

## Session Summary

### The Role of Watersheds in Reconciling Fisheries with Conservation

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Several keynote speakers at the Fourth World Fisheries Congress emphasized the importance of understanding ecosystem processes if we are to effectively reconcile fisheries with conservation. Nowhere is this more important than in watershed management. Watershed processes determine the properties of freshwater ecosystems and thereby regulate the productivity of local fisheries, as well as other fisheries whose target species spend part of their life cycles in freshwater ecosystems. Fish are but one of many natural resources that comprise the spectrum of ecological "goods and services" watersheds provide (drinking water, irrigation, hydroelectric power, water for industrial processes, and others) and, as such, are subject to inevitable tradeoffs and compromises that accompany different interests with competing water needs. In watersheds, reconciling fisheries with conservation means not only balancing exploitation with the need for conserving the long-term viability of fish populations, it also means balancing the aquatic ecosystem requirements of fish with other societal needs for water. Oral and poster presenters in the Watershed Session offered a wide range of ideas on how these balances might be achieved. Their ideas fell into several general categories.

#### Watershed Management Requires a Hierarchical Approach

Several presenters noted the inadequacy of managing strictly at the local level, which meant deciding harvest, conservation or restoration issues based on the perceived conditions at a particular location in a watershed without giving due consideration to the context of the surrounding landscape. A hierarchical approach involves setting objectives and strategies at the watershed scale and making local decisions based on actions that are compatible with these overarching goals. A thorough, watershed-wide assessment of environmental conditions affecting fishery resources is often the necessary first step, followed by an agreed upon plan that sets general goals for the watershed and permits increased specificity in decision making at the local level.

#### Reconciling Fisheries with Conservation in Watersheds must be Viewed as One of Many Competing Demands for Water

A number of the papers in the session addressed conflicts between fisheries and other land and water uses. Several, for example, dealt

with the impact of forestry operations on aquatic habitats and fish populations, and one paper described the conflict between protecting the habitat of an endangered shad population and the development of a water supply reservoir for more than a half million people. Such conflicts are never easy to resolve and scientific experts employed by competing interests usually advocate opposing positions. Within the last two decades or so, committees of independent scientists have been assembled to study watershed issues and provide objective descriptions of the likely outcomes of management alternatives based on the best current science; such committees do not make policy, but they do inform politicians about the risks and benefits of different actions. One innovative paper in the session noted that the effect of national water security programs on freshwater fisheries was poorly understood at both a local and global scale.

### Watershed Processes Determine Appropriate Management Strategies

The dynamic nature of ecological processes operating at the watershed scale was addressed by several presenters. Some of the biophysical processes affecting fisheries and conservation included climate change, disturbance-based patterns of erosion and runoff, and the introduction of non-native species. There was a clear consensus that management strategies will be more effective if they include provisions for accommodating watershed change, whether mediated by shifts in climate, periodic natural disturbances such as fires and floods, and the intentional or unintentional establishment of exotic species. Two papers emphasized the identification of biological hotspots, locations in the watershed likely to support high aquatic production (e.g., tributary junctions), as special places that require conservation. Long-term habitat benefits of

natural disturbance processes were recognized in several presentations. One paper even noted that management of disturbances caused by a wildlife species (beaver) could be used to enhance fish stocks in the Yukon River, Canada.

### Watershed Governance Systems Influence the Balance Between Exploitation and Conservation

In the past, watershed management has been the responsibility of governmental organizations with regulatory authority, but more recently management decisions have been shared with a variety of nongovernmental organizations. Some of the most successful have been "watershed councils," which are composed of groups of stakeholders charged with recommending habitat improvement projects, educating the public regarding watershed processes, and promoting collaboration between traditional adversaries. As one paper points out, watershed councils can also help support monitoring programs by engaging activists in the monitoring process and by providing timely feedback to stakeholders regarding the efficacy of restoration projects. However, other papers note that losses of aquatic habitats are continuing in most areas and many restoration projects are not living up to expectations. Local organizations often seem ill equipped to deal with restoration failure, while larger organizations (federal and state/provincial agencies) seem better equipped to document broad-scale habitat declines but often lack local support to effect remedies.

### New Decision Support Tools Assist Landscape-Scale Analyses

Advances in geospatial mapping technology, remote environmental sensing, spatial and temporal modeling, and the ability to share

data via the internet have all contributed to the development of tools to aid watershed decision makers in reconciling fisheries with conservation. The session included papers on spatially explicit modeling of land development on Pacific salmon, landscape models of stream channel dynamics in Ontario, Canada, and coastal Oregon, USA, water temperature models for evaluating the adequacy of riparian buffers along forested streams, and a Geographic Information System (GIS)-based model of stream shading and steelhead *Oncorhynchus mykiss* growth. All of these papers presented information that transcended the reach scale typical of freshwater habitat studies, thus giving policy makers a better opportunity to view the big picture.

