

Nutrient Limitation to Primary Productivity in a Secondary Savanna in Venezuela¹

Nichole N. Barger²

Graduate Group in Range Science, University of California, Berkeley, California 94720-3114, U.S.A.

Carla M. D'Antonio

Department of Integrative Biology, University of California, Berkeley, California 94720-3140, U.S.A.

Thaura Ghneim

Centro de Ecología, Instituto Venezolano de Investigaciones Científicas, Caracas, Venezuela

Kearly Brink

Energy and Resources Group, University of California, Berkeley, California 94720, U.S.A.

and

Elvira Cuevas

Centro de Ecología, Instituto Venezolano de Investigaciones Científicas, Caracas, Venezuela

ABSTRACT

We examined nutrient limitation to primary productivity in a secondary savanna in the interior branch of the Coastal Range of Venezuela, which was converted from forest to savanna more than 100 years ago. We manipulated soil nutrients by adding nitrogen (+N), phosphorus and potassium (+PK), and nitrogen, phosphorus, and potassium (+NPK) to intact savanna. Eleven months after fertilization, we measured aboveground biomass and belowground biomass as live fine roots in the top 20 cm of soil, and species and functional group composition in response to nutrient additions. Aboveground biomass was highest in the NPK treatment ([mean g/m²]; control = 402, +N = 718, +PK = 490, +NPK = 949). Aboveground production, however, appeared to be limited primarily by N. Aboveground biomass increased 78 percent when N was added alone but did not significantly respond to PK additions when compared to controls. In contrast to aboveground biomass, belowground biomass increased with PK additions but showed no significant increase with N (depth 0–20 cm; [mean g/m²]; control = 685, +N = 443, +PK = 827, +NPK = 832). There was also a 36 percent increase in root length with PK additions when compared to controls. Whole savanna shoot:root ratios were similar for control and +PK (0.6), while those for +N or +NPK fertilization were significantly higher (1.7 and 1.2, respectively). Total biomass response (above + belowground) to nutrient additions showed a strong N and PK co-limitation ([mean g/m²]; control = 1073, +N = 1111, +PK = 1258, +NPK = 1713). Aboveground biomass of all monocots increased with N additions, whereas dicots showed no response to nutrient additions. *Trachypogon* spp. (*T. plumosus* + *T. vestitus*) and *Axonopus canescens*, the two dominant grasses, made up more than 89 percent of the total aboveground biomass in these sites. *Trachypogon* spp. responded to NPK, whereas *A. canescens*, sedges, and the remaining monocots only responded to N. Even though nutrient additions resulted in higher aboveground biomass in N and NPK fertilized plots, this had little effect on plant community composition. With the exception of sedges, which responded positively to N additions and increased from 4 to 8 percent of the plant community, no changes were observed in plant community composition after 11 months.

RESUMEN

En este estudio se examinaron las limitaciones nutricionales en la productividad primaria de una sabana secundaria de más de 100 años localizada en el brazo interior de la Cordillera de la Costa de Venezuela. Se manipularon los nutrientes del suelo mediante la adición de nitrógeno (+N), fósforo y potasio (+PK), y nitrógeno, fósforo, y potasio (+NPK) al suelo de la sabana. Después de once meses de iniciarse los experimentos se midió la respuesta a la adición de nutrientes en términos de producción de biomasa aérea, biomasa de raíces finas vivas en los primeros 20 cm de suelo, y cambios en la composición de especies y grupos funcionales. La biomasa aérea fue mayor en las parcelas fertilizadas con N o en combinación de NPK ([promedio g/m²]; control = 402, +N = 718, +PK = 490, +NPK = 949) indicando que la producción aérea está limitada principalmente por N. No hubo respuesta estadísticamente significativa a la adición de PK con respecto a los controles. La biomasa de raíces finas aumentó con la adición de

¹ Received 28 January 2002; revision accepted 19 September 2002.

² Current address: Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, Colorado 80523, U.S.A.; e-mail: nichole@nrel.colostate.edu

PK y NPK mientras que no hubo aumento significativo con N (profundidad 0–20 cm; [promedio g/m²]; control = 685, +N = 443, +PK = 827, +NPK = 832). La adición de PK modificó la arquitectura radical con un aumento de 36 por ciento en la longitud de las raíces con respecto al control. La relación vástago/raíz fue similar en los tratamientos control y +PK (0.6), pero significativamente mayor en +N (1.7) y +NPK (1.2) indicando nuevamente una limitación principal por N. La respuesta de la biomasa total (vástago + raíces vivas) a la adición de nutrientes refleja una colimitación de N y PK ([promedio g/m²]; control = 1073, +N = 1111, +PK = 1258, +NPK = 1713). La biomasa aérea de las monocotiledóneas aumentó con la adición de N, mientras que no hubo respuesta significativa a la adición de nutrientes en las dicotiledóneas. *Trachypogon* spp. (*T. plumosus* + *T. vestitus*) and *Axonopus canescens*, las dos gramíneas dominantes, representaron más del 89 por ciento de la biomasa total en las parcelas. *Trachypogon* spp. respondieron a NPK, mientras que *A. canescens*, ciperáceas, y las otras monocotiledóneas sólo respondieron a N. No hubo cambios significativos en la composición de especies como respuesta a la adición de nutrientes, con la excepción de las ciperáceas que respondieron significativamente a la adición de N con un aumento de 4 a 8 por ciento.

Key words: fertilization; nitrogen; nutrient limitation; phosphorus; savanna; *Trachypogon*; Venezuela.

