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ECOSYSTEMS

Temporal Asynchrony in Soil Nutrient Dynamics and Plant Production in a Semiarid Ecosystem

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ABSTRACT

A central goal of ecosystem ecology is to understand how the cycling of nutrients and the growth of organisms are linked. Ecologists have repeatedly observed that nutrient mineralization and plant production are closely coupled in time in many terrestrial ecosystems. Typically, mineralization rates of limiting nutrients, particularly of nitrogen, during the growing season determine nutrient availability while pools of mineral nutrients remain low and relatively constant. Although several previous reports suggest nitrogen mineralization has the potential to vary seasonally and out of phase with plant production, such a phenomenon has been poorly documented. Here we report results from a semiarid savanna ecosystem characterized by distinct temporal asynchrony in rates of soil nitrogen cycling and plant production. Periods of positive plant growth following the onset of rains coincide with periods of low N turnover rates, whereas higher rates occur late in the wet season following plant senescence and throughout dry seasons. Plant uptake from the substantial mineral N pool present early in the growing season is sufficient to explain most of the N allocation to aboveground plant biomass during the growing season, even in the absence of any wet-season mineralization. The mineral N pool is subsequently recharged by late wet- and dry-season mineralization, plus urine inputs at sites with high levels of ungulate activity. These findings suggest fundamental changes in the quality of substrates available to decomposers over a seasonal cycle, with significant implications for the partitioning of limiting nutrients by plant species, the seasonal pattern of nutrient limitations of aboveground production, and the effective use of N fertilizers in semiarid ecosystems.

Key words: grazing; grassland; inorganic nitrogen; Kenya; mineralization; nutrient cycling; phosphorous; rangeland; savanna.

INTRODUCTION

The simplest nutrient cycle within an ecosystem consists of nutrient uptake and incorporation into organic molecules by plants and the release of nutrients from organic to inorganic forms by decomposers. Plant and microbial activity in many temperate ecosystems are temporally synchronized by seasonal temperature fluctuations, with minimal activity during fall-winter and a pulse of growth and nitrogen mineralization during spring- summer (Nadelhoffer and others 1984; Pastor and others 1984; Vitousek and Matson 1985; Wedin and Tilman 1990; Burke 1989; Hatch and others 1991; Frank and Groffman 1998; Wilson and others 1999). Similar patterns have been documented for the tropics, where rainfall initiates a pulse of synchronous plant production and significant N mineralization (Marrs and others 1991; McNaughton and others 1997; Singh and others 1989, 1991). Funda-

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mental characteristics of all these ecosystems include low and relatively constant inorganic N pools over time, high rates of annual net N mineralization relative to inorganic pool fluctuations, and N supplied to plants via growing-season mineralization.

More recently, studies of N cycling in some ecosystems have identified ecologically significant rates of N mineralization occurring out of phase with the growing season. For example, in alpine tundra, large increases in the inorganic N pool have been documented during snowmelt (Brooks and others 1998) and the highest rates of N mineralization occur during late summer or early fall, after plant senescence (Jaeger and others 1999). In California annual grasslands, soil inorganic N pools and microbial biomass N increase during dry seasons, indicating N flux out of phase with plant growth (Jackson and others 1988). Similarly, in monocultures of the grass *Agrostis scabra*, most N mineralization occurs in August when this species is dormant (Wedin and Tilman 1990).

Greater understanding of the temporal patterns of inorganic N turnover and plant growth in ecosystems is needed because these patterns can influence at least four important aspects of community and ecosystem dynamics. First, asynchrony in plant growth and inorganic N availability can allow significant N losses in surface waters to occur even from N-limited ecosystems (Brooks and others 1998; Vitousek and others 1998). Second, despite the low and variable rainfall characteristic of semiarid grasslands and savannas, many studies have shown that both N and P availability can limit primary productivity and influence community composition (Penning de Vries and others 1980; Hooper and Johnson 1999; Paschke and others 2000; Snyman and others 2002). In semiarid ecosystems, seasonal fluctuations in the size of the inorganic N pool has been hypothesized to underlie temporal variation in the degree to which N versus P limits net primary productivity (Penning de Vries and others 1980), but data examining this idea are lacking. Third, greater understanding of temporal fluctuations in inorganic N dynamics can provide insight on the degree to which decomposers are regulated by seasonal changes in substrate quality and availability versus fluctuations in soil moisture and temperature (Burke 1989; Jaeger and others 1999). Fourth, traditional models of plant species coexistence have been predicated on a constant supply rate of limiting nutrients (Tilman 1988), but more recent work has shown that coexisting plant species can be differentiated in terms of both the chemical form and the timing of N acquisition (McKane and others 2001).

We studied the temporal pattern of inorganic N turnover and plant growth in a semiarid savanna ecosystem in central Kenya. Our objective was to evaluate the linkages between plant production and net N mineralization on nutrient-rich grassland glades dominated by lawns of *Cynodon plectostachyus*, and in the surrounding nutrient-poor *Acacia* bushland, dominated by a more diverse perennial, herbaceous community (Young and others 1995). Specifically, we examined relationships among rainfall, aboveground net primary production (ANPP), N allocated to aboveground net primary production (ANPP-N), inorganic N pool dynamics, and in situ net N-mineralization rates during 6–8-month study seasons in 3 disparate years: a relatively dry year in 1999 (417 mm rainfall), a drought year in 2000 (296 mm), and a wet year in 2001 (658 mm).