How well did the papers address the central theme of reconciling fisheries with conservation in watersheds? Overall, most papers focused more on successes than failures. This is typical of many watershed presentations, where there is a reluctance to highlight projects that did not work. Only a few papers dealt with the fact that, in most areas, freshwater habitats are being lost more rap-

idly than they are being restored and the global capacity of freshwater ecosystems to increase capture fisheries has apparently reached its limit. Several papers recognized that collaboration among stakeholders and improved systems of watershed governance were the keys to the reconciliation process, but examples of real successes (i.e., fisheries that recovered as a result of better watershed management) were largely absent.

On the other hand, a number of authors presented exciting examples of new technologies that can be used to inform management decisions. These tools, if applied properly, will lead to an improved understanding of the tradeoffs between fishing, habitat conservation, and other natural resource management actions. The session contained a useful cross section of papers dealing with the complex issues involved in reconciling fisheries with conservation in watersheds. Readers will find examples of both technically and socially oriented attempts to achieve effective conservation that, hopefully, will stimulate new ideas and creative approaches to a very difficult problem.

# Nutrient resorption and patterns of litter production and decomposition in a Neotropical Savanna

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## Summary

1. Deposition of nutrients due to anthropogenic activities has the potential to change nutrient availability in nutrient-limited ecosystems with consequences for plant and ecosystem processes.
2. Species-specific and ecosystem responses to the addition of nutrients were studied in a field experiment conducted in a Savanna (*Cerrado sensu stricto*) on dystrophic soil in central Brazil. Three fertilization treatments (N, P and N plus P additions) and unfertilized control were replicated in four 15 × 15 m plots per treatment.
3. Five of the dominant woody species were studied. Specific leaf area (SLA) was not affected by the treatments, but species responded differently in terms of foliar nutrient concentration, resorption efficiency and proficiency to the increased soil N and P availability.
4. Responses of N and P resorption suggested different levels of regulation for these two limiting elements, with a decrease in N and P resorption proficiency depending on the treatment. In general, under N fertilization, senesced leaves presented higher N concentration, whereas combined fertilization with N and P resulted in senesced leaves richer in P. The concomitant variation in P resorption efficiency and proficiency indicates a stronger regulation between them compared to N.
5. Results indicated a highly efficient and complete P resorption, while N concentrations in senesced leaves indicated intermediate or incomplete resorption efficiencies, supporting the idea that Cerrado plants might be more limited by P than by N.
6. At the ecosystem level, higher N concentration in the leaf litter was measured at the end of the dry season in the +NP-fertilized plots, resulting in a significantly faster decomposition rate in relation to the control treatment. Responses of litterfall and decomposition rates indicated that the system was generally more responsive to the combined addition of N and P than to fertilization with N or P alone over the relatively short time span of this study.

**Key-words:** Cerrado, fertilization, nitrogen and phosphorus resorption, N : P ratio

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## Introduction

Human activities and population growth have more than doubled the production rate of reactive nitrogen on the land surface (Galloway *et al.* 2004). According to Filoso *et al.* (2006), vast deforestation, rapid conversion of natural vegetation into agricultural lands accompanied by intensification of agriculture,

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expansion of nitrogen-fixing crops, increasing rates of fertilizer consumption, population growth and fast urbanization rates are the common drivers altering the nitrogen cycle in the tropics. These authors examined the changes in the nitrogen cycle associated with human activities in Brazil, the largest tropical country in the world. They concluded that the intensive agricultural activities (pastures and soybean) in the Brazilian Savanna region (Cerrado) account for much of the anthropogenic N inputs in the country.

The Cerrado forms the second most extensive plant formation in tropical South America, covering about 2 million km<sup>2</sup> of area. Containing more than 7000 plant species, it is the most species-rich Savanna in the world (Solbrig 1996) and, doubtless, one of the most species-rich ecosystems of any type. Although annual rainfall in the region is relatively high (1500 mm), there is a prolonged 4-month dry season from June through September. In addition to the pronounced seasonality of rainfall, there is predominance of old and highly weathered soils, with low nutrient availability, especially N and P, considered the major constraint on plant growth (Haridasan 2001). These features of the Cerrado environment have probably been acting as forces selecting for species with high capacity to take up and retain nutrients in their tissues. Cerrado plants seem to have developed efficient and conservative mechanisms to minimize nutrient losses, including scleromorphic leaves and high resorption rates of nutrients, which results in production of litter with high C : N and C : P ratios and slow decomposition rates (Resende 2001; Nardoto *et al.* 2006). Nutrient cycling in the Cerrado is also likely to be influenced by the diverse patterns of leaf phenology (Franco *et al.* 2005) in relation to seasonal variations of precipitation and soil nutrient availability.