LAND USE CHANGE IN TROPICAL ECOSYSTEMS, especially the conversion of tropical forests to pasture, has led to a dramatic increase in land coverage of "anthropogenic" or secondary savannas (Houghton *et al.* 1983, Detwiler & Hall 1988). Short-term effects of forest to pasture conversion on soil nutrient dynamics have been well documented in the last decade (Reiners *et al.* 1994, Feigl *et al.* 1995, Neill 1997, Kauffman 1998, Jin *et al.* 2000, Garcia-Montel *et al.* 2000, Hughes *et al.* 2000), but few studies have investigated the longer-term biogeochemical characteristics of permanent secondary savannas. In addition, there is little information on nutrients that limit production in tropical ecosystems generally. In this study, we examined nutrient limitation to primary productivity in a secondary Venezuelan savanna that was converted from forest more than 100 years ago.

Natural savannas in Venezuela cover a large area of the lowlands in the central and northern part of the country and are some of the most well studied savannas in the world (Sarmiento 1984, Solbrig 1996). In contrast, secondary savannas generally occur at higher elevations and are a result of forest removal and the subsequent colonization by native savanna species (Ramia 1967). As a result, species composition is similar between the two savanna types despite differences in soils and climatic zones. Soils in secondary savannas tend to be more fertile, with up to twice the amount of nitrogen (N) and phosphorus (P) relative to lowland savannas (Baruch & Gomez 1996). Even though lowland and secondary savannas receive similar amounts of rainfall, the drought period is more intense in the lowland savannas (Baruch & Gomez 1996). The higher fertility soils in addition to the less intense drought period in secondary savannas is believed to contribute to higher plant available nutrients throughout the growing season (Baruch & Gomez 1996).

Despite the fact that secondary savanna soils

are more fertile than lowland savannas, soils in this region are Ultisols that are characterized by low nutrient and base cation availability (Cuenca 1987). Savanna ecosystems in general also have a high potential for N loss due to volatilization of N during fire (Medina *et al.* 1978, Medina 1982). Evidence from lowland fertilization studies has shown that both N and P strongly limit primary production (Garcia-Miragaya *et al.* 1983); however, in a postfire environment, production appeared to respond primarily to N and to a lesser extent P (Medina *et al.* 1978). Whether these patterns hold in secondary mid-elevation savannas that differ from lowland savannas in soil nutrients and climate is not known.

We hypothesized that primary production in secondary savannas is limited by both N and PK. In this paper, we report on N and PK limitation to primary production, community composition, and plant allocation patterns in a mid-elevation secondary savanna that was converted from forest more than 100 years ago and has burned every 2–6 years for the past decade. Because fire is important to both the biogeochemistry and persistence of savannas, we carried out our experiment during the postfire regeneration period (San Jose & Farinas 1983).

METHODS AND MATERIALS

STUDY SITE.—We conducted a factorial fertilization experiment in a secondary savanna within the boundaries of the Instituto Venezolano de Investigaciones Científicas (IVIC), which is located *ca* 15 km from Caracas, Venezuela, in the coastal cordillera. Mean annual temperature is 17.9°C and mean annual precipitation is 1063 mm. Eighty percent of the precipitation occurs from May through December (Cuenca 1987). We established sites at 1200 m elevation. Prior to the last century, this region was largely forested. Once the forests were

removed, native savanna species consisting mainly of grasses and sedges colonized these areas. The plant community is dominated by *Trachypogon* spp. (*T. plumosus* + *T. vestitus*) and *Axonopus canescens* (Poaceae) with no major woody component. Soils are Typic Haplohumults and are characterized by low pH (3.9–4.2) and low base saturation.

Savannas within IVIC are protected from grazing but burn every 2–6 years. The most recent fire event was a wildfire in March 1996, 4 months before the experiment was initiated. Final biomass harvests were conducted 15 months after fire (June 1997). Since peak biomass for the different species occurs at different times throughout the year, we chose to conduct the final harvest 1–2 months after the dry season ended, during peak carbon gain for many of the species.

FERTILIZATION EXPERIMENT.—We conducted a factorial experiment in which we fertilized with two levels of N and PK. We created 40 1 × 1 m plots in which 10 plots received no nutrients (control), 10 received nitrogen only (+N), 10 received phosphorus and potassium only (+PK), and 10 received a combination of nitrogen, phosphorus, and potassium (+NPK). Phosphorus additions were always coupled with K due to the unavailability of fertilizer containing P alone. Fertilization occurred on 29 July, 5 August, and 2 November 1996. On these dates, N was added at a rate of 50, 50, and 100 kg/ha of N in the form of urea; P was added at a rate of 50, 50, and 100 kg/ha in the form of KH_2PO_4 ; and potassium (K) was added at a rate of 63, 63, and 126 kg/ha of K in the form of KH_2PO_4 . We added a total of 200 kg/ha/yr of N and P and 252 kg/ha/yr of K. The fertilizer was dissolved in water and misted onto the soil surface for the July and August fertilization events. We observed tissue damage to small seedlings within the plots after the September fertilization; therefore, we injected fertilizer directly into the soil for the November fertilization. We injected 20 ml of fertilizer on a 20 × 20 cm grid within each plot for a total of 25 injection points/m².