METHODS

Study Area

All research was conducted at the Mpala Research Centre and associated Mpala ranch (MRC) which encompasses 190 km^2 of semiarid savanna within the Laikipia district of central Kenya (37°53′E, 0°17′N). Topography consists of gently rolling hills and occasional granitic inselbergs. Mean annual rainfall during 1972–2000 was 508 mm (1 SD = 226 mm; CV = 0.44). Rainfall occurs in a trimodal fashion with wet seasons typical during April–May, August, and October, and a consistent dry season during January–March. Our studies of plant and nutrient dynamics were initiated in the January–March dry season and encompassed wet seasons during April–August in 1999, 2000, and 2001.

The landscape at MRC contains a two-phase vegetation mosaic with discrete, short-grass glades lacking woody vegetation (1% of the landscape) embedded within the background *Acacia*-dominated community (99% of the landscape; Young and others 1995). These short-grass glades are a legacy of cattle management practices in the region. For at least the past 200 years, cattle at MRC have been contained overnight in semipermanent brush-ringed corrals or ''bomas'' where significant quantities of dung and urine accumulate. Bomas are typically abandoned after several years of use and subsequently colonized by a unique plant community as the manure layer becomes mixed with mineral soil (Stelfox 1986; Young and others 1995; Reid and others 1995). Soil carbon and nutrient content declines dramatically during the first 4 decades after boma abandonment, but bomas more than 40 years old remain enriched in nutrients relative to surrounding bushland soils for an unknown time period (Augustine 2003a), possibly up to several centuries (Blackmore and others 1990). Abandoned bomas that are more than 40 years old (''glades'' hereafter) are typically 0.5–1.0 ha in size and contain 1.6 times more total soil C and N than surrounding bushland soils (Augustine 2003a).

We studied four grassland glades (all more than 40 years old based on 1961 aerial photos) and four nearby *Acacia* bushland sites in 1999 and 2000, and three glade and three bushland sites in 2001. Glades and bushland sites were both underlain by friable sandy loams developed from metamorphic parent material (Ahn and Geiger 1987), and both types of study sites had similar soil texture (75% sand, 8%–14% clay), were located at similar upper topographic positions, and received the same rainfall. Glades were dominated by *Cynodon plectostachyus* and the annual forb *Tribbalus terrestris* and lacked shrubs. Bushland sites in 1999–2000 were dominated by *Cynodon dactylon* between shrubs and *Cynodon dactylon* and *Digitaria milanjiana* beneath shrub canopies. Bushland sites in 2001 were dominated by *Cynodon dactylon* and *Digitaria milanjiana* between shrubs and *Enteropogon macrostachyus* and *Cymbopogon pospischillii* beneath shrubs. Dominant shrubs were *Acacia mellifera* and *Acacia etbaica*. Dominant grazers in the study area were cattle and impala (*Aepyceros melampus*), which occurred at average densities of 12.2 and 20.3 km^{-2} respectively (Augustine 2002).

Plant Productivity and Nitrogen Cycling

Measures were initiated during the January–March dry season each year. In 1999 and 2000, studies encompassed two distinct dry–wet cycles, whereas studies in 2001 encompassed a single 6-month dry–wet cycle. Aboveground net primary productivity (ANPP) of the herbaceous layer was measured each study season by sequential measures of biomass inside and outside 1-m^3 movable grazing cages (McNaughton and others 1996; $N = 4$ cages and 8 grazed plots per glade, 6 cages and 12 grazed plots per bushland site in 1999–2000; 6 cages and 12 grazed plots per glade, 12 cages and 24 grazed plots per bushland site in 2001). This method was used because grazing pressure in this ecosystem is intense, and we wanted a measure of productivity that included plant biomass consumed by ungulates. Live biomass and standing dead biomass were measured on each cage and control plot by canopy interception (see Augustine 2003b for regression equations) at 22–30-day intervals during early wet seasons, and 30–40-day intervals during late wet and dry seasons. For each study site, ANPP was calculated as the sum of positive increases in live biomass inside cages for all measurement intervals where this increase was statistically significant at the $\alpha \leq 0.1$ level. Because the cages temporarily prevent ungulate consumption during the measurement interval, this method measures the ANPP of grazed vegetation including consumption by large herbivores (McNaughton and others 1996). Sampling at bushland sites was stratified between and beneath shrub canopies. We also clipped a 20 × 20-cm subsample of plant tissue from caged plots at each sampling date and returned tissues to Syracuse University for C and N determination. A rain gauge was maintained at each of the study sites.

