

Nutrient Sequestering by the Understorey Strata of Natural *Pinus caribaea* Stands Subject to Prescription Burning

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ABSTRACT

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The capacity of understorey shrub and graminoid strata to conserve Ca, Mg, K and P by rapidly resprouting after fires was examined in prescription-burned stands of *Pinus caribaea* var. *hondurensis* Morelet growing on infertile savanna soils in Belize, Central America. Vegetative resprouting by both strata was vigorous and resulted in above-ground biomass accumulations, after 1 year, of approximately 800 and 1500 kg ha⁻¹ for shrubs and graminoids, respectively. Thereafter, accumulation was slower and consisted mainly of stemwood in shrubs and standing dead material in grasses and sedges. After 5 years, total above-ground mass accumulation in shrubs and graminoids was approximately 2400 and 3400 kg ha⁻¹, respectively. Despite this difference in mass, higher nutrient concentrations in shrub tissues resulted in larger nutrient accumulations in this stratum than in graminoids for all elements except P, which showed a large accumulation in the standing dead tissues of grasses and sedges. Accumulation in either layer represented a significant proportion of the total system storages and fluxes. However, because of the generally larger accumulation of nutrients in the shrub layer, and the resistance of its tissues to ignition during fire, we conclude that this stratum should be preferred for nutrient conservation when this ecosystem is managed.

INTRODUCTION

The importance of biomass as a nutrient sink in oligotrophic tropical ecosystems has been stressed by many authors (Richards, 1952; Jordan and Kline, 1972; Golley, 1983). This phenomenon is manifested in the large proportion of system nutrient capital present in the biomass of many tropical forests (Nye and Greenland, 1960). It can also be seen in the inability of low-biomass ecosystems to retain large quantities of nutrients in their soil compartments, even when these remain unsaturated. For example, in the Mountain Pine Ridge

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savannas of Belize, grassland-covered soils remain at very low fertility levels after 35 years of fire suppression, despite possessing highly base-unsaturated cation exchange capacities and being subject to a continual input of nutrients from atmospheric sources (Kellman and Carty, 1986). This has been attributed to an enlarged biomass nutrient compartment and enriched nutrient cycle at these sites. Thus, while these soils are capable of resisting acute short-term leaching losses by rapidly immobilizing nutrients (Kellman and Sanmugadas, 1985), they are apparently incapable of preventing gradual chronic losses in the absence of a large biomass sink.

Prescription burning is being used increasingly as a management tool in forestry. In the tropics, fire is likely to be of greatest use in native conifer woodlands and savannas (Munro, 1966), and in conifer plantations in savanna environments, where fire is a normal ecosystem component. When applied to oligotrophic systems, such as the native pine savannas of Central America, fire represents a potentially serious source of cumulative nutrient depletion, as nutrients stored in plant tissues are mineralized and possibly lost through leaching or sheet wash (Hudson et al., 1983a, b). Kellman et al. (1985) examined leaching losses immediately after fire in the Mountain Pine Ridge savanna and found that soil immobilization effectively suppresses these losses. The speed of plant uptake of these temporarily retained nutrients presumably determines the proportion that is lost by longer-term chronic leaching. Some data on this phenomenon are available from the cerrado savannas of Brazil, where Cavalcanti (1978) recorded a sharp increase in the quantities of exchangeable nutrients in topsoils after fire, followed by a gradual return to preburn levels over the following 3 months. The author attributed the decline to plant uptake, although some leaching losses could also have been involved.

At present no data exist on the speed and effectiveness with which nutrients, released by fires in the Mountain Pine Ridge savanna and retained temporarily in soil storage, are immobilized in plants. In particular, the effectiveness of the pine stratum in this capacity is unknown. However, nutrient uptake experiments over a 2-month period with seedlings of *Pinus caribaea* have shown them to have a very limited capacity to absorb a simulated post-fire nutrient flush (K. Robertson, York University, unpublished data, 1986), and declining soil fertilities have been recorded at rain forest sites planted to the species (Cornforth, 1970). The limited uptake capacity by pine that these data suggest may be further exacerbated after fires by the partial crown scorching that often occurs when stands of this species are burned.