The responses of Cerrado vegetation to an increase in nutrient availability are not known. Fertilization experiments in other nutrient-poor systems have found that plants responded to N and P amendments by changing leaf morphology, nutrient concentration, carboxylation capacity, nutrient-use efficiency, chlorophyll content, leaf life span (Cordell *et al.* 2001a,b), resorption efficiency and decomposability of leaf litter (Vitousek 1998), above- and below-ground biomass and root length (Garcia-Miragaya, San José & Hernández 1983; Barger *et al.* 2002). At the community level, fertilization might alter species diversity (Aerts, de Caluwe & Beltman 2003).

We conducted a fertilization experiment involving repeated additions of N, P and N + P combined in an area of intact Cerrado vegetation in order to assess potential impacts of removal of soil nutrient limitations at the individual species and ecosystem levels. The responses of five abundant woody species and some key attributes related to nutrient cycling were analyzed. We tested the hypotheses that nutrient additions to the soil would: (i) enhance foliar nutrient concentration; (ii) decrease leaf nutrient resorption

efficiency (NRE) and nutrient resorption proficiency; and (iii) result in litter with lower C : N and C : P ratios that would decompose faster. The present study synthesizes the responses in the soil-plant system during the first 2 years after the beginning of the fertilizations.

## Materials and methods

### STUDY AREA AND CLIMATE

The study was initiated in October 1999 at the Ecological Reserve of the IBGE (Brazilian Institute for Geography and Statistics, <www.recor.org.br>), 35 km south of Brasília (15°56' S, 47°53' W). The study site represents the most common physiognomy found in the Cerrado region, known as Cerrado *stricto sensu*, characterized by a continuous ground layer dominated by grass and a woody layer of trees and shrubs varying in ground cover from 10% to 60% (Eiten 1994). A survey performed at the beginning of the experiment estimated a density of woody plants (with height > 100 cm and stem diameter at 20 cm above the soil surface > 4.0 cm) of 1527 plants per hectare (unpublished data). Mean height was 295.0 ± 9.9 cm and mean stem diameter 8.4 ± 0.3 cm (Bucci *et al.* 2006). Soil is characterized as Latossolo Vermelho (Brazilian Soil Taxonomy) which corresponds to Oxisols (US Soil Taxonomy). It is acidic, with high aluminum levels, low cation exchange capacity and 0.6%–2.4% organic matter content.

Total precipitation in 1999 was 1206.6 mm (Fig. 1). Although there were some rain events in September and at the beginning of October, the rainy season, as a continuous period characterized by frequent rains, started in the middle of October. In 2000, total precipitation was 1559.1 mm. The first 4 months received 65% more precipitation than the same period in 1999, and August and September were also wetter in 2000. Mean air temperature was 22.3 °C in 1999 and 2000.

### FERTILIZATION TREATMENTS

The field design consisted of three fertilization treatments and an unfertilized control replicated four times in sixteen 15 × 15 m plots separated by at least 10 m from each other. Treatments were randomly assigned to plots. The treatments were given as follows: +N (100 kg of N per ha per year as (NH<sub>4</sub>)<sub>2</sub>SO<sub>4</sub>), +P (100 kg of P per ha per year as Ca(H<sub>2</sub>PO<sub>4</sub>)<sub>2</sub> + CaSO<sub>4</sub>·2H<sub>2</sub>O), and +NP (100 kg of N + 100 kg of P per ha per year in the preceding forms). An additional area of 1-m width surrounding the 15 × 15 m plots was also fertilized. Nutrients were applied over the litter layer to avoid major disturbance in the plots and in granular form in order to release N and P more slowly. The amount of fertilizers was based on recommendations for removing nutrient limitations in *Eucalyptus* plantations in the Cerrado region, and was divided into two applications; one at the beginning and the other at the end of the rainy season. Fertilizer was first applied at the beginning of