On each sampling date, we also collected 5-cm-diameter × 15-cm-deep bulk soil cores for determination of inorganic N pools (4 cores per glade and 8 cores per bushland site in 1999–2000; 6 cores per glade and 12 cores per bushland site in 2001) and incubated the same number of cores in situ in 5-cm–diameter × 15-cm-deep PVC tubes until the subsequent measurement interval (McNaughton and others 1997). In July 1999, we also collected bulk cores from 0–15-, 15–40-, and 40–65-cm soil depths and evaluated changes in the inorganic N pool with depth (Augustine 2003a). Initial and incubated soil cores were maintained on ice or refrigerated until a 15-g subsample was extracted with 1 M KCl within 48 h of collection. An additional subsample (2.5 g) from each initial core was extracted with Mehlich 3 solution (Mehlich 1984) for determination of extractable P content. Total soil and plant C and N were determined by Dumas combustion with a Carlo-Erba CN Analyzer and ammonium and nitrate concentrations were measured by autoanalyzer methods on the KCl extracts. Extractable P concentrations were determined by inductively coupled plasma spectroscopy (Leman Labs PS3000, Hudson, MA) in simultaneous mode using sample preparation procedures described by McNaughton (1988).

During the studies in 1999–2001, we did not measure potential leaching losses of N from the bottom of the PVC mineralization tubes. Two additional studies conducted during the 2002 wet season quantified this potential source of N loss from mineralization tubes. Specifically, we measured leaching from PVC mineralization tubes at six study sites that varied widely in the size of the initial inorganic N pool size, and we conducted irrigation studies that varied rainfall from 68 to 128 mm at sites with both high and low initial inorganic N pools (Augustine 2002). Briefly, mineralization was measured in the same way as during 1999–2001, but we also placed nylon bags containing 2 level tablespoons (29.6 ml) of mixed-bed ion-exchange resin (Dowex MR-3, a 1:1 mixture of HCRS[H^+] and SBR[OH^-]) at the bottom of each 5-cm–diameter × 15-cm-deep PVC tube during the incubation. In addition, a second, paired resin bag was placed in a PVC cylinder measuring only 5-cm-diameter × 2-cm deep; this small cylinder was buried at a depth of approximately 13–15 cm beneath undisturbed soil in the immediate vicinity of the 15-cm tube. Leaching loss was estimated as the difference in resin-N adsorption rates beneath mineralization tubes (where plant uptake of N was prevented) versus resin-N adsorption rates beneath bulk soil where plant roots were present. A multiple regression analysis showed that both rainfall and initial mineral N pool size were significant predictors of leaching rate, yielding the relationship: [Leached N (g N m^{-2}) = 0.00536*(mm rain) + 0.1315*(initial g mineral N m^{-2}) − 0.1977; $F_{2,113} = 64.5$, $P < 0.001$, $r^2 = 0.53$, $t_{\text{rain}} = -3.74$, $P = 0.0003$; $t_{\text{mineralN}} = 8.99$, $P < 0.0001$]. This relationship was used to correct estimates of mineralization rates in the studies conducted during 1999–2001 for leaching losses based on monthly rainfall and initial mineral N pool size. Resin bags incubated at the bottom of mineralization tubes and in bulk soil during May 2000 showed no leaching with rainfall of 32 mm, so the regression was applied only in months where rainfall exceeded 40 mm.

N Mineralization and Plant ANPP-N Comparisons

Monthly net N mineralization was the difference between ($NH_4^+ - N + NO_3^- - N$) from incubated versus initial soil cores, after correcting for leaching loss. Due to occasionally extreme local heterogeneity in inorganic N concentrations, in all analyses of net N-mineralization rates, samples exceeding the mean by ±3 standard deviations were excluded from analyses. To compare net N mineralization and plant growth in the same units, we calculated monthly rates of N allocation to aboveground production (ANPP-N, in units of g N m^{-2} $month^{-1}$) as ANPP times the N content of live biomass (Biondini and Manske 1996).

For two complete dry-wet season cycles during March–May in 1999 and 2001, we compared ANPP-N with the magnitude of potential sources of inorganic N. Potential N supplied to plants by the inorganic N pool alone (without mineralization) was calculated by difference for the duration of net plant growth at each site (Mar–Apr at five sites and Mar–May at three sites in 1999; Mar–May at all six sites in 2001). Urine deposition during the growing season was calculated from dung deposition rates measured monthly at each site using eight 20 × 2-m transects per site. Ratios for calculation of grams urine-N deposited per gram of dung-N deposited were derived from Holter and others (1979) for impala and Scholefield and others (1991) for cattle. All reported standard errors reflect among-site variation (that is, variation among true replicates at the landscape scale). All soil N values reported on a g m^{-2} basis are to a depth of 15 cm.

Seasonal changes in net N mineralization rates and the inorganic N pool were tested using repeated-measures analysis of variance (ANOVA) applied to the monthly means for each study site, with a block term included to account for pairing of glade and bushland sites (von Ende 1993). Each year was analyzed separately due to major differences among years in rainfall and the fact that different bushland sites were studied during 2001 than during 1999–2000.