In contrast to this slow response is the rapid vegetative resprouting by fire-tolerant plants of the shrub and graminoid layers that form the understorey in these pine savannas. Nutrient uptake by these strata could, in theory, be characterized as competition with pine. Indeed, considerable effort has been expended in the Mountain Pine Ridge savanna over the past three decades on hand-clearing the broadleaved trees and shrubs that coexist with pine and are

assumed to compete with it. However, the magnitude of this competitive effect is strictly limited by the small stature of plants in the subordinate shrub and herb strata, and by the fact that any nutrients immobilized in them are periodically mineralized by fire and so become potentially available to the pine overstorey. Consequently, we suggest that the coexistence of these strata with a pine overstorey may provide long-term cumulative benefits to this tree crop that outweigh any brief periods of competition in the immediate post-fire period.

In this paper we estimate the magnitude of nutrient immobilization in above-ground tissues of these strata and assess the effectiveness of these layers as temporary nutrient sinks in prescription-burned pine savannas.

METHODS

Data were gathered in the western part of the Mountain Pine Ridge savanna of Belize (lat. 17°N, long. 89°W), which consists of a granite plateau of approximately 500 m elevation, experiencing a total annual rainfall of 1560 mm, and having a pronounced dry season from February to April (Walker, 1973). Soils are coarse-textured Ultisols of exceptionally low fertility. Cation exchange capacities are low (2–20 meq per 100 g), as are base saturations (2–10%) and pH (4.7–5.0; Kellman, 1979). Wildfires in the savanna have been suppressed for the past three decades to encourage recruitment of *Pinus caribaea*, and today much of the savanna is covered by an open woodland of this species.

The study makes use of a prescription-burning experiment that was established in the savanna in 1976 to examine the feasibility of using fire as a management tool for fuel reduction (Hudson, 1976). Data collected in 1981, 1982 and 1983 on these experimental plots were used to analyse the response of shrubs to repeated burning and to develop a computer simulation model of post-fire shrub regrowth (Miyanishi, 1984; Miyanishi and Kellman, 1986b). Tissue samples of the most abundant shrub species, *Miconia albicans* (Swartz) Triana, were sampled for nutrient analysis in 1982 and 1983, and the results used in combination with the shrub growth simulation to estimate nutrient immobilization after fire. A more limited sample of mass and nutrient accumulation in the graminoid layer was taken in 1983 for comparison with the shrub nutrient immobilization data.

Prescription burning experiment

The prescription burning experiment comprised a randomized block design of 20 factorial treatments (five burning cycles \times two burning seasons \times two burning intensities) plus five controls, with replications in four sites within the savanna. Each plot was 25 \times 40 m in area. At the start of the experiment, all sites had been under fire control for 20 years and pine had been thinned



Fig. 1. A stand of *Pinus caribaea* in the Mountain Pine Ridge savanna, Belize, with a shrub understorey composed primarily of *Miconia albicans* (in flower).

once to densities of approximately 500 stems ha^{-1} . The shrub understorey was also cut back during the thinning operation. For logistical reasons, data were gathered in our study on plots of only one burning season (end of the dry season). Furthermore, since burn intensity treatments (headfire/backfire) proved not to differ significantly due to frequent wind shifts, this factor was disregarded. All sampling took place under early wet-season conditions during the months of May–July. Data on shrub performance were collected at the replicate site possessing the highest shrub density, while those on the graminoid layer were collected at the site possessing the lowest shrub density and best-developed stratum of grasses and sedges.

Shrub stratum

The shrub layer in this savanna is dominated overwhelmingly by *Miconia albicans* (Kellman, 1976; Fig.1). At the time of sampling, the density of *Miconia* plants on the experimental-burn plots exceeded 8000 ha^{-1} (Miyanishi, 1984). Estimates of nutrient immobilization by the shrub layer have been confined to this species and, consequently, are conservative estimates for the layer as a whole. The species is a multi-stemmed evergreen melastomataceous shrub that is widely distributed in neotropical savannas and is capable of reaching 5 m in height if protected from fire for long periods. Stem and leaf tissues are non-flammable but extremely fire-sensitive, and *Miconia* experiences 100% top kill after even cool fires. Scorched leaves on dead stems are shed slowly over several months after a fire, during which time vigorous resprouting of new stems takes

place from the root collar at ground level. Resprouting capacity is closely linked to root carbohydrate reserves (Miyanishi and Kellman, 1986b): these are progressively depleted by annual burns, and extinction of a shrub of average size after 21 years of this treatment has been predicted. However, burns at intervals of 2 years or longer allow replenishment of these reserves and indefinite persistence of shrub populations. For this reason, only burn cycles of 2 years or longer are considered here. Seedlings of the species are estimated to require approximately 13 years to achieve fire tolerance (Miyanishi and Kellman, 1986a), and the dense populations that now exist in the savanna probably derive from the three decades of fire suppression in this area. Prior to fire control, the species was reported only along the edges of riparian woodland within the savanna (Lundell, 1940).