SOIL NUTRIENT AVAILABILITY.—We measured soil N and P availability 2 months after each fertilization event using ion exchange resin bags as described in Giblin *et al.* (1994). Resin bags were made out of commercial nylon stockings. The bags were soaked in 0.1 N HCl for one hour and rinsed in deionized water before resins were placed in them. We placed a 50.2 cm² coated wire ring within each bag to increase the surface area of soil that would be in

contact with the resins. Five cm³ each of cation and anion exchange resins (anion resins, Dowex 1-X8, 20–50 mesh, chloride form; August fertilizations, cation resins, Dowex 50W-X8, 20–50 mesh, hydrogen form; November fertilization, cation resins, Dowex 50W, 16–40 mesh, hydrogen form) were loaded into a single nylon bag and placed in the upper 5 cm of soil for one month. A total of four sets of resin bags were placed in the soil during August, September, November, and December (Barger 1998), although data are presented here one month after each fertilization event. We were unable to obtain the same cation resin type after the July and August nutrient additions. As a result, we do not compare changes in soil N and P availability after the different fertilization events but rather focus on differences among treatments. Once the bags were removed from the soil, they were rinsed with deionized water and frozen. Ammonium, NO_3^- , and PO_4^{3-} were extracted from the resins with 100 ml of 0.1 M NaCl and analyzed on a Lachat Autoanalyzer at UC Berkeley.

BIOMASS RESPONSE TO NUTRIENT ADDITIONS.—Of the ten plots within each treatment, we randomly chose five plots to examine species level and functional group response to nutrient additions. At the species level, we separated biomass of the dominant grasses, *Trachypogon* spp. (*T. plumosus* + *T. vestitus*) and *A. canescens*. The remaining material was separated into three groups: (1) sedges, (2) dicots, and (3) remaining monocots. In the remaining five plots, we clipped and bulked all aboveground biomass and samples were dried at 65°C for 48 hours.

We randomly selected four plots per fertilization treatment to measure live root biomass and root length. Samples were collected with a 10 cm diameter core and separated into 0–5, 5–10, 10–15, and 15–20 cm depths. Samples were refrigerated immediately after collection. In the lab, we used an elutriator (Bel-Arte Products) to separate organic matter, which included roots, from the mineral soil. Each sample was placed in a large funnel that was connected to a water and air source. As air and water were pumped through the funnel, organic matter rose to the surface and heavier mineral soil was left at the bottom. Live roots were then removed from the organic material by hand. All calculations of root biomass and length were based on live root material. Total root length for each sample was calculated using the method described in Tennant (1975). Each root sample was spread over a square grid and the length was calculated as ($\pi/4$) × number of intersections

TABLE 1. Soil N and P availability in response to fertilization. Time points are one month after each fertilization event. Values are average resin bag N ($\text{NH}_4^+ + \text{NO}_3^-$ $\mu\text{g/day}$) and P (PO_4^{3-} $\mu\text{g/day}$) in each treatment (± 1 SE). Fertilizer was applied in two events during July and August, and one event in November. Letters within each column examine the main effects of N (a and b) and PK (c and d). Main effects are statistically different at $P < 0.05$ where a different letter appears within a column. An * above a column denotes a significant $\text{N} \times \text{PK}$ interaction on soil nutrient levels.

	August ($\mu\text{g NH}_4^+ + \text{NO}_3^-/\text{day}$)	August ($\mu\text{g PO}_4^{3-}/\text{day}$)	November ($\mu\text{g NH}_4^+ + \text{NO}_3^-/\text{day}$)	November ($\mu\text{g PO}_4^{3-}/\text{day}$)
			*	
Control	1.08 (0.23) a, c	0.27 (0.24) a, c	0.87 (0.25) a, c	0.01 (0.004) a, c
+N	20.29 (5.27) b, c	0.57 (0.17) a, c	4.65 (2.77) b, c	0.10 (0.03) a, c
+PK	2.22 (0.86) a, c	15.33 (3.97) a, d	1.07 (0.48) a, c	0.70 (0.39) a, c
+NPK	22.56 (9.80) b, c	16.13 (5.13) a, d	12.34 (7.31) b, c	0.84 (0.66) a, c

with grid lines X grid unit. A 3 cm grid allowed a sufficient number of intersections in each sample to assume precision on the order of ± 1 percent for each root length estimate. Root samples were oven-dried at 65°C and then weighed.

INDIVIDUAL PLANT RESPONSE.—We marked one *T. plumosus* plant within each plot at the beginning of the experiment ($N = 10$) to examine individual plant response to nutrient additions. We selected plants that were away from the plot edge and had an elliptical base and canopy. Canopy diameter was the best predictor of initial biomass for *T. plumosus* based on harvested plants from outside the plots. Final change in aboveground biomass for *T. plumosus* was calculated using estimated initial dry weight based on canopy diameter minus final dry weight of the plant.

Of the ten marked *T. plumosus* plants, we randomly selected five in which we measured both aboveground and belowground biomass. We collected belowground biomass by extracting the root ball along with the aboveground biomass. We defined the root ball as a 20 cm diameter circle around the base of each plant. In the lab, we washed the soil from the root system and clipped the root system from the aboveground biomass. Biomass was then separated into live leaves, dead leaves, stems, roots, and rhizomes. Plant samples were dried at 65°C for 48 hours. Since plant size varied, we expressed biomass for *T. plumosus* plant parts on percent allocation to each tissue type.

We measured total C, N, and P on a subsample of *T. plumosus* live leaves collected from each marked plant. Samples were ground on a Wiley Mill and then on a Wig-L-Bug amalgamator (Crescent Dental). Total C and N was measured on a NA1500 Fisons Instruments CHN Analyzer. We measured total phosphorus using sulfuric acid Kjel-

dahl digestion and PO_4^{3-} was then measured on a Lachat autoanalyzer. We analyzed the data using Systat 5.0. All analyses were conducted with a two-way analysis of variance with the main effects of N and PK and their interaction, with significance levels evaluated at $P < 0.05$ unless otherwise noted.