RESULTS

Plant Production and Inorganic N Dynamics

In all three study seasons during 1999–2001, net N-mineralization rates and inorganic N pool sizes fluctuated significantly over seasonal cycles (Table 1). No difference was detected between glade and bushland communities in terms of net N-mineralization rates in 1999, although a significant month × community interaction was observed for net N mineralization in 2000 and 2001 (Table 1) reflecting lower rates in glades compared to bushland during wet seasons (August 2000 and April–May 2001; Figures 1 and 2). Large, highly significant monthly fluctuations in the inorganic N pools were observed in all 3 years (Table 1). In 1999, a significant month × community interaction was detected, reflecting more rapid inorganic N accumulation in glades than in bushland soils during dry seasons, but declines to similarly low inorganic N pool sizes in both communities during the wet season (Figure 3). In 2001, a weakly significant month × community interaction was again observed ($P = 0.08$, Table 1), also reflecting greater inorganic N pool size in glades during the dry but not the wet season (Figure 3). Inorganic N increased in both communities throughout the drought in 2000 and was significantly higher in

Table 1. Results of Repeated-Measures ANOVAs Examining Variation in Net N-Mineralization Rates and the Inorganic N Pool Size in Terms of Seasonality (month effect) and Differences between Glades versus Bushland Sites (community effect)

	N mineralization				Inorganic N pool		
Effect	*df*	*F*	*P*		*df*	*F*	*P*
				1999			
Block	3,3	1.41	0.729		3,3	1.75	0.329
Community	1,3	0.14	0.393		1,3	8.52	0.062
Month	6,36	2.58	0.035		6,36	6.33	0.0001
Community × Month	6,36	1.13	0.367		6,36	2.80	0.024
				2000			
Block	3,3	6.00	0.088		3,3	0.88	0.542
Community	1,3	5.83	0.095		1,3	19.97	0.021
Month	4,24	3.38	0.025		4,24	6.21	0.001
Community × Month	4,24	4.69	0.006		4,24	1.84	0.154
				2001			
Block	2,1	1.04	0.570		2,1	1.17	0.548
Community	1,2	0.03	0.886		1,2	1.67	0.325
Month	4,16	6.58	0.003		5,20	17.52	0.0001
Community × Month	4,16	3.21	0.041		5,20	2.31	0.083

glades than bushland throughout this period (Table 1 and Figure 3).

In all 3 years of the study, periods of rapid plant growth consistently were temporally separated from high rates of net N mineralization (Figure 1). ANPP, ANPP-N, and seasonal fluctuations in net N mineralization were greater in glades than bushland, but both production (ANPP) and plant demand for nitrogen (ANPP-N) were temporally asynchronous with N-mineralization rates at all sites (Figures 1 and 2). Significantly positive net N mineralization coincided with the onset of the wet season only during brief middrought showers in May 2000, which stimulated minimal plant growth (Figures 1 and 2). N-mineralization rates were near zero or slightly negative during the four periods with the highest rates of plant growth and N demand: April 1999, August 1999, August 2000, and April–May 2001 (Figures 1 and 2). Both net nitrification and net ammonification rates were typically negative or zero early in the wet season. Net nitrification rates peaked late in the wet season (more than 80% of net mineralization) and declined during dry seasons, whereas net ammonification increased as dry seasons progressed.

In 2001, rainfall during April averaged 65 mm and initiated significant plant growth across the landscape, but it was associated with a lack of net N mineralization (Figure 1). ANPP peaked in May following an additional 122 mm of rainfall. Late in the growing season, rainfall during July (57 mm) and August (74 mm) was similar in magnitude to April rains, but new plant production remained low as grasses matured. Soil N dynamics averaged across all sites switched from no net mineralization (-0.11 ± 0.42 g N m^{-2}; $\bar{x} \pm 1$ SE) in April to net positive mineralization (1.47 ± 0.25 g N m^{-2}) in August (paired $t_5 = 4.81$, $P = 0.005$) despite similar levels of rainfall in both months.

In contrast to the strong seasonality we found for inorganic N dynamics, inorganic P pools were relatively constant over the seasonal cycle (Figure 4). During the drought in 2000, Mehlich-extractable P did not vary across months (repeated-measures ANOVA, test for month effect: $F_{2,12} = 0.72$, $P = 0.51$) but was significantly greater in glades than bushland sites ($F_{1,3} = 14.16$, $P = 0.033$). During the long rains in 2001, extractable P was again constant over time ($F_{5,15} = 0.21$, $P = 0.95$) and, considering the low power of the statistical test, significantly greater in glades than bushland sites ($F_{1,2} = 11.84$, $P = 0.075$; Figure 4). Furthermore, Mehlich-extractable P pools were similar in drought and wet years (Figure 4).

At first glance, the low rates of net N mineralization documented during growing seasons suggest N availability severely limits plant production. However, significant mineralization during the transition from wet to dry seasons, continued dry-season mineralization, and urine deposition in glades recharged mineral N pools each seasonal cycle, leading to maximal inorganic N availability at