The simulation model of the performance of populations of this species has been described elsewhere (Miyanishi, 1984). The model is based upon observed shrub resprouting capacity, and seedling establishment and growth patterns after varying post-fire periods. The model provides estimates of the fresh above-ground mass of each individual on a 100-m² plot at yearly intervals after fires of 1-5 years' regular recurrence interval. In this study, a randomly generated starting population possessing a density and size distribution similar to the shrub population in the prescription burning plots was simulated through 70 years of 2-, 3- and 5-year burn cycles, at which time shrub biomass had stabilized. A post-fire recovery cycle was then simulated for each burn cycle and the predicted mass of individual shrubs at annual intervals was used to estimate nutrient accumulation. Nutrient accumulation in 4-year burn cycles was not attempted, as no 4-year-old shrub tissues were available for nutrient content analysis at the time of field work (see below).

During 1981 and 1982, when shrub tissues were collected for nutrient content analysis, resprouted shoots of 1, 2, 3, and 5 years of age were available for sampling (Table 1). Ten randomly-selected shrubs were harvested for mass analysis in each of three treatment plots in 1981, and a further sample of 20 shrubs per plot was taken in six treatment plots in 1982. The fresh weight of each shrub was measured at harvest, then each was divided into four tissue types: young non-lignified stems, old stems, leaves, reproductive structures. Each tissue type was oven-dried at 60°C and then weighed. The dry mass of each tissue type was then regressed upon total shoot fresh weight for the shrub (Table 2). Using these regressions, the mass of the four tissue types in each shrub of the simulated populations was estimated at annual post-fire intervals, from the total shoot fresh weights generated by the model.

A subsample of the four tissue types was taken from ten randomly-selected shrubs in each fire treatment plot sampled, and was analysed for Ca, Mg, K and P content. The differences in mean tissue nutrient content between shrub ages was tested by Duncan's multiple range test (Table 5), and those tissues showing insignificant differences ($P > 0.05$) with tissues of any age were pooled

TABLE 1

Actual burn histories of the experimentally burned plots used in this study

Burn cycle	Year							
	1976	1977	1978	1979	1980	1981	1982	1983
Control	X							
One	X	X	X	X	X		X	
Two	X		X			X	X	
Three	X			X			X	
Four	X				X			
Five	X					X		

'X' indicates a burn. Burning irregularities in 1981 and 1982 resulted in some departure from the planned schedule at 1- and 2-year burn cycle plots

TABLE 2

Regression and determination coefficients of equations for *Miconia* tissue type mass on total fresh mass of the shrub

Tissue age (years)	No. of burns	N	a	b	r ²
<i>Old stems</i>					
1	5	10	—	—	—
1	2	37	0.046	-0.412	0.787
2	2	40	0.101	-0.616	0.937
3	2	48	0.233	-9.725	0.976
5	1	10	0.297	-5.594	0.980
<i>Young stems</i>					
1	5	10	0.063	0.021	0.977
1	2	37	0.103	-1.620	0.952
2	2	40	0.083	2.414	0.962
3	2	48	0.061	3.957	0.957
5	1	10	0.055	1.222	0.987
<i>Leaves</i>					
1	5	10	0.337	1.462	0.996
1	2	37	0.333	-8.433	0.982
2	2	40	0.282	-0.721	0.953
3	2	48	0.227	-4.615	0.908
5	1	10	0.162	4.904	0.940
<i>Reproductive structures</i>					
1	5	10	—	—	—
1	2	37	—	—	—
2	2	40	—	—	—
3	2	48	0.050	-1.201	0.865
5	1	10	0.049 ^a	-0.992 ^a	0.868 ^a

All equations of the form: Component oven-dry mass (g) = a · total fresh mass (g) ± b

^aData from 3- and 5-year-old tissues combined as insufficient data from 5-year-old tissues.

with these to provide a mean nutrient concentration estimate for tissue of that age. These concentrations were combined with the mass estimates of tissue types on each simulated shrub, to provide an estimate of nutrients sequestered by them at annual intervals, and these were summed across all shrubs to provide an estimate for sequestering by the stratum.

