- Jones, M. B., C. C. Delwiche, and W. A. Williams
1977. Uptake and losses of ^{15}N applied to annual grass and clover in lysimeters. *Agron. J.* 69:1019-23.
- Jones, M. B., W. E. Martin, and W. A. Williams
1968. Behavior of sulfate sulfur and elemental sulfur in three California soils in lysimeters. *Soil Sci. Soc. Am. Proc.* 32:535-39.
- Jones, M. B., J. E. Street, and W. A. Williams
1974. Leaching and uptake of nitrogen applied to annual grass and clover-grass mixtures in lysimeters. *Agron. J.* 66:256-58.
- Jones, M. B. and R. G. Woodmansee
1979. Biogeochemical cycling in annual grassland ecosystems. *Bot. Rev.* 45:111-14.
- Katznelson, J.
1977. Phosphorus in the soil-plant-animal ecosystem. *Oecologia* 26:325-34.
- Kennedy, R. K.
1972. Preliminary network evaluation on methods of primary biomass estimation. *In* Preliminary producer data synthesis, 1970 comprehensive sites. US/IBP Grassland Biome Tech. Rep. No 161, ed. P.G. Resser, 30-46. Fort Collins: Colo. State Univ.
- Kitson, R. E., and M. G. Mellow
1944. Colorimetric determination of phosphorus as molybdovanadophosphoric acid. *Anal. Chem.* 16:379-83.
- Knudsen, D., G. A. Petersen, and P. F. Pratt
1982. Lithium, sodium, and potassium. *In* Methods of soil analysis, part 2. 2d ed, ed. A.L. Page, *Agronomy* 9: 225-46. Madison, Wis.: Am. Soc. Agron.
- Loneragan, J. F., and K. Snowball
1969. Calcium requirements of plants. *Aust. J. Agric. Res.* 20:465-78.
- Marion, G. M.
1982. Nutrient mineralization in Mediterranean-type ecosystems. *In* Proceedings of the symposium on dynamics and management of Mediterranean-type ecosystems, eds. C.E. Conrad and W.C. Oechel, 313-20. Gen. Tech. Rep. PSW-58. Pacific Southwest Forest and Range Exp. Sta., USDA, Forest Service.
- Martin, W. E.
1958. Sulfur deficiency widespread. *Calif. Agr.* 12(11):10-12.
- McKell, C. M., M. B. Jones, and E. R. Perrier
1962. Root production and accumulation of root material on fertilized annual range. *Agron. J.* 54:459-64.
- McKell, C. M., A. M. Wilson, and M. B. Jones
1961. A flotation method for easy separation of roots from soil samples. *Agron. J.* 53:56-57.

- McNaughton, S. J.
1968. Structure and function in California grasslands. *Ecology* 49:962-72.
- Metson, A. J.
1974. Magnesium in New Zealand soils. I. Some factors governing the availability of soil magnesium: a review. *N. Z. J. Exp. Agric.* 2:277-319.
- Mokwunye, A. U., and S. W. Melsted
1972. Magnesium forms in selected temperate and tropical soils. *Soil Sci. Soc. Am. Proc.* 36:762-64.
- Molina, J. A. E., C. E. Clapp, M. J. Shaffer, F. W. Chichester, and W. E. Larson
1983. NCSOIL, a model of nitrogen and carbon transformation in soil: description, calibration, and behavior. *Soil Sci. Soc. Am. J.* 47:85-91.
- Munz, P. A., and D. D. Keck
1949. California plant communities. *El Aliso* 2:87-105.
- Myrold, D. D.
1988. Denitrification in ryegrass and winter wheat cropping systems of western Oregon. *Soil Sci. Soc. Am. J.* 52:412-16.
- Odum, E. P.
1960. Organic production and turnover in old field succession. *Ecology* 41:34-49.
- Ozanne, P. G., J. Keay, and E. F. Biddiscombe.
1969. The comparative applied phosphate requirements of eight annual pasture species. *Aust. J. Agric. Res.* 20:809-18.
- Parton, W. J., D. S. Schimel, C. V. Cole, and D. S. Ojima
1987. Analysis of factors controlling soil organic matter levels in Great Plains grasslands. *Soil Sci. Soc. Am. J.* 51:1173-79.
- Parton, W. J., J. W. B. Stewart, and C. V. Cole
1988. Dynamics of C, N, P and S in grassland soils: a model. *Biogeochem.* 5:109-31.
- Pastor, J., and J. G. Bockheim
1984. Distribution and cycling of nutrients in an aspen-mixed hardwood-spodosol ecosystem in northern Wisconsin. *Ecology* 65:339-53.
- Paul, E. A., and N. G. Juma
1981. Mineralization and immobilization of soil nitrogen by microorganisms. *In* Terrestrial nitrogen cycles. Processes, ecosystem strategies and management impacts, eds. F. E. Clark and T. Rosswall. *Ecol. Bull. Stockholm* 33:179-204.
- Pendleton, D. W., J. W. Menke, W. A. Williams, and R. G. Woodmansee
1983. Annual grassland ecosystem model. *Hilgardia* 51(1):1-44.
- Perrier, G. K., W. A. Williams, and J. W. Menke
1982. Tarweed, an unloved annual-type range plant. *Rangelands* 4:144-50.
- Phillips, D. A., D. M. Center, and M. B. Jones
1983. Nitrogen turnover and assimilation during regrowth in *Trifolium subterraneum* L. and *Bromus mollis* L. *Plant Physiol.* 71:472-74.
- Phillips, D. A., M. B. Jones, D. M. Center, and C. E. Vaughn
1983. Estimating symbiotic nitrogen fixation by *Trifolium subterraneum* L. during regrowth. *Agron. J.* 75:736-41.
- Pitt, M. D., and H. F. Heady
1978. Responses of annual vegetation to temperature and rainfall patterns in northern California. *Ecology* 59:336-50.
- Reisenauer, H. M.
1975. Soil assays for the recognition of sulphur deficiency. *In* Sulphur in Australasian agriculture, ed. K.D. McLachlan, 182-87. Sydney, Australia: Sydney Univ.Press.