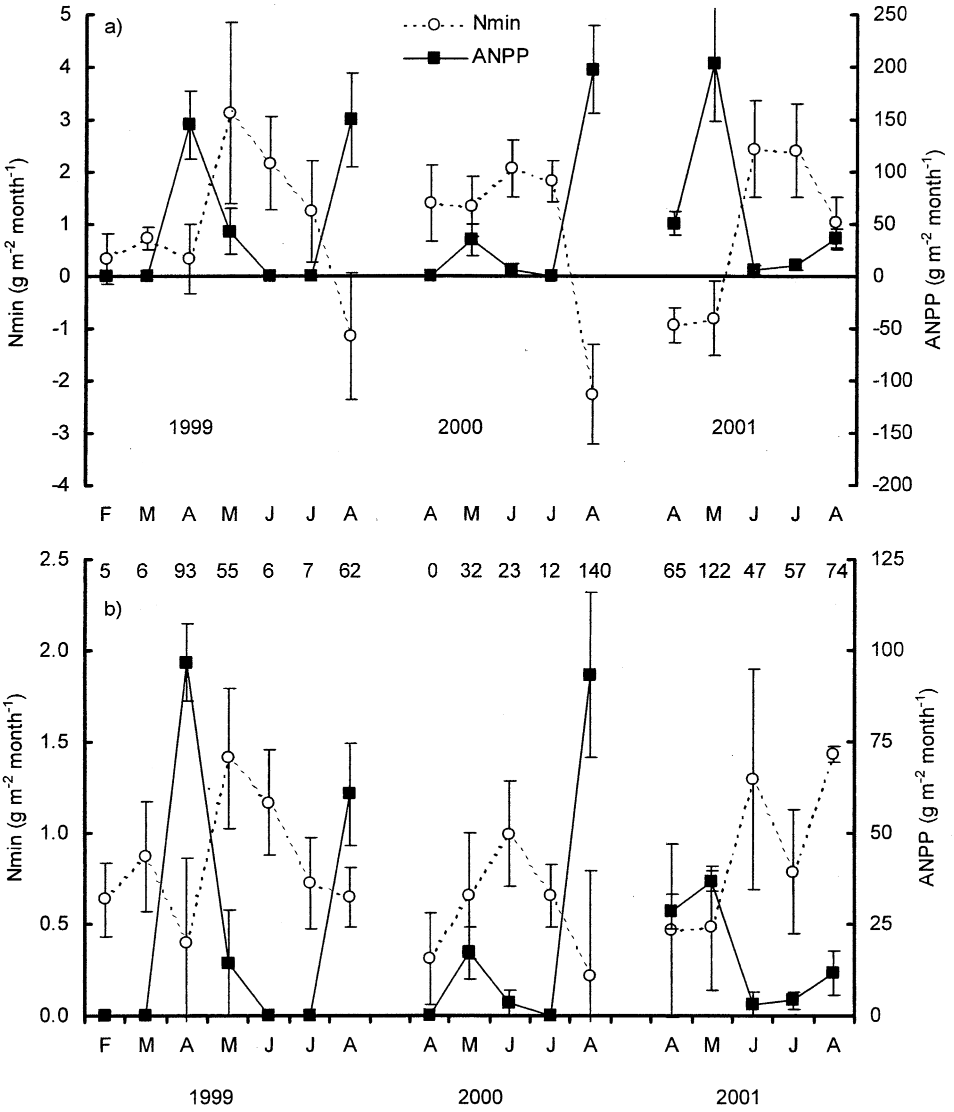

Figure 1. Seasonal patterns of ANPP and in situ net N mineralization for nutrient-rich glades (**a**) and nutrient-poor acacia bushland (**b**) at Mpala, Kenya. Studies encompassed a dry year (1999), a drought year (2000), and a wet year (2001). The numbers below each month along the *x*-axis in **a** show rainfall (mm) during that measurement interval. These rainfall data also apply to the bushland sites in **b**. Note differences in the scaling of axes between **a** and **b**. Error bars show 1 SE.

the onset of the next rainy season (Figure 3). Furthermore, inorganic N pool sizes increased throughout the drought (April–August 2000) and were much larger in July 2000 and March 2001, at the end of long dry seasons, compared with inorganic N pool sizes in February and July 1999, which followed short dry seasons (Figure 3). Large declines in the inorganic N pool coincided with pulses of aboveground production in April 1999 and April–May 2001, both in glades and bushland sites (Figure 3). Positive aboveground production only coincided with increasing inorganic N pools during May 1999 and 2000 (Figure 3). In May 1999, plant production was low and declining, some plants were beginning to senesce, and net N mineralization occurred at the highest rate recorded during the 3-year study for both glades and bushland sites (Figure 1). In 2000, rainfall during May was much lower than in most years, plant productivity was correspondingly low, and net N mineralization rates were similar to dry-season months.

To evaluate whether seasonal fluctuations in pool size alone can account for plant N requirements during the growing season, we calculated the total amount of N allocated to aboveground plant production during the growing season in April–May 1999 and during a second growing