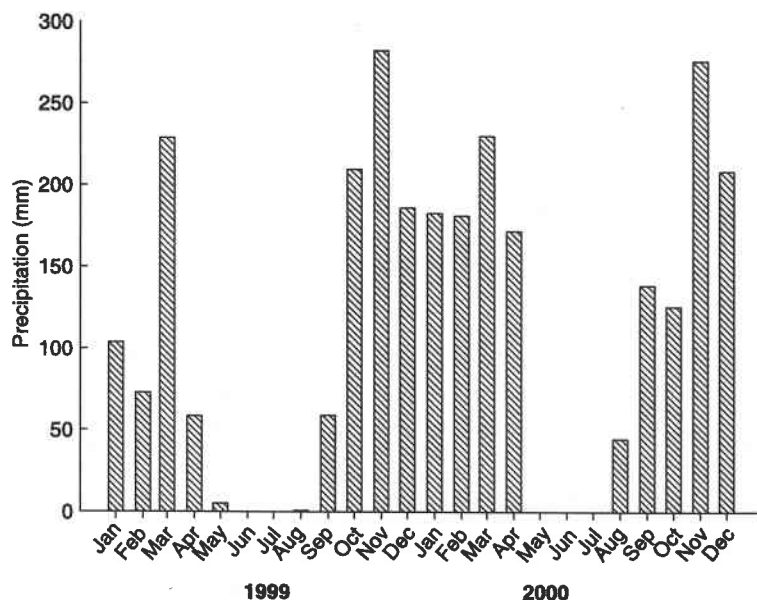


Fig. 1. Monthly precipitation at the Reserva Ecológica do Roncador – IBGE during 1999 and 2000.

the rainy season in October of 1998. Subsequent fertilizations occurred in April 1999, October 1999 and March 2000.

#### PLANT SPECIES

Five woody species were chosen for the study. Three are brevideciduous (*Blepharocalyx salicifolius* Berg, Myrtaceae; *Caryocar brasiliense* Camb., Caryocaraceae; *Qualea parviflora* Mart., Vochysiaceae) and two are ever-green species (*Schefflera macrocarpa* Seem, Araliaceae and *Ouratea hexasperma* (St. Hil.) Baill., Ochnaceae). *Caryocar brasiliense* and *Q. parviflora* normally show a peak of leaf loss at the end of the dry season, *B. salicifolius* shows a peak of leaf loss at the beginning of the dry season, *S. macrocarpa* produces and loses leaves continuously throughout the entire year and *O. hexasperma* begins losing leaves and developing new ones with the onset of the first rains during the dry-to-wet season transition.

#### SOIL ANALYSES

Soil samples were collected at 0–5, 5–10, 10–20 and 40–50 cm depth before (September 1998) and 7 months after (May 1999) the first fertilization. Three samples were collected per plot and mixed to form a composite sample, resulting in four replicates per treatment. Samples were analyzed for available P (Mehlich I), pH in  $\text{CaCl}_2$  and KCl and total nitrogen (Kjeldahl). Analyses were performed by the Embrapa–Cerrados, the Brazilian Research Center for Agriculture in Cerrado Region (Embrapa 1998).

Availability of ammonium and nitrate in the soil (0–5 cm) was determined monthly from August 1999

to July 2000. Three samples were collected in each plot using a 5-cm-diameter PVC coring device. The field-moist soil samples were extracted with 1 M KCl for 1 h, and the inorganic N concentrations were determined by colorimetry.  $\text{N-NH}_4$  was analyzed through reaction with Nessler reagent and  $\text{N-NO}_3$  by UV absorption according to the method proposed by Meier (1991).

#### LEAF NUTRIENT CONCENTRATION, RESORPTION EFFICIENCY AND SPECIFIC LEAF AREA (SLA)

To estimate resorption of foliar nutrients, green, fully expanded leaves of three individuals of each species per treatment were collected during the rainy season (December 1999 to March 2000). Two branches per plant were enclosed in cloth bags (2 mm mesh) in order to facilitate the collection of abscised leaves in the following dry season (June to August 2000). The bags did not interfere with transpiration and photosynthesis. Determinations of N, P and C concentrations in leaves were performed by Embrapa–Cerrados. Resorption efficiency was calculated as the difference in nutrient concentration between the green and the abscised senescent leaves expressed as percentage of the nutrient concentration in green leaves. To avoid underestimations due to leaf mass loss during the senescence period, measured resorption values were recalculated as described by van Heerwaarden, Toet & Aerts (2003) considering a Fractional Change of Measurement Basis of 0.21. Nutrient resorption was also quantified by resorption proficiency that describes the level to which a nutrient is reduced during senescence (i.e. the nutrient concentration measured in the senesced leaves), with higher proficiencies corresponding to lower final nutrient concentration (Killingbeck 1996). SLA was determined for five leaves per tree (three individuals per treatment) during the rainy season. Leaves were scanned and their area was calculated through the program AREA 2.1C (Caldas *et al.* 1992). Leaf dry mass was measured after drying for 48 h at 65 °C in an oven.