Graminoid stratum

Experimentally burned plots possessing a heterogeneous assemblage of burn histories were available in 1983, when the graminoid layer was sampled (Table 1). The most common time since burning was 1 year, and data from these plots, together with those from adjacent unburned sites outside the plot boundaries, were used to provide estimates of likely minimum and maximum nutrient storage in graminoid layers. This sampling design also permitted some assessment of whether repeated fires were reducing storage in this compartment. In the edaphically similar Llanos savannas of Venezuela, graminoid biomass achieves an equilibrium approximately 5 years after a fire (Sarmiento, 1984). Consequently, it is probable that the data from the long-unburned areas beyond plot boundaries provide reasonable estimates of the condition of the graminoid layer at 5 years of age. Two sets of 1-year post-burn plots that had previously been burned three, four and six times were sampled. To these were added data from two other plots (and their adjacent unburned controls) from elsewhere in the savanna: these were also 1 year post-burn, but the burn from which they were recovering had been the first in two decades.

Each plot was sampled with 20 randomly-located 0.25-m² quadrats, with those falling beneath shrub canopies being rejected. All live and standing dead grass and sedge tissue within each quadrat was clipped at 6.5 cm above ground level, the approximate height of stubble remaining after a prescription burn. Material was sorted into live and dead tissue for each of the five species that make up most of the graminoid mass (Table 6), with a residual component of minor species whose tissues were bulked and treated as a further 'species'. All material was oven-dried at 60°C and weighed, after which composite subsamples for nutrient concentration analysis were taken separately from live and dead tissues of each species in every plot. Total biomass and necromass for each species in every plot were converted to nutrient-content estimates using these concentrations, and were summed across all species to provide an estimate of total nutrient sequestering by the graminoid layer in each plot.

Chemical analysis

Tissue samples were dry-ashed at 450°C for 12 h after grinding in a Wiley mill (No. 40 mesh screen), and the ash taken up in 1N HCl. Cations in solution

TABLE 3

Estimated mass accumulation after fire in the *Miconia albicans* shrub layer subjected to 2-, 3- and 5-year burn cycles for 70 years (kg ha^{-1} , oven-dry mass)

Cycle and year	Old stems	Young stems	Leaves	Reproductive structures	Total
2-year cycle: year 1	72	162	510	—	744
year 2	238	203	673	—	1114
3-year cycle: year 1	88	198	623	—	909
year 2	319	283	901	—	1503
year 3	806	253	808	175	2042
5-year cycle: year 1	76	168	528	—	772
year 2	283	194	799	—	1276
year 3	629	204	633	137	1603
year 5	1252	244	731	123	2350

were determined by atomic absorption spectrophotometry, and P concentration measured by the molybdophosphoric blue method, using an autoanalyser.

RESULTS

Plant mass

In *Miconia*, leaf and young stem biomass appeared to equilibrate after 2 years at 600–900 and 200–300 kg ha^{-1} , respectively, while old stem tissue continued to accumulate, and reproductive tissue only appeared in measurable quantities after 3 years (Table 3). Total mass accumulation in the graminoid layer was approximately 1.8 times that in the shrub layer at 1 year after a fire, and 1.5 times that of the shrubs at 5 years (Table 4). Increase in the graminoid layer after 1 year is attributable mainly to increases in the standing dead material, as there were no significant differences between biomass in 1-year plots and adjacent unburned areas (paired *t*-test, $t=1.75$; $P>0.05$), while significant differences existed in the quantity of standing dead material ($t=5.03$; $P<0.01$). However, a comparison between accumulation of necromass on 1-

TABLE 4

Mean mass accumulation in the graminoid layer of savanna at 1 year and 5+ years after fire (kg ha^{-1} oven-dry mass, ± 1 SD)