RESULTS

RESIN BAG N AND P.—Fertilization with N and PK elevated plant available forms of nitrogen and phosphorus in the soil. One month after each fertilization event, resin bag N ($\text{NH}_4^+ + \text{NO}_3^-$) increased on average 9-fold in the N addition plots relative to minus N plots ($F_{1, 30} = 14.6$, $P = 0.001$), whereas resin bag P increased on average 48-fold with PK additions relative to minus P plots ($F_{1, 30} = 28.4$, $P < 0.001$; Table 1). After the November fertilization only, the presence of PK resulted in an increase in resin bag N as well as PK, shown by the significant $\text{N} \times \text{PK}$ interaction ($F_{1, 30} = 4.3$, $P = 0.05$). In September, we observed the only significant effect of fertilization on soil moisture with a 13 percent decrease in soil moisture with N additions (Barger *et al.* in press).

ABOVEGROUND AND BELOWGROUND RESPONSE TO FERTILIZATION.—Total aboveground biomass of savanna species more than doubled when N and PK were added in combination relative to controls (Fig. 1). Both N and PK additions resulted in an increase in aboveground biomass (+N, $F_{1, 40} = 49.3$, $P < 0.001$; +PK, $F_{1, 40} = 8.3$, $P = 0.007$), with no significant $\text{N} \times \text{PK}$ interaction. Aboveground production, however, appeared to be more limited by N relative to PK. Aboveground biomass increased 78 percent when N was added alone (Tukey HSD, $P < 0.001$) but did not respond signif-

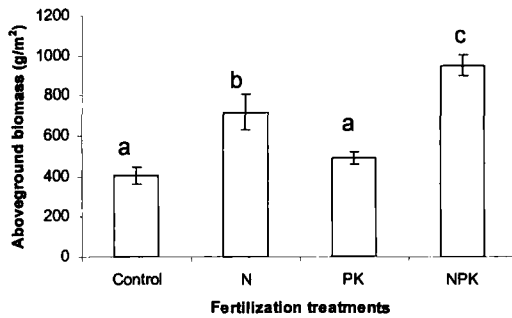


FIGURE 1. Total aboveground biomass of savanna vegetation (g/m^2). Values are average plot biomass per fertilization treatment ± 1 SE ($N = 10$). The main effects of both N and PK additions were significantly different at $P < 0.05$. Since we were interested in individual treatment effects, a different letter over a bar represents a significant difference at $P < 0.05$ (Tukey HSD).

icantly to PK additions when compared to controls.

In contrast to the aboveground response to nutrient additions, 0–20 cm live root biomass increased 53 percent with PK additions relative to minus PK plots, with no response to N ($F_{1, 16} = 9.6$, $P = 0.008$; Fig. 2B). The increase in live root biomass with PK additions occurred at depths greater than 10 cm (Fig. 2A). Even though N alone did not have an effect on 0–20 cm live root biomass, there was an interactive effect of N and PK at 0–5 cm depth ($F_{1, 16} = 8.4$, $P = 0.01$), whereby N additions counteracted the positive effect of PK (Fig. 2). At 15–20 cm, there was a significant increase in root biomass with PK additions (PK; $F_{1, 16} = 17.3$, $P = 0.001$), but the presence of N in combination with PK led to a decrease in root biomass (N \times PK; $F_{1, 16} = 3.9$, $P = 0.07$; Fig. 2A). Root length also increased with additions of PK, while there was no effect of N additions ([mean root length at 0–20 m/m²]; +PK = 292, –PK = 191; $F_{1, 16} = 27.3$, $P < 0.001$; Fig. 3B). Root length increased with PK additions at all depths greater than 5 cm (5–10 cm, $F_{1, 16} = 9.8$, $P = 0.007$; 10–15 cm, $F_{1, 16} = 30.8$, $P < 0.001$; 15–20 cm, $F_{1, 16} = 10.2$, $P = 0.006$), with no effect in the surface 5 cm (Fig. 3). Again there was an interactive effect of N and PK at 15–20 cm; live root length increased with PK additions but decreased in the presence of N ($F_{1, 16} = 114.5$, $P < 0.001$).

SPECIES-LEVEL AND FUNCTIONAL-GROUP RESPONSE TO FERTILIZATION.—*Trachypogon* spp., which comprise more than 50 percent of the standing aboveground

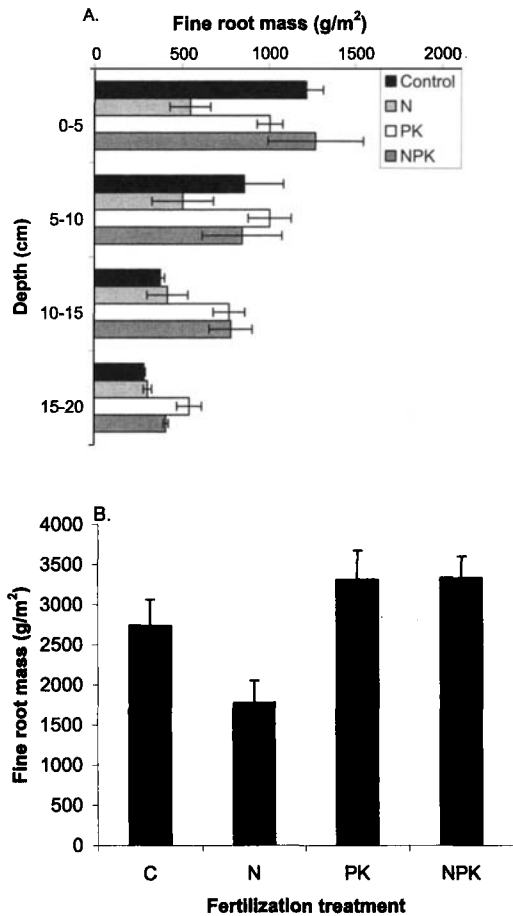


FIGURE 2. Standing stock of live fine root mass with nutrient additions by depth and summed across depths to 20 cm (inset). Values are mean live fine root mass of four soil cores collected from within each fertilization treatment ± 1 SE.