#### LITTER PRODUCTION AND QUALITY

Litter production at the community level was quantified monthly from January 1999 to June 2000. Three litter traps (50 × 50 cm, 2-mm mesh) per plot (12 traps per treatment) were randomly installed at 15 cm from the soil surface. Litter samples were oven-dried for 72 h, separated into leaves and other parts (including reproductive structures, stems, etc.) and weighed. Grass and animal tissues were excluded. Leaf litter nutrient concentration was measured monthly from the transition between the dry and rainy seasons (September 1999) to the peak of the rainy season (January 2000). The leaf fraction was ground for subsequent determinations of total N (Nessler method, Oliveira 1986), P (inductively coupled plasma-atomic emission spectrometry) and C (wet combustion). The analyses

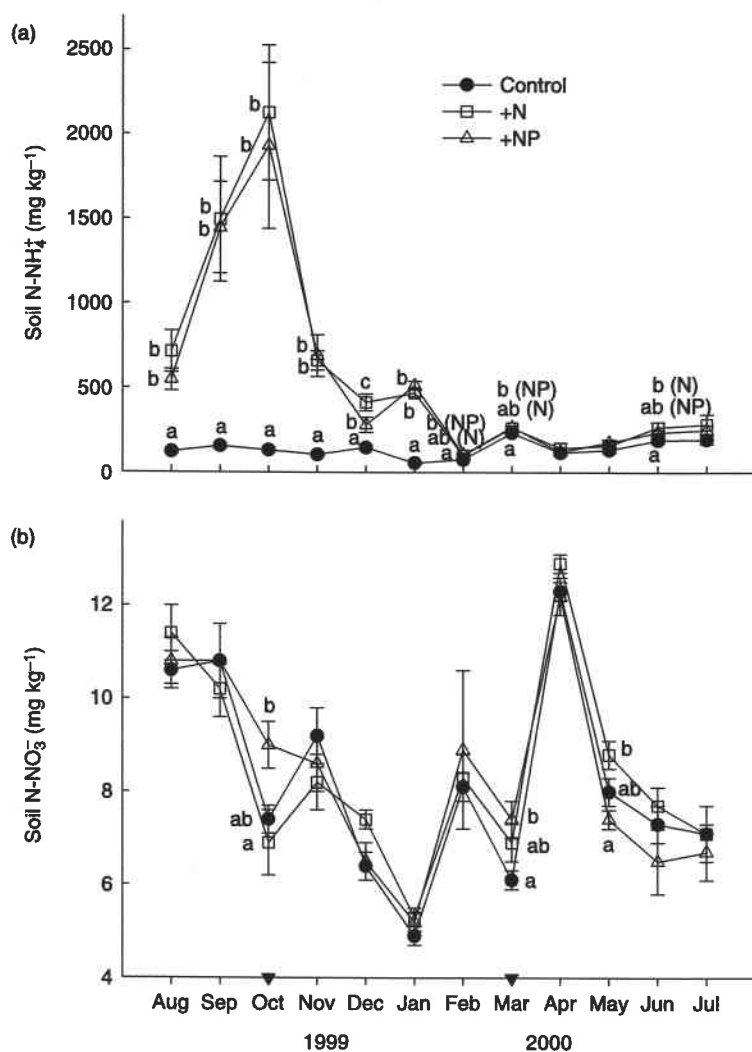


Fig. 2. Nitrate (mg N-NO<sub>3</sub> kg<sup>-1</sup> soil dry wt) and ammonium (mg N-NH<sub>4</sub> kg<sup>-1</sup> soil dry wt) concentrations in Cerrado soils (0–5 cm) from August 1999 until July 2000. Inverted triangles on the x-axis indicate dates of fertilization. Different letters indicate significant differences ( $P < 0.1$ ) among treatments within the same month.

were performed by Embrapa–Cerrados. Data related to P concentration in the +P plots in September and October are not presented due to technical problems.

#### LITTER DECOMPOSITION RATE

Litter samples collected from the traps in October 1999 (1 year after the first fertilization) were used for the determination of decomposition rates. Fresh subsamples were dried to constant weight and 10 g were put into litter bags (20 × 20 cm, 2 mm mesh). Three bags were placed under the litter layer in each plot and were collected after 5 months (April 2000) of incubation *in situ* spanning the rainy season. The content of the bags was dried and weighed for the determination of mass losses. The decomposition constant,  $K$ , was calculated using the negative exponential model (Lavelle *et al.* 1993).

$X_t = X_0 \cdot e^{-Kt}$ , where  $X_t$  represents the litter dry mass after a period of incubation days ( $t$ ), and  $X_0$  is the initial litter dry mass.

#### STATISTICAL ANALYSES

Data were first analyzed for normal distribution using the Kolmogorov–Smirnov test. In the case of non-normal distribution, the data were log-transformed. Differences in soil parameters, SLA, foliar nutrient concentration and resorption efficiency and decomposition rate among treatments were tested using ANOVA. Repeated measures ANOVA was used to test month and treatment differences in mineral nitrogen availability, litterfall and leaf litter quality. Due to the variability of data and the limitation of sample size associated with the field experiment conditions, the acceptance level,  $P$ , was 0.1, which increases the power of the hypothesis tests and reduces the probability of making a type II error (Peterman 1990). Analyses were performed by the SPSS program version 10.0.