Years since fire	Biomass	Necromass	Total mass
1	598 \pm 183	857 \pm 416	1455 \pm 572
5+	752 \pm 151	2528 \pm 903	3413 \pm 850

TABLE 5

Mean nutrient content (%) of *Miconia albicans* tissues

Tissue age (years)	No. of previous burns	Ca	Mg	K	P
<i>Old stems</i>					
1	5	—	—	—	—
1	2	0.123a ¹	0.125a ¹	0.454a ¹	0.026a ¹
2	2	0.101a ²	0.106ab ²	0.327ab ²	0.016b ²
3	2	0.098a	0.098ab	0.337ab	0.014b
5	1	0.091a	0.076b	0.251b	0.012b
<i>Young stems</i>					
1	5	0.207c	0.292a	1.033a	0.035ab
1	2	0.228bc	0.285a	1.096a	0.044a
2	2	0.185c	0.296a	0.789b	0.026b
3	2	0.305a	0.213a	0.785b	0.026b
5	1	0.282ab	0.234a	0.649b	0.022b
<i>Leaves</i>					
1	5	0.654b	0.285ab	0.692c	0.044b
1	2	0.967a	0.304a	0.896a	0.076a
2	2	0.736b	0.245ab	0.857ab	0.054b
3	2	0.729b	0.207b	0.680c	0.043b
5	1	0.697b	0.211b	0.761bc	0.040b
<i>Reproductive structures</i>					
1	5	—	—	—	—
1	2	—	—	—	—
2	2	—	—	—	—
3	2	0.553a ³	0.277a ³	1.109a ³	0.069a ³
5	1	0.568a ³	0.270a ³	0.968a ³	0.074a ³

Means with the same letter subscript for a tissue type and element are not significantly different between tissue age ($P < 0.05$, Duncan's multiple range test). $N = 10$, except where otherwise indicated: ¹ $N = 9$; ² $N = 7$; ³ $N = 6$.

year-old plots, relative to adjacent controls, and number of previous burns yielded an insignificant correlation ($r = -0.08$). Consequently, we conclude that, so far, repeated burning had no detectable effect upon the accumulation of either live or dead graminoid material at these sites. At 1 and 5 years after fire, total mass accumulation in both shrub and graminoid layers represented 2.6% and 6.6% of that present in the above-ground tissues of a 30-year-old thinned stand of *Pinus caribaea* sampled by Stewart and Kellman (1982).

Nutrient concentration in tissues

The nutrient content of *Miconia* tissues did not show strong age-related differences (Table 5), although there was a tendency for many elements to be

TABLE 6

Nutrient content ($\bar{x} \pm 1$ SD) of live tissues of the five major species comprising the savanna graminoid layer, at 1 year after burning and in adjacent unburned areas

Species	Ca		Mg		K		P	
	1 year	Unburned	1 year	Unburned	1 year	Unburned	1 year	Unburned
<i>Axonopus purpurssi</i>	0.170 ± 0.021	0.153 ± 0.018	0.164 ± 0.034	0.140 ± 0.021	0.840 ± 0.110	0.885 ± 0.113	0.010 ± 0.001	0.011 ± 0.001
<i>Mesosetum filifolium</i>	0.039 ± 0.010	0.043 ± 0.015	0.172 ± 0.041	0.157 ± 0.033	0.765 ± 0.055	0.846 ± 0.113	0.032 ± 0.015	0.031 ± 0.014
<i>Paspalum plicatum</i>	0.083 ± 0.014	0.063 ± 0.020	0.163 ± 0.032	0.141 ± 0.031	1.222 ± 0.249	1.465 ± 0.326	0.017 ± 0.008	0.037 ± 0.031
<i>Paspalum</i> sp.	0.210 ± 0.088	0.189 ± 0.027	0.188 ± 0.055	0.168 ± 0.047	1.188 ± 0.095	1.291 ± 0.163	0.120 ± 0.016	0.107 ± 0.011
<i>Trachypogon plumosus</i>	0.086 ± 0.014	0.100 ± 0.023	0.083 ± 0.012	0.075 ± 0.014	0.760 ± 0.043	0.697 ± 0.096	0.019 ± 0.011	0.038 ± 0.025

For 1-year tissues, $N = 8$; for unburned tissues, $N = 6$; two unburned sites each served as controls for burned plots.