biomass in our sites, increased with both N ($F_{1, 20} = 5.5$, $P = 0.03$) and PK ($F_{1, 20} = 5.0$, $P = 0.03$) additions and the response to these nutrients was additive (Fig. 4); however, *A. canescens*, the second most common grass species, only responded to N additions ($F_{1, 20} = 4.9$, $P = 0.04$). Likewise, monocot and sedge biomass also increased with N additions but there was no effect of PK (monocot, $F_{1, 20} = 5.3$, $P = 0.03$; sedge, $F_{1, 20} = 24.9$, $P < 0.001$). Dicots, which contributed less than 1 percent to standing aboveground biomass, did not respond to any combination of nutrient additions. Although we observed an increase in total biomass with nutrient additions, percent composition within the community remained the same for most groups with the exception of sedges. Sedges in-

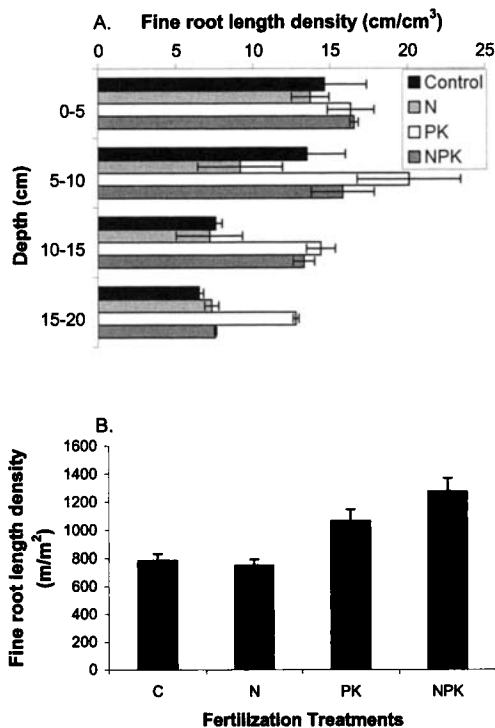


FIGURE 3. Fine root length density with nutrient additions by depth (A) and summed across depths to 20 cm (B). Values are mean live fine root length density of four soil cores collected from within each fertilization treatment ± 1 SE.

creased significantly from 4 to 8 percent of the community with N additions ($F_{1, 20} = 24.9$, $P < 0.001$).

The biomass response to fertilization by individually marked *T. plumosus* plants mirrored that of the total plot level response. Again, *T. plumosus* biomass increased only when N and PK were added in combination, showing no response when N and PK were added alone (Fig. 5). The biomass response by *T. plumosus* may be partially explained by changes in nutrient uptake. *Trachypogon plumosus* live leaf N increased by 16 percent with N additions, whereas P in live leaves nearly doubled with P additions (Table 2). The increase in P concentrations in live leaf tissue led to an increase in P:N ratios in +PK plots (Table 2). Although aboveground biomass of *T. plumosus* plants significantly increased with nutrient additions, we observed little change in allocation strategies.

DISCUSSION

Even though forested areas adjacent to our secondary savanna sites have shown strong P limitation to

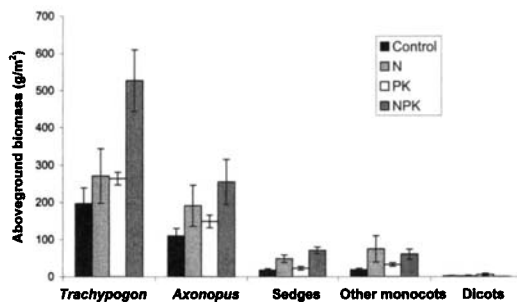


FIGURE 4. Community response to nutrient additions. We separated aboveground biomass into two species groups, *Trachypogon* spp. (*T. plumosus* + *T. vestitus*) and *Axonopus canescens*. The remaining vegetation was separated into three functional groups: (1) monocots, (2) dicots, and (3) sedges. Values are mean aboveground biomass (g/m^2) per fertilization treatment ± 1 SE ($N = 5$).

primary production (Marulanda 1997), aboveground production in the secondary savannas appeared to be more limited by N and only responded to PK addition once N was added. Total soil N in adjacent forests near our sites is nearly double that of the secondary savanna (Barger & D'Antonio, pers. obs.), indicating loss of ecosystem N over the last century.