#### Results

##### SOIL pH AND NUTRIENT AVAILABILITY

Values of soil pH, total N and available P concentrations did not differ among treatment plots before the first fertilization (September 1998), indicating that they were homogeneous in terms of soil conditions. Soil pH values were about 4.7 in CaCl<sub>2</sub> and varied from 3.9 (0–5 cm) to 4.3 (40–50 cm) in KCl. Comparing the nutrient concentrations in the 0–5 cm and 40–50 cm soil layers, total N decreased from 2.6 to around 1.3 g kg<sup>-1</sup>, respectively, and available P concentration decreased from 1.2 to 0.1 µg kg<sup>-1</sup> (data not shown).

After fertilization, significantly lower values of pH were found in the +N (0–20 cm) and +NP (0–10 cm) treatments, whereas P addition did not affect soil pH. Available P concentration in the first 5 cm of soil was enhanced by 7.3 (+NP) and 3.2 (+P) times compared to the control plots, although the differences were significant only in the +NP treatment. Although N and NP fertilizations did not alter total N in the soil, +N and +NP treatments led to an increase in available inorganic N, especially NH<sub>4</sub><sup>+</sup> during the dry season of 1999 when NH<sub>4</sub><sup>+</sup> concentration was about 5.2 times and 9.4 times higher than in the control in August and September, respectively (Fig. 2a, see Table S1 in Supplementary material). Immediately after the third fertilization (October 1999), the difference increased to 15.5 times, falling to much lower values with the onset of the rainy season. Fertilization in the rainy season (March 2000) did not enhance NH<sub>4</sub><sup>+</sup> availability. Significantly higher NO<sub>3</sub><sup>-</sup> concentrations compared to the control were only found in the +NP plots immediately after the two fertilization events (October 1999 and March 2000, Fig. 2b).

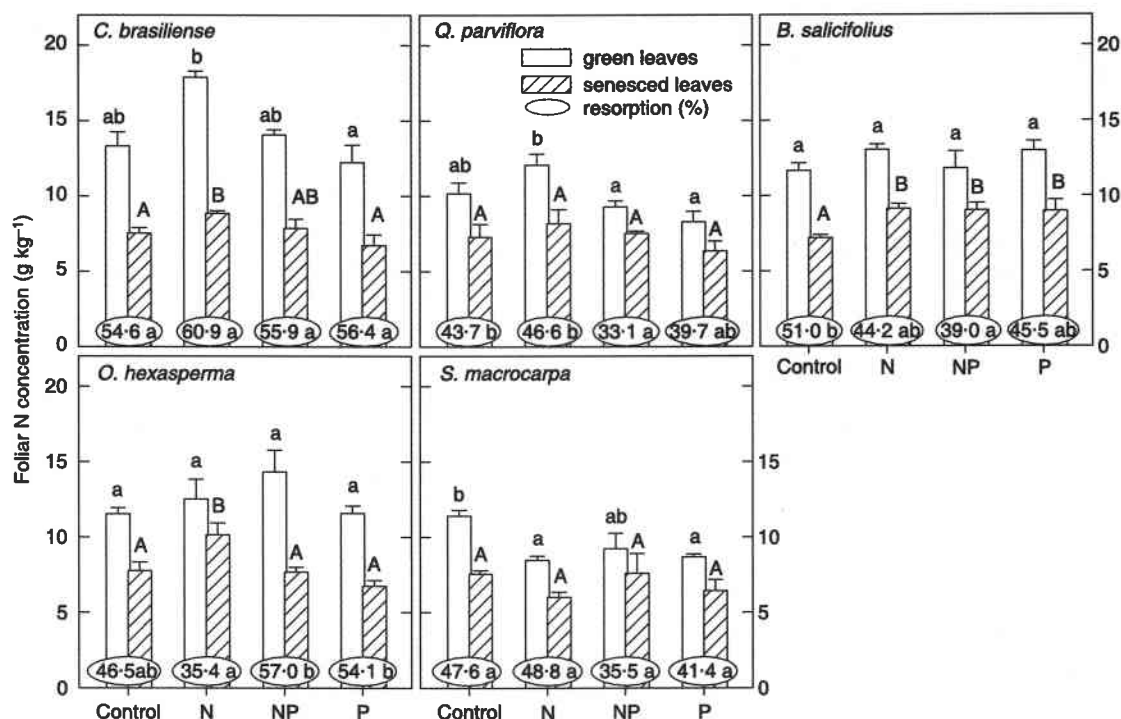


Fig. 3. Nitrogen concentration (bars) in green and senesced leaves of the five Cerrado species growing in the control and fertilized plots (+N, +NP and +P). Numbers within the ellipses represent the resorption efficiency (%). Different letters indicate significant differences ( $P < 0.1$ ) among treatments.