TABLE 7

Nutrient accumulation (kg ha^{-1}) in above-ground tissues of *Miconia albicans* and graminoids, compared to other nutrient storages and fluxes for the pine savanna ecosystem

Component or flux	Ca	Mg	K	P
1-year-old <i>Miconia</i>	5.57	2.11	6.71	0.49
1-year-old graminoids	1.39	1.79	6.52	0.42
1-year-old total	6.96	3.90	13.23	0.91
5-year-old <i>Miconia</i>	8.16	4.19	12.98	0.72
5-year-old graminoids	3.09	3.21	9.05	1.38
5-year-old total	11.25	7.40	22.03	2.10
Mean annual accumulation in 25-year-old unthinned pine ^a	5.84	0.36	0.53	0.68
Total above-ground accumulation in 30-year-old thinned pine ^a	65	20	55	7
Estimated annual atmospheric input ^b	2.15	0.39	3.68	0.15
Exchangeable nutrients in 30 cm of topsoil ^a	73.8	48.9	104.2	3.8

^aData from Stewart and Kellman (1982).

^bData from Kellman and Carty (1986).

significantly more concentrated in the 1-year-old tissues of shrubs burned only twice than in the tissues of older shrubs. However, this difference had largely disappeared in the 1-year-old tissues of shrubs subjected to five previous annual burns, presumably reflecting the deterioration in shrub performance that was found at these sites (Miyaniishi and Kellman, 1986b).

Differences between nutrient concentrations of graminoid tissues in burned and unburned plots were small (Table 6), and paired *t*-tests showed only one significant difference (P concentration in *Paspalum* spp. tissues: burned > unburned). Consequently, burning treatments applied over the 7 years of the experiment had not had any widespread effect on the nutrient content of graminoid tissues, and any differences in accumulation in this layer must be attributed to storage in standing dead material.

Nutrient accumulation

Accumulation of nutrients in shrubs showed an initial rapid increase during the first year, followed by slower accumulation rates during subsequent years (Table 7, Fig. 2). Calcium accumulation by shrubs was superior to that by the