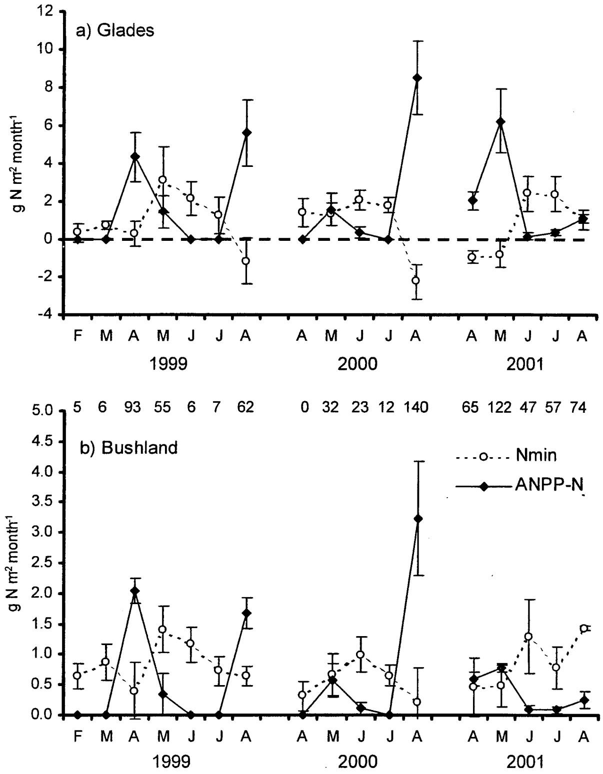

Figure 2. Seasonal patterns of N allocated to aboveground net primary production of the herbaceous layer (ANPP-N) and in situ net N mineralization for nutrient-rich glades (**a**) and nutrient-poor acacia bushland (**b**). Rates for ANPP-N and net N mineralization are both expressed in g N m^{-2} $month^{-1}$. Studies encompassed a dry year (1999), a drought year (2000), and a wet year (2001). The numbers below each month along the x-axis in **a** show rainfall (mm) during that measurement interval. These rainfall data also apply to the bushland sites in **b**. Note differences in the scaling of axes between **a** and **b**. Error bars show 1 SE.

season in April–May 2001. Declines in the inorganic N pool during the growing season (0–15-cm depth) accounted for 88% of the N in aboveground plant production at glades and 39% of the N in aboveground plant production at bushland sites during 1999 (Table 2). Corresponding estimates for 2001 were 55% at glades and >100% at bushland sites. In contrast, net N mineralization was a much smaller source of inorganic N relative to pool size fluxes in both years, especially in glades (Table 2).

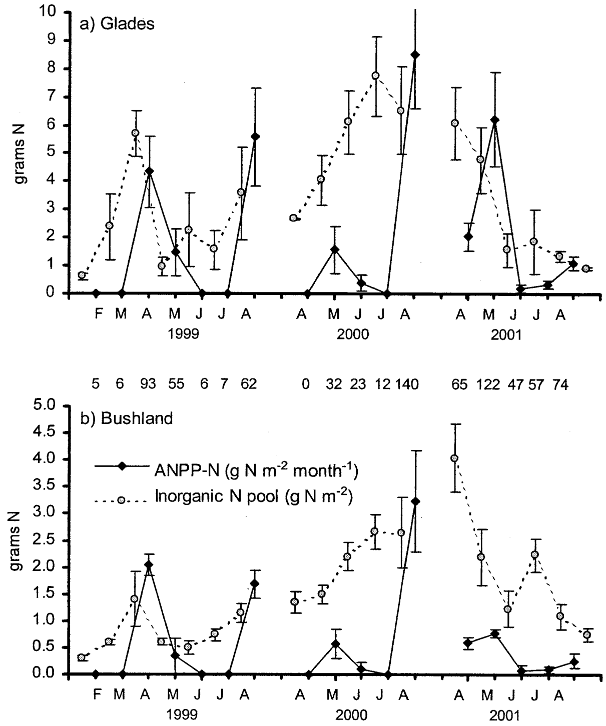

Figure 3. Seasonal patterns of N allocated to aboveground net primary production of the herbaceous layer (ANPP-N) and changes in soil inorganic N pool size over 3 years for nutrient-rich glades (**a**) and nutrient-poor acacia bushland (**b**). The numbers below each month along the x-axis in **a** show rainfall (mm) during that measurement interval. These rainfall data also apply to the bushland sites in **b**. Note differences in the scaling of axes between **a** and **b**. Error bars show 1 SE.

DISCUSSION

Results from this study demonstrate distinct temporal asynchrony between plant production and soil N turnover. Soil inorganic N at the onset of wet seasons is sufficient to support observed levels of plant production, but this pool is rapidly depleted during 1–2-month growing seasons. Significant mineralization during plant senescence and dry-season months, combined with urine inputs in glades, recharges the mineral N pool. In contrast to many terrestrial ecosystems, seasonal fluctuations in extractable mineral N are large and, in the case of bushland study sites, similar in magnitude to net mineralization during late wet-season and early dry-season months. Sustained rainfall over several months leads to continually low soil inorganic N levels as late wet-season mineralization is offset by plant production and uptake.

This temporal pattern has significant implications for four aspects of ecosystem ecology and management. First, it explains seasonal shifts in the degree to which N versus P limits grass production in semi-arid ecosystems (Penning de Vries and others 1980), with maximal N limitation occurring in high-rainfall years with short dry seasons. This

Table 2. N Allocation to ANPP (ANPP-N), Changes in $NH_4^+ + NO_3^- - N$ Pools, and Net N-Mineralization Rates during Periods of Active Plant Growth in March–May 1999 and 2001.