Repeated burning of secondary savannas may cause a shift from P limitation to production in adjacent forests to N limitation in secondary savanna. Ecosystem N loss often exceeds P loss during fire (Kauffman *et al.* 1993, 1994; Carreira & Niell 1995) since P is retained in the surface ash

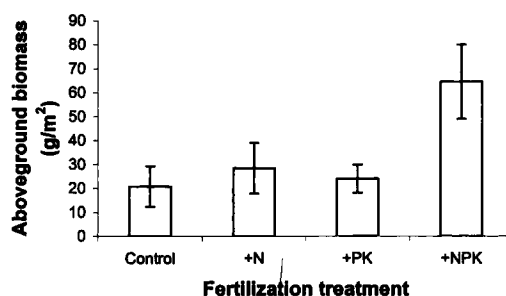


FIGURE 5. Total aboveground biomass for individual *Trachypogon plumosus* plants. Values are the change in individual *T. plumosus* aboveground biomass 11 months after fertilization (final aboveground biomass—estimated initial biomass). Plant biomass was estimated at the beginning of the experiment by regression of canopy diameter for *T. plumosus* plants collected from the site as a function of aboveground biomass. Values are means ± 1 SE ($N = 10$). The main effect of N additions was significant at $P < 0.05$ and the main effect of PK additions was significant at $P < 0.10$.

TABLE 2. *Nutrient concentrations in Trachypogon plumosus live leaves and allocation patterns in individually marked plants. Root weight ratios were calculated as root dry weight/(root + shoot dry weight). Values are means of 10 plants \pm 1 SE. The first letter in each column examines the main effect of N (a and b) and the second examines the effect of PK (c and d). Main effects are statistically different at $P < 0.05$ where a different letter appears within a column.*

	Percent N	Percent P	P:N	Shoot:Root	Root Wt. Ratio
Control	1.40 (0.11) a, c	0.06 (0.01) a, c	0.04 (0.006) a, c	26 (8) a, c	0.05 (0.009) a, c
+N	1.57 (0.12) b, c	0.06 (0.01) a, c	0.04 (0.002) a, c	23 (5) a, c	0.05 (0.01) a, c
+PK	1.25 (0.05) a, c	0.13 (0.02) a, d	0.11 (0.016) a, d	16 (4) a, c	0.07 (0.01) a, c
+NPK	1.51 (0.10) b, c	0.11 (0.01) a, d	0.08 (0.008) a, d	25 (4) a, c	0.04 (0.008) a, c

layer, whereas N may be volatilized in the combustion process. Even though N losses after fire may be high in savanna ecosystems, these losses may be offset by N fixation, since savanna ecosystems often have a high diversity of leguminous species (Medina & Bilbao 1991). Because dicots in our site made up less than 1 percent of the species composition, we expected symbiotic N fixation to be low; however, the importance of non-symbiotic N fixation in these sites is not known. With high potential N losses from frequent fires events and low N fixation potential, we would expect these secondary savannas to maintain long-term N limitation.

Although fire results in losses of both N and P in combustion and erosional processes, there is often a temporary increase in extractable N and P after fire, which may positively affect plant growth and nutrient concentrations (Singh *et al.* 1991, Singh 1993, Carreira *et al.* 1994, Singh 1994, Carreira & Niell 1995, Materechera *et al.* 1998). Fire may be an important process by which bound P is converted to more labile forms, especially on highly weathered soils characterized by low P availability. Even though fire may result in an increase in labile P fractions, this effect may last only a few weeks (Carreira & Neill 1995). Fire in our sites occurred four months before the experiment began, which may partially explain the lack of an aboveground response to P alone.

Even though aboveground biomass did not respond to P alone, leaf P concentrations increased significantly with P fertilization in our study. Luxury consumption of phosphorus, which is the increase in nutrient uptake in excess of what is required for growth, is a common response in savanna grasses (Medina & Bilbao 1991). It has been hypothesized that nutrients in excess of what is required for growth may be stored and remobilized during periods of low nutrient availability (Chapin 1980). Therefore, luxury consumption of nutrients

may be especially important in savanna ecosystems that are characterized by strong seasonal patterns in nutrient availability.

Rooting density often increases in zones of P fertilizer, although the effect is largely in combination with N (Marschner 1995). Even though we were not able to separate the effect of P from K additions on changes in fine root biomass and root length density in this study, there is evidence that P fertilization stimulates root production in forested ecosystems (Cuevas & Medina 1988). In addition to root production, fertilization may also have an affect on standing stocks of live roots through changes in root mortality and turnover rates. An extensive review by Ostertag (2001) of belowground response to nutrient additions showed that root mortality tends to increase or remain the same with N additions, but there was no generalizable effect of N or NPK additions on root turnover rates (Haynes & Gower 1995, Katterer *et al.* 1995, Pregitzer *et al.* 1995, Majdi & Nyland 1996, Majdi & Kangas 1997, Tingey *et al.* 1997). Therefore, changes in fine root mass and root length density with PK additions in our study were most likely due to increased root production rather than a decrease in root mortality. The few studies on root response to nutrient additions in temperate grasslands ecosystems have suggested that standing root stocks (live + dead roots) tend to increase or remain the same with N additions (Black & Wight 1979; Power 1980, 1981).

Whole savanna shoot:root ratios (aboveground: fine root) support the idea that N is the primary limiting nutrient in these savannas. Shoot:root ratios were similar for control and PK fertilization (0.6), whereas there was a stronger aboveground response with N additions (1.7 for N and 1.2 for NPK); however, this pattern was not seen at the individual plant level. Shoot:root ratios for the dominant species *T. plumosus* remained unchanged with fertilization. The maintenance of a large ab-

sorption surface either under natural conditions or with PK additions can be construed as a mechanism to maximize nutrient and water uptake, especially when a resource (in this case, N) is strongly limiting for growth or when ratios among specific soil nutrients are unusually skewed (Lajtha & Harrison 1995). Even though root absorption area increased with PK additions, this belowground response did not overcome the N limitations on aboveground growth. Overall, these secondary savanna sites showed an aboveground response to nutrients similar to lowland savannas that had previously burned; N was the primary limiting nutrient and once N was present, plants responded to additions of PK. Summing the above- and belowground response to nutrients, ecosystem productiv-

ity in our sites appears to be strongly co-limited by N and PK (Total above and belowground biomass g/m²; control = 1073, +N = 1111, +PK = 1258, +NPK = 1713).