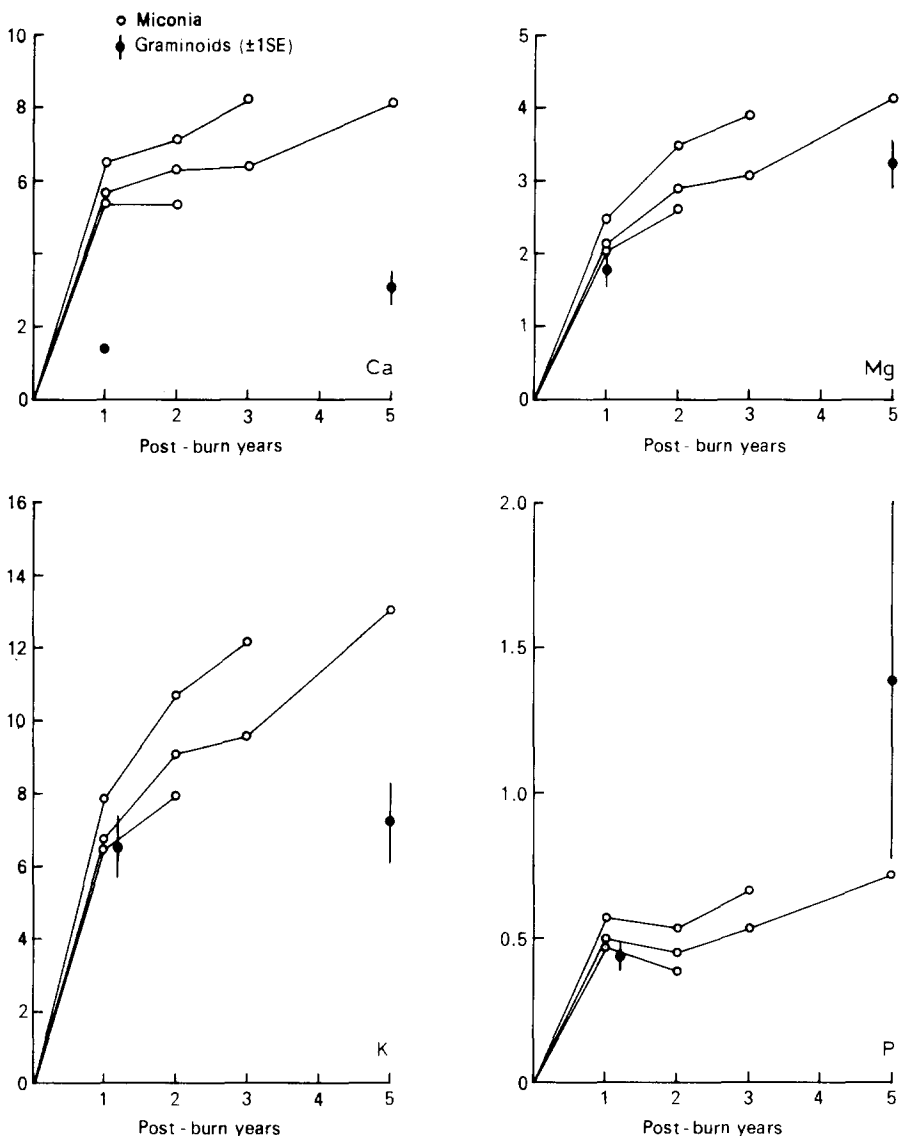


Fig. 2. Accumulation of Ca, Mg, K and P (kg ha^{-1}) in above-ground tissues of *Miconia albicans* after regular prescription burning at 2-, 3-, and 5-year intervals, and in the graminoid layer at 1 and 5+ years after burning.

graminoids under all treatments. First-year accumulation of Mg, K and P was approximately equal in the two layers. Thereafter, shrub accumulation of Mg and K exceeded that by the graminoid layer. However, P accumulation in the dead material of the graminoid layer far exceeded that by the shrubs in subsequent years.

DISCUSSION

Potassium and P concentration in *Miconia* leaves are broadly similar to those in live grass and sedge tissues, but Mg concentrations are somewhat higher, and Ca concentrations substantially so (Tables 5 and 6). The nutrient concentrations in graminoid tissues from the Mountain Pine Ridge savanna fall within the range of those of other neotropical grasses and sedges (Sarmiento, 1984). Those of *Miconia* also fall within the range of nutrient concentrations in leaf tissues of savanna shrubs from Trinidad (Ahmad and Jones, 1969) and Venezuela (Montes and Medina, 1977). Concentrations of Ca, Mg and K in *Miconia* leaves are also within the range of those in tropical forest trees (Sarmiento, 1984), but P concentrations are generally lower than these. The nutrient concentrations of *Miconia* leaves measured here also very similar to the overall mean concentrations of the same elements in the leaves of ten tree and shrub species from the Mountain Pine Ridge savanna that were analysed by Kellman (1976). These leaf tissues contained approximately double the concentrations of Ca, Mg and K that pine foliage possessed, and approximately equal concentrations of P. Nutrient concentration in the stemwood of *Miconia* (Table 5) was two to seven times that of pine (Stewart and Kellman, 1982). These data indicate that the dicot shrubs of neotropical savannas are capable of maintaining concentrations of most nutrients in their tissues at levels similar to those of tropical forest trees, despite the extreme infertility of the soils upon which they grow. As such, they comprise high-quality nutrient storage tissue relative to that of pine, whose success on these infertile soils depends upon a combination of low nutrient demands and slow growth.

The estimates of nutrient sequestering in the graminoid layer are probably reasonable estimates of the maximum achievable in this type of understorey, since sampling was restricted to shrub-free areas. However, the estimate for shrubs is conservative as it ignored the quantities sequestered in the low-density graminoid layer beneath shrubs as well as the contribution of minor species in the shrub layer. Consequently, a reasonable estimate of the maximum sequestering achievable in both understorey layers combined probably lies between that for the shrub layer and the shrub + graminoid layer estimates provided in Table 7. These estimates do not include nutrients sequestered in a litter compartment which, on these sites, is composed mainly of pine needles. However, while an appreciable litter layer can develop beneath pine stands after a long period of fire suppression (Hutchinson, 1977), this is normally reduced to a very small size under regular prescribed burning.