	March–May 1999		March–May 2001	
	Glades	Bushland	Glades	Bushland
ANPP-N (g N m^{-2})	5.80 (0.67)	2.38 (0.53)	8.27 (2.49)	1.37 (0.11)
Decline in Inorganic N pool (g N m^{-2})	5.10 (0.76)	0.92 (0.48)	4.51 (1.19)	2.81 (0.34)
Net N mineralization (g N m^{-2})	0.44 (0.90)	0.57 (0.48)	−1.74 (0.41)	0.94 (0.80)
Urine deposition	1.42 (0.30)	0.17 (0.06)	0.56 (0.06)	0.08 (0.03)
% of ANPP-N accounted for by decline in N pool in 0.15-cm soil layer	88	39	55	>100

Values shown are means of 4 glade and 4 bushland sites in 1999 and 3 glade and 3 bushland sites in 2001; values in parenthesis are 1 SE.

seasonal variation in the magnitude of N limitation indicates that the use of N fertilizers in temporally asynchronous ecosystems needs to be carefully tailored to yearly rainfall conditions. N fertilization early in the growing season, when natural N pools are already extremely high, could exacerbate losses from other pathways such as volatilization (Ball and Ryden 1984) and denitrification (Hall and Matson 1999), whereas fertilization only a month later could be highly effective.

Second, results provide insight to the role seasonal patterns may play in the retention of N in semiarid ecosystems (Vitousek and others 1998). The degree to which fluctuations in the inorganic N pool size accounted for aboveground plant production varied among years and communities, ranging from 39% to greater than 100% (Table 1). Because these calculations do not account for N allocated to aboveground production from root reserves or from soils below 15-cm depth, they indicate that the inorganic N pool just prior to the onset of rains is a major source of N for plant growth, and far exceeds the importance of wet-season mineralization. A significant portion of plant N uptake could occur beneath the 0–15-cm soil layer, particularly in bushland communities. Inorganic pools in the 0–15-cm soil layer represent 55% of total inorganic N to a depth of 65 cm in glades and only 29% of total inorganic N to 65 cm in bushland (Augustine 2003a). At Mpala, both the inorganic N pool and total soil N content decline with depth (Augustine 2003a), and studies in other tropical grassland soils show that N mineralization in deeper soil layers occurs at lower rates (but with the same temporal pattern) than in the surface layer (S. J. McNaughton, unpublished). As a result, we believe it is unlikely (but still possible) that wet-season N mineralization in deep soils supports plant N uptake. Rather, based on the simple assumption that inorganic N uptake from different soil layers occurs in proportion to the size of the inorganic N pool in those layers (for example, in glades, 54% from the 0–15-cm layer, 28% from the 15–40-cm layer, and 17% from the 45–65-cm layer), all of the N allocated to aboveground plant production can be accounted for by depletion of the soil inorganic N pool alone. In addition, root biomass in tropical grasslands reaches a maximum during dry seasons and a minimum during wet seasons (San José and others 1982; Kinyamario and Imbamba 1992; McNaughton and others 1998), such that some N allocated aboveground during the wet season may also be derived from roots. Finally, urine inputs during the growing season represent another N source, which is substantial in glades where both impala and cattle concentrate their grazing activities (Table 2). The rapid dry-season increase in mineral N pools in glades, particularly in 1999 (Figure 3), is likely also related to urine input because impala deposit significant quantities of urine and dung on glades in dry seasons (Augustine 2002). All of these lines of evidence support the conclusion that the accumulation of mineral N during late-wet and dry seasons, rather than N mineralized during the primary period of plant growth, plays a major role in supplying plant N requirements. At the same time, we also acknowledge that because net N-mineralization assays measure the balance between gross mineralization and gross immobilization, they can underestimate N supply if plants or their mycorrhizal symbionts are capable of competing effectively with soil microbes for N (for example, Kaye and Hart 1997). Measures of gross mineralization rates and ^{15}N tracer studies could provide further insight to the importance of microbial activities in supplying N to plants during growing seasons.

In this study, soil inorganic N levels at bushland sites switched from 39% of herbaceous production in 1999 to nearly double the amount required for

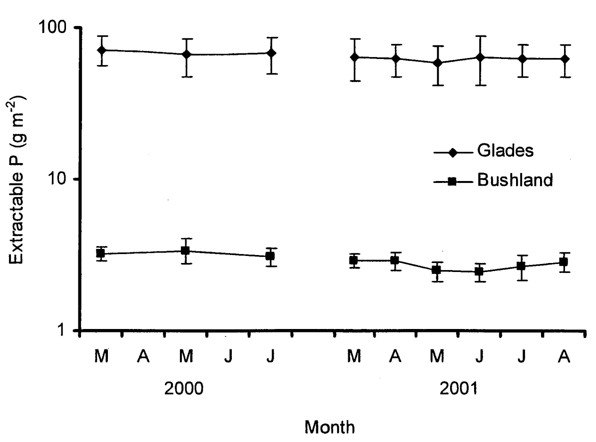

Figure 4. Seasonal changes in the pool of Mehlich-extractable inorganic P in the 0–15-cm layer of glade and bushland soils at MRC during a drought in 2000 and a long wet season in 2001. Note the logarithmic scale. Error bars show ±1 SE.

herbaceous production in 2001. This switch reflects a significant decline in herbaceous productivity from 1999 (which followed a high-rainfall year in 1998) to 2001 (which followed a severe drought in 2000). Grass tuft mortality during the drought, exacerbated by intense grazing, may be an important cause of the low plant demand for inorganic N in 2001. Thus, substantial accumulation of inorganic N in soil during the 2000 drought (Figure 3) followed by low plant demand in subsequent wet seasons on drought- and grazing-affected sites (2001 bushland sites, Table 1), could potentially cause significant leaching and erosional and gaseous losses of N during that first postdrought rainy season. Although further study is needed to quantify pathways of N loss, this drought-induced asynchrony in inorganic N availability and plant demand provides initial empirical support for Vitousek and others' (1998) hypothesis that semiarid ecosystems may be characterized by pulsed losses of N, even if N is limiting to plant growth. The significant accumulation of soil inorganic N that we documented during the drought also provides the first confirmation that temporal patterns within climatically variable semiarid ecosystems are similar to spatial patterns previously reported across gradients of increasing aridity (Austin and Vitousek 1998; Austin and Sala 1999; Handley and others 1999). In other words, in both space and time, greater aridity is associated with a larger inorganic N pool in the soil.