ACKNOWLEDGMENTS

We would like to thank Heather Swartz for providing valuable logistical assistance in the initial setup of the experiment. Hailin Zhong provided tremendous analytical help in the laboratory and Eric Berlow gave advice on statistical analysis. Members of the D'Antonio lab gave feedback on experimental design and data interpretation. We also appreciate the administrative support provided by IVIC and the lab of Dr. Ernesto Medina. Special thanks to Whendee Silver and two anonymous reviewers for making valuable comments on the manuscript. This work was supported by NSF BSR 9119618 and an REU supplement to Carla D'Antonio.

LITERATURE CITED

- BARGER, N. N. 1998. Controls over colonization by an African grass (*Melinis minutiflora*) and grassland productivity in a Venezuelan savanna. M.S. thesis. Graduate Group in Range Science, University of California, Berkeley, California.
- , C. M. D'ANTONIO, T. GHNEIM, AND E. CUEVAS. Constraints to colonization and growth of the African grass, *Melinis minutiflora*, in a Venezuelan savanna. Plant Ecol. In press.
- BARUCH, Z., AND J. A. GOMEZ. 1996. Dynamics of energy and nutrient concentration and construction cost in a native and two alien C₄ grasses from two Neotropical savannas. Plant Soil 181: 175–184.
- BLACK, A. L., AND J. R. WIGHT. 1979. Range fertilization: Nitrogen and phosphorus uptake and recovery over time. J. Range Manage. 32: 349–353.
- CARREIRA, J. A., AND F. X. NIELL. 1995. Mobilization of nutrients by fire in a semiarid gorse–scrubland ecosystem of southern Spain. Arid Soil Res. Rehab. 9: 73–89.
- , ———, AND K. LAJTHA. 1994. Soil nitrogen availability and nitrification in Mediterranean shrublands of varying fire history and successional stage. Biogeochemistry 26: 189–209.
- CHAPIN, F. S., III. 1980. The mineral nutrition of wild plants. Annu. Rev. Ecol. Syst. 11: 233–260.
- CUENCA, G. 1987. Mecanismos de tolerancia al aluminio en la vegetación ceciendo en suelos ácidos. Ph.D. dissertation. Instituto de Ecología, Instituto Venezolano de Investigaciones Científicas, Caracas, Venezuela.
- CUEVAS, E., AND E. MEDINA. 1988. Nutrient dynamics within Amazonian forest: II. Fine root growth, nutrient availability and leaf litter decomposition. Oecologia 76: 222–235.
- DETWILER, R. P., AND C. A. S. HALL. 1988. Tropical forests and the global carbon cycle. Science 239: 242–247.
- FEIGL, B. J., J. MELILLO, AND C. C. CERRI. 1995. Changes in the origin and quality of soil organic matter after pasture introduction in Rondonia (Brazil). Plant Soil 175: 21–29.
- GARCIA-MIRAGAYA, J., J. J. SAN JOSE, AND J. I. HERNANDEZ. 1983. Effect of added nitrogen, phosphorus and potassium on aboveground biomass production and nutrient content of *Trachypogon* savanna grasses. Trop. Ecol. 24: 33–42.
- GARCIA-MONTEL, D. C., C. NEILL, J. MELILLO, T. SUZANNE, P. A. STEUDLER, AND C. C. CERRI. 2000. Soil phosphorus transformations following forest clearing for pasture in the Brazilian Amazon. Soil Sci. Soc. Am. J. 64: 1792–1804.
- GIBLIN, A. E., J. A. LAUNDRE, K. J. NADELHOFFER, AND G. R. SHAVER. 1994. Measuring nutrient availability in arctic soils using ion exchange resins: A field test. Soil Sci. Soc. Am. J. 58: 1154–1162.
- HAYNES, B. E., AND S. T. GOWER. 1995. Belowground carbon allocation in unfertilized and fertilized red pine plantations in northern Wisconsin. Tree Physiol. 15: 317–325.
- HOUGHTON, R. A., J. E. HOBBIE, J. M. MELILLO, B. MOORE, B. J. PETERSON, G. R. SHAVER, AND G. M. WOODWELL. 1983. Changes in the carbon content of terrestrial biota and soils between 1860 and 1980: A net release of CO₂ to the atmosphere. Ecol. Monogr. 53: 235–262.
- HUGHES, F. R., B. J. KAUFFMAN, AND V. J. JARAMILLO. 2000. Ecosystem-scale impacts of deforestation and land use in a humid tropical region of Mexico. Ecol. Appl. 10: 515–527.
- JIN, V. L., L. T. WEST, B. L. HAINES, AND C. J. PETERSON. 2000. P retention in tropical pre-montane soils across forest–pasture interfaces. Soil Sci. 165: 881–889.
- KATTERER, T., A. FABIAO, M. MADEIRA, C. RIBEIRO, AND E. STEIN. 1995. Fine-root dynamics, soil moisture, and soil carbon content in *Eucalyptus globulus* plantations under different irrigation and fertilisation regimes. Forest Ecol. Manage. 74: 1–12.