#### SPECIFIC LEAF AREA (SLA), NUTRIENT CONCENTRATION IN LEAVES, AND RESORPTION PROFICIENCY AND EFFICIENCY

Fertilization did not significantly change SLA of the species studied, with exception of *C. brasiliense*, which showed higher SLA under the +N treatment (data not shown). Brevideciduous species showed higher SLA values ( $8\text{--}15\text{ m}^2\text{ kg}^{-1}$ ) than evergreen species ( $4\text{--}8\text{ m}^2\text{ kg}^{-1}$ ).

Since SLA was not affected by fertilization, patterns of nutrient concentration on leaf area and leaf dry mass basis were similar. In the control, the mean N concentration in mature green leaves ranged from  $14.4\text{ g kg}^{-1}$  in *C. brasiliense* to  $9.5\text{ g kg}^{-1}$  in *S. macrocarpa* (Fig. 3). Foliar N concentration was not affected by fertilization, except in *S. macrocarpa*, which showed significantly lower N concentration in the +N and +P treatments compared to the control (Fig. 3). Similarly, leaf P concentration of *S. macrocarpa* was also significantly lower in the +P plots compared to the control (Fig. 4). A significant increase in the P concentration in response to +P treatment was only found for *B. salicifolius*.

The N : P ratio in green leaves was not significantly influenced by the fertilization treatments, and mean values in *Q. parviflora* (20.7), *S. macrocarpa* (19.8) and *B. salicifolius* (18.4) were significantly higher than in *C. brasiliense* (11.8) and *O. hexasperma* (11.6).

In the control plots, average N and P concentrations in the senesced leaves was about  $7.5$  and  $0.32\text{ g kg}^{-1}$ ,

respectively, and did not significantly differ among species (Figs 3 and 4). In the +N plots, N concentrations in senesced leaves were significantly higher in *C. brasiliense*, *B. salicifolius* and *O. hexasperma* in comparison to the control. In *B. salicifolius*, N concentration in senesced leaves in both the +NP and +P plots was 25% greater than in the control. In the other species, N concentration in senesced leaves did not appear to be influenced by +NP and +P addition. Phosphorus concentration in senesced leaves was significantly higher in *B. salicifolius* (33%), *C. brasiliense* (68%) and *S. macrocarpa* (32%) in the +NP plots compared to the control, but no significant differences were observed under the +P treatment. Thus, in general, N fertilization tended to result in the abscission of leaves with higher N content (Fig. 3), whereas the combined fertilization with N and P promoted a leaf litter richer in P (Fig. 4), indicating a decrease in N and P resorption proficiency depending on the treatment.

Generally, higher resorption efficiencies were found for P (Fig. 4) than for N (Fig. 3). In the control plots, about 80% of the foliar P of *C. brasiliense* and *O. hexasperma* was retranslocated before leaf abscission. *Schefflera macrocarpa* and *B. salicifolius* retranslocated about 62%–67% of foliar P, while in *Q. parviflora*, resorption rates were around 31%. N resorption also differed among species but to a lower extent, varying from 44% in *Q. parviflora* to 55% in *C. brasiliense*. The N and P treatments did not affect N and P resorption efficiencies. On the other hand, the addition of N and P combined led to a significant reduction in the N resorption