- Robson, N. J.
1973. The growth and development of simulated swards of perennial ryegrass. I. Leaf growth and dry weight change as related to ceiling yield of a seedling sward. *Ann. Bot.* 37:387-500.
- Savelle, G. D.
1977. Comparative structure and function in a California annual and native bunchgrass community. Ph.D. thesis. Univ. Calif., Berkeley.
- Schlesinger, W. H., and M. M. Hasey
1981. Decomposition of chaparral shrub foliage: losses of organic and inorganic constituents from deciduous and evergreen leaves. *Ecology* 62:762-74.
- Sharpley, A. N.
1985. Phosphorus cycling in unfertilized and fertilized agricultural soils. *Soil Sci. Soc. Am. J.* 49:905-11.
- Sharpley, A. N.
1986. Disposition of fertilizer phosphorus applied to winter wheat. *Soil Sci. Soc. Am. J.* 50:953-58.
- Sharpley, A. N., C. A. Jones, C. Gray, and C. V. Cole
1984. A simplified soil and plant phosphorus model: II. Prediction of labile, organic, and sorbed phosphorus. *Soil Sci. Soc. Am. J.* 48:805-09.
- Shock, C. C., M. B. Jones, W. A. Williams, and D. M. Center
1984. Competition for S and N by associations of three annual range species in lysimeters. *Plant Soil* 81:311-21.
- Shock, C. C., W. A. Williams, M. B. Jones, D. M. Center, and D. A. Phillips
1984. Nitrogen fixation by subclover associations fertilized with sulfur. *Plant Soil* 81:323-32.
- Simpson, J. R.
1965. The transference of nitrogen from pasture legumes to an associated grass under several systems of management in culture. *Aust. J. Agric. Res.* 16:915-26.
- Simpson, J. R.
1976. Transfer of nitrogen from three pasture legumes under periodic defoliation in a field experiment. *Aust. J. Exp. Ag. Anim. Husb.* 16:863-70.
- Singh, J. S., W. K. Lauenroth, and R. K. Steinhorst
1975. Review and assessment of various techniques for estimating net aerial primary production in grasslands from harvest data. *Bot. Rev.* 41:181-232.
- Stinner, B. R., E. P. Odum, and D. A. Crossley, Jr.
1983. Nutrient uptake by vegetation in relation to other ecosystem processes in conventional tillage, no-tillage, and an old field system. *Agric., Ecosystems, Environ.* 10:1-13.
- Stinner, B. R., D. A. Crossley, Jr., E. P. Odum, and R. L. Todd
1984. Nutrient budgets and internal cycling of N, P, K, Ca, and Mg in conventional tillage, no-tillage, and old field ecosystems on the Georgia piedmont. *Ecology* 65:354-69.
- Tabatabai, M. A., and J. M. Bremner.
1970. A simple turbidimetric method of determining total sulfur in plant materials. *Agron. J.* 62:805-06.
- Tiesen, H., J. W. B. Stewart, and J. R. Bethany
1982. Cultivation effects on amounts and concentrations of carbon, nitrogen, and phosphorus in grassland soils. *Agron. J.* 71:831-35.

Van Hook, R. I., Jr.

1971. Energy and nutrient dynamics of spider and orthopteron populations in a grassland ecosystem. *Ecol. Monogr.* 41:1-26.

Varian Techtron

1972. Analytical methods for flame spectroscopy. Melbourne, Australia: Varian Techtron Property, Ltd.

Vaughn, C. E. and A. H. Murphy

1982. Long-term effects of fertilization and subclover seeding on northern California annual range. *J. Range Manage.* 35:92-95.

Vaughn, C. E., D. M. Center, and M. B. Jones

1986. Seasonal fluctuations in nutrient availability in some northern California annual range soils. *Soil Sci.* 141:43-51.

Whitehead, D. C.

1970. The role of nitrogen in grassland productivity. Bull. No. 48. Farnham Royal, Bucks., England: Commonwealth Agric. Bureau.

Whittaker, R. H., G. E. Likens, F. H. Bormann, J. S. Eaton, and T. G. Siccama

1979. The Hubbard Brook ecosystem study: Forest nutrient cycling and element behavior. *Ecology* 60:203-20.

Woodmansee, R. G., and D. A. Duncan

1980. Nitrogen and phosphorus dynamics and budgets in annual grasslands. *Ecology* 61:893-904.

Woodmansee, R. G., J. L. Dodd, R. A. Bowman, F. E. Clark, and E. E. Dickenson

1978. Nitrogen budget of a shortgrass prairie ecosystem. *Oecologia (Berlin)* 34:363-76.