- KAUFFMAN, B. J. 1998. Fire in the Brazilian Amazon. 2. Biomass, nutrient pools and losses in cattle pastures. *Oecologia* 113: 415–427.
- , D. L. CUMMINGS, AND D. E. WARD. 1994. Relationship of fire, biomass and nutrient dynamics along a vegetation gradient in the Brazilian Cerrado. *J. Ecol.* 82: 519–531.
- , R. L. SANFORD JR., D. L. CUMMINGS, I. H. SALCEDO, AND E. V. S. B. SAMPAIO. 1993. Biomass and nutrient dynamics associated with slash fires in Neotropical dry forests. *Ecology* 74: 140–151.
- LAJTHA, K., AND A. F. HARRISON. 1995. Strategies of phosphorus acquisition and conservation by plant species and communities. *In* H. Tiessen (Ed.). *Phosphorus in the global environment*, pp. 139–147. John Wiley and Sons, Chichester, England.
- MAJDI, H., AND P. KANGAS. 1997. Demography of fine roots in response to nutrient applications in a Norway spruce stand in southwestern Sweden. *Ecoscience* 4: 199–205.
- , AND J. NYLUND. 1996. Does liquid fertilization affect fine root dynamics and lifespan of mycorrhizal short roots? *Plant Soil* 185: 305–309.
- MARSCHNER, H. 1995. *Mineral nutrition of higher plants*. Academic Press, London, England.
- MARULANDA, L. O. 1997. Efectos de los cambios florísticos y estructurales en la dinámica de raíces finas y el flujo de CO₂ del suelo en un mosaico sucesional de la Cordillera de la Costa, Altos de Pipe, Venezuela. Centro de Estudios Avanzados. Instituto Venezolano de Investigaciones Científicas, Caracas, Venezuela.
- MATERECHERA, S. A., O. T. MANDIRINGANA, P. M. MBOKODI, AND K. NYAMAPPENE. 1998. Organic matter, pH and nutrient distribution in soil layers of a savanna Thornveld subjected to different burning frequencies at Alice in the Eastern Cape. *S. Afr. J. Plant Soil* 15: 109–115.
- MEDINA, E. 1982. Nitrogen balance in the *Trachypogon* grasslands of central Venezuela. *Plant Soil* 67: 305–314.
- , AND B. BILBAO. 1991. Significance of nutrient relations and symbiosis for the competitive interaction between grasses and legumes in tropical savanna. *In* G. Esser and D. Overdieck (Eds.). *Modern ecology: basic and applied aspects*, pp. 24–36. Elsevier Science, Amsterdam, The Netherlands.
- , A. MENDOZA, AND R. MONTES. 1978. Nutrient balance and organic matter production in the *Trachypogon* savannas of Venezuela. *Trop. Agr.* 55: 243–253.
- NEILL, C. 1997. Net nitrogen mineralization and net nitrification rates in soils following deforestation for pasture across the southwestern Brazilian Amazon basin landscape. *Oecologia* 110: 243–252.
- OSTERTAG, R. 2001. Effects of nitrogen and phosphorus availability on fine-root dynamics in Hawaiian montane forests. *Ecology* 82: 485–499.
- POWER, J. F. 1980. Response of semiarid grassland sites to nitrogen fertilization: I. Plant growth and water use. *Soil Sci. Soc. Am. J.* 44: 545–550.
- . 1981. Long-term recovery of fertilizer nitrogen applied to a native mixed prairie. *Soil Sci. Soc. Am. J.* 45: 782–786.
- PREGITZER, K. S., D. ZAK, P. S. CURTIS, M. E. KISKE, J. A. TEERI, AND C. S. VOGEL. 1995. Atmospheric CO₂, soil nitrogen and turnover of fine roots. *New Phytol.* 129: 575–585.
- RAMIA, M. 1967. Tipos de sabanas en los llanos de Venezuela. *Bol. Soc. Venez. Cienc. Nat.* 27: 264–288.
- REINERS, W. A., A. F. BOUWMAN, W. F. J. PARSONS, AND M. KELLER. 1994. Tropical rain forest conversion to pasture: Changes in vegetation and soil properties. *Ecol. Appl.* 42: 363–377.
- SAN JOSE, J. J., AND M. FARINAS. 1983. Changes in tree density and species composition in a protected *Trachypogon* savanna in Venezuela. *Ecology* 64: 447–458.
- SARMIENTO, G. 1984. *The ecology of Neotropical savannas*. Harvard University Press, Cambridge, Massachusetts.
- SINGH, R. S. 1993. Effect of winter fire on primary productivity and nutrient concentration of a dry tropical savanna. *Vegetatio* 106: 63–71.
- . 1994. Changes in soils nutrient following burning of dry tropical savanna. *Int. J. Wildland Fire* 4: 187–194.
- , A. S. RAGHUBANSHI, AND J. S. SINGH. 1991. Nitrogen-mineralization in dry tropical savanna effects of burning and grazing. *Soil Biol. Biochem.* 23: 269–274.
- SOLBRIG, O. T. 1996. The diversity of the savanna ecosystem. *In* O. T. Solbrig, E. Medina, and J. F. Silva (Eds.). *Biodiversity and savanna ecosystem processes*, pp. 1–30. Springer-Verlag, Berlin, Germany.
- TENNANT, D. 1975. A test of a modified line intersect method of estimating root length. *J. Ecol.* 63: 995–1001.
- TINGEY, D. T., D. L. PHILLIPS, M. G. JOHNSON, M. J. STORM, AND J. T. BALL. 1997. Effects of elevated CO₂ and N fertilization on fine root dynamics and fungal growth in seedling *Pinus ponderosa*. *Environ. Exp. Bot.* 37: 73–83.