Third, the seasonal patterns we documented suggest fundamental changes in the type of substrates used by decomposers over a seasonal cycle. Changes in substrate composition are also believed to underlie increased mineralization following plant senescence in alpine tundra ecosystems (Jaeger and others 1999), California annual grassland (Jackson and others 1988; Schimel and others 1989) and monocultures of the grass *Agrostis scabra* (Wedin and Tilman 1990), and they may reflect increased inputs of proteins and amino acids from root turnover, root exudation, surface litter inputs, and dung beetle activity as grasses senesce. Low rates of mineralization early in the growing season at MRC may reflect the mirror image of factors driving mineralization after plant senescence. Depletion of labile organic compounds, particularly the first month after plant senescence but also throughout the dry season, may limit the amount and quality of organic matter available to microbial populations early in the growing season, when fresh litter inputs are not available. Use of low-N substrates for microbial growth early in the growing season may, in turn, be accompanied by significant immobilization of inorganic N sources. A lack of net N mineralization during the growing season has also been reported in temperate mixed-grass prairie grazed by bison (Fahnestock and Detling 2002) and by cattle (Shariff and others 1994). Intense grazing by mammalian herbivores at MRC (62%–80% of ANPP in glades; Augustine 2002) may also limit organic matter availability to decomposers, such that soil microbial activity is closely linked to recent litter inputs. Analyses of natural ^{15}N abundance in various components of a West African savanna also indicate that most plant N is derived from rapid turnover of roots rather than recalcitrant soil organic matter (Abbadie and others 1992).

In addition to the pulse in N mineralization the first month after plant senescence, mineralization rates remained significantly positive throughout dry seasons, even when gravimetric soil moisture fell below 5% and rainfall was less than 10 mm (Figure 1). Soil drying has been shown to increase the availability of labile fractions of organic soil N ($CaCl_2$-extractable organic N; Appel 1998) and is believed to provide the substrate responsible for flushes of mineral N often released when dry soils are rewetted (Birch 1958; Pulleman and Tietma 1999). We hypothesize that labile organic N made available during soil drying may also provide substrate during dry seasons, resulting in mineralization even without soil rewetting. Dry-season N mineralization has also been reported in another tropical grassland (McNaughton and others 1997) and in California annual grassland (Jackson and others 1988). The pattern does not appear to be associated with tropical versus temperate ecosystems because many temperate studies and some tropical studies (for example, Marrs and others 1991; Singh and others 1991) report a lack of dormant-season mineralization. Rather, a consistent factor may be the seasonality and composition of organic matter inputs to the soil.

Fourth, asynchrony in plant growth and N mineralization could clearly affect competition between plants and microbes (Kaye and Hart 1997) and among plant species (McKane and others 2001) for inorganic N sources. During the first month following rains, competition may be alleviated by the high initial inorganic pool size, but plant-microbe competition could contribute significantly to N limitation in high-rainfall years with longer growing seasons (Penning de Vries and others 1980). Microbial competition during the growing season could, in turn, create different niches for plant species based on temporal patterns of N acquisition. Theoretical analyses of plant competition for a limited soil nutrient are often based on a constant supply rate and long-term mean pool size (Tilman 1988), but both pool sizes and mineralization rates fluctuate significantly over time. The dominance of *Cynodon* species and certain annual forbs (*Tribbalus terrestris* and *Gynandropsis gynandra*) in this ecosystem may be related to their capacity for rapid uptake of inorganic N early in the growing season, thus exploiting the period of greatest N availability. These two annual forb species not only grow rapidly at a time of maximal N availability, but their short aboveground tenure limits losses to large grazers. Other strategies of plant N acquisition could include effective competition with microbes during the growing season when pools are low and N accumulation late in the growing season when mineralization occurs (Legard and others 1988; Jackson and others 1989; McKane and others 2001).

This study documents distinct asynchrony in soil nitrogen turnover and plant production in a natural ecosystem. Nitrogen dynamics are uniquely characterized by fluctuations in the inorganic N pool similar in magnitude to seasonal N-mineralization rates. These findings are robust across years differing widely in rainfall intensity, and robust across nutrient-rich and nutrient-poor communities. Whether these patterns are characteristic of semiarid and arid ecosystems (Jackson and others 1989), are related to specific aspects of topography and soil texture (Burke 1989; Schimel and others 1985; Ruess and Seagle 1994), or represent a stable ecosystem state attained by plantsoil feedbacks (Wedin and Tilman 1990) will require further attention to this temporal phenomenon.

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