The quantities of nutrients stored in these understorey layers represent a significant proportion of total system storages and fluxes. For example, accumulation by shrubs during the first year after a fire equals the mean annual accumulation of Ca in 25-year-old unthinned pine stands, and far exceeds the annual accumulation of Mg and K in these stands (Table 7). Only P shows

greater annual accumulation rates in the pine stands. Storage in shrubs at 1 year also exceeds the estimated annual influx from atmospheric sources for all elements (Kellman and Carty, 1986). Storage in shrubs at 5 years is approximately 10% of that in the exchangeable nutrient compartment of the soil, and represents 10–20% of that stored in above-ground tissues of a thinned pine overstorey. The quantities will also normally exceed those mineralized in a controlled fire, as complete fuel consumption does not normally occur in prescription burning. The magnitude of understorey nutrient sequestering will probably decline as the pine overstorey develops and increasing quantities of nutrients are immobilized in this layer. However, few stands of pine older than 35 years exist in the savanna at this time, making it impossible to predict the pattern of understorey nutrient storage over the 60+ -year rotation that will be required for timber production. We suggest that the proportionately large quantities of nutrients that can be immobilized in these understorey layers, and the speed with which this immobilization can be achieved, indicate an important nutrient conservation role for this ecosystem component in an oligotrophic environment. This role will be particularly important after periodic prescription burning, and after thinning and harvesting of the pine overstorey when tree root uptake capacity is reduced or eliminated and large quantities of nutrients are deposited in slash.

Under annual burning only a graminoid layer can be sustained in this savanna (Miyanihi, 1984), and it seems probable that under these circumstances some net loss of nutrients, especially of Ca, would occur. Burning of the graminoid layer normally results in relatively complete mineralization of its stored nutrients, and significant increases in the quantities of exchangeable Ca and Mg have been recorded at sites subjected to multiple annual burns (Kellman et al., 1985). This indicated a net transfer of these elements to the soil, an inability of pine to fully immobilize them, and their susceptibility to long-term chronic leaching from the soil compartment. Burning at fire cycles longer than 1 year permits the existence of a shrub layer, and we believe that there are cogent reasons to prefer this understorey as a nutrient sink to one composed exclusively of graminoids. With the exception of P, the shrub layer is capable of storing more nutrients than is the graminoid layer. Moreover, while larger quantities of P can be stored in the dead tissues of grasses and sedges, this element is rapidly immobilized by soil fixation (Kellman, 1985; Kellman and Sanmugas, 1985) and so is unlikely to be lost from the site. However, we suggest that the major advantage of the shrub layer studied here lies in its non-flammability. Because of this property, stored nutrients are not mineralized instantaneously in fires, but are gradually released in the post-fire period as scorched leaves are shed and they, and stems, gradually decompose. Under these circumstances, volatilization of N is also much less likely. Furthermore, long-term computer simulations of *Miconia* populations show a stabilization

of densities at equivalent levels irrespective of the burn cycle length (Miyaniishi, 1984). This suggests a demographically highly resilient stratum.

The ultimate test of the efficacy of a shrub understorey in maintaining site fertility and increasing pine growth would require long-term monitoring of tree growth rates on sites with and without this stratum. An earlier analysis of the effects of dicot trees and shrubs on pine growth (Kellman, 1976) showed neither significant inhibition nor augmentation. However, most pines in that study were under 20 years in age, and it is unlikely that the postulated cumulative effects would become detectable at such an early stage of stand development. While data on pine growth over longer time spans does not now exist, we suggest that the information presented here provides strong circumstantial evidence in favour of a facilitative role (*sensu* Connell and Slatyer, 1977) for coexisting shrubs. However, in emphasizing *Miconia* in this study, we are not suggesting that this species provides a unique solution to the nutrient conservation problem. Although its fire tolerance, local dominance, and wide-spread occurrence in other neotropical savannas suggests a locally promising resource, equivalent species possessing comparable properties almost certainly exist elsewhere. For example, Grove and Malajczuk (1985) have demonstrated the potentially important nutrient-cycling role that the understorey shrubs *Trymalium spathulatum* and *Bossiaea laidlawiana* play in prescription-burned *Eucalyptus diversicolor* stands in Western Australia. We reiterate the appeal that these authors have made for a fuller understanding of the dynamics of understorey shrub strata in managed forests and an evaluation of their role in maintaining site fertility and productivity.

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