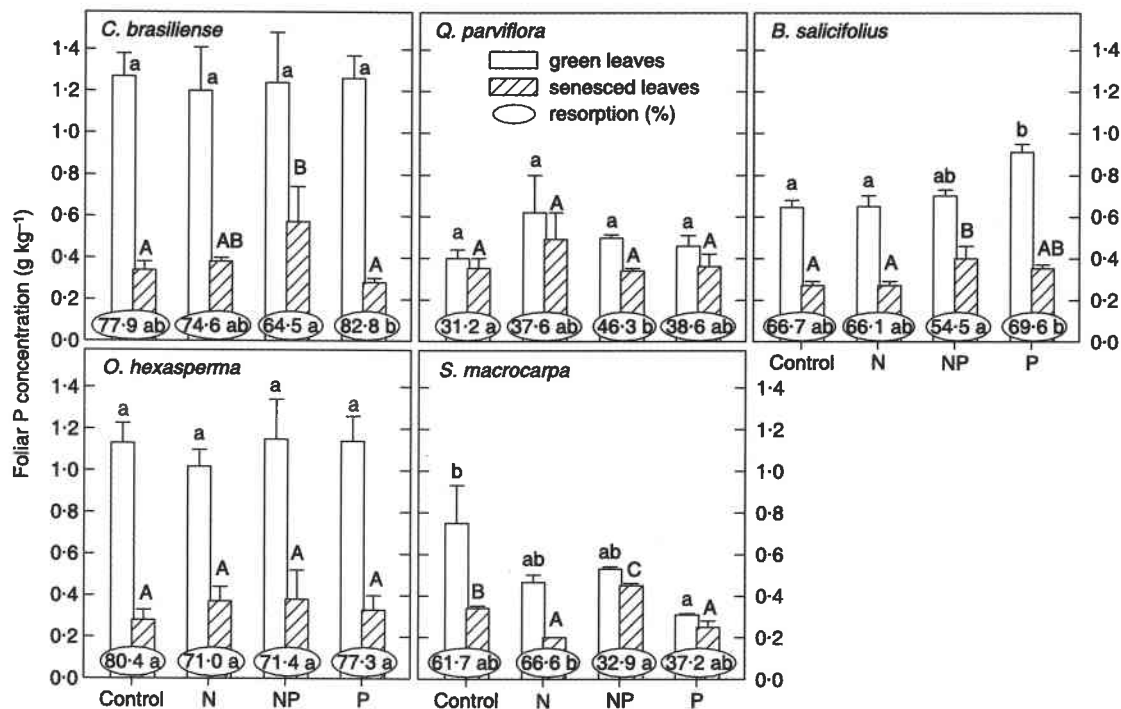


Fig. 4. Phosphorus concentration (bars) in green and senesced leaves of the five Cerrado species growing in the control and fertilized plots (+N, +NP and +P). Numbers within the ellipses represent the resorption efficiency (%). Different letters indicate significant differences ( $P < 0.1$ ) among treatments.

efficiency in *Q. parviflora* and *B. salicifolius*. In terms of P, only *Q. parviflora* showed significant higher P resorption in the +NP plots compared to control.

Analyzing functional groups separately, there was no significant effect of treatments in evergreen species regarding the resorption efficiency of N and P as well as their contents in green and senescent leaves. On the

other hand, in the brevideciduous species, there was a significant reduction of N resorption efficiency under the +NP treatment.

#### LITTER PRODUCTION AND QUALITY

The mean annual litter production in 1999 was about  $151 \pm 29$  g m<sup>-2</sup> in the control plots and did not differ significantly from that in the +N ( $149 \pm 28$  g m<sup>-2</sup>), +NP ( $141 \pm 33$  g m<sup>-2</sup>) and +P ( $102 \pm 27$  g m<sup>-2</sup>) plots. Treatments also did not significantly influence litter production from January to June 2000.

The mean monthly leaf litterfall (Fig. 5) in the control plots varied significantly throughout the study period showing two peaks of leaf litterfall: from the beginning to the middle of dry season (May–July) and at the transition to the wet season (October) in 1999 and from the beginning to middle of the dry season (May and June) in 2000 (see Supplementary Table S1). Similar behaviour was observed in the fertilized plots. Comparison of monthly litterfall among treatments indicated that it was significantly lower in relation to the control only in July (+P) and in September (+N) 1999.

Changes in nitrogen concentration in the leaf litter occurred at the end of the dry season, with significantly higher concentration in the +NP and +P plots in October 1999 (see Supplementary Table S2). Also, comparing treatments, leaf litter from the +NP plots had significantly higher N concentrations in September and October (Fig. 6a), with no significant differences among treatments during the remaining months.

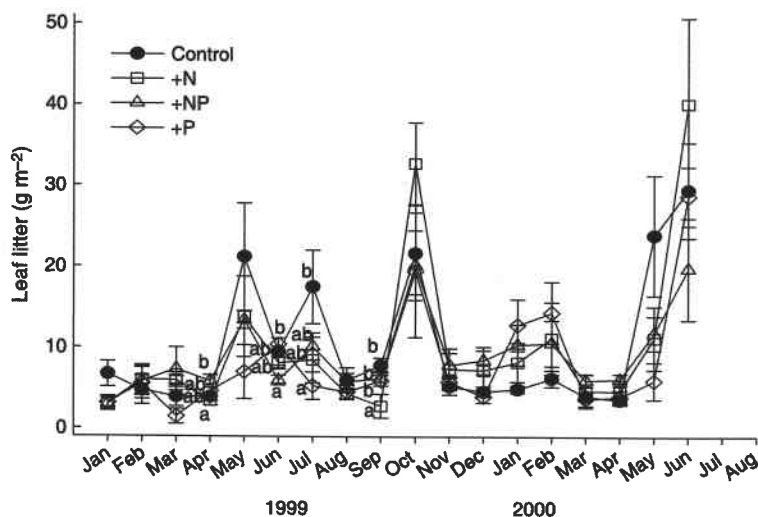


Fig. 5. Monthly leaf litter mass produced between January 1999 and June 2000 in the control and fertilized (+N, +NP and +P) plots. There were no significant differences among treatments within a same month. Comparing with the background values, significantly ( $P < 0.1$ ) higher litterfall was observed in the control plots in May and October 1999, and in May and June 2000, and in all fertilized plots in October 1999 and June 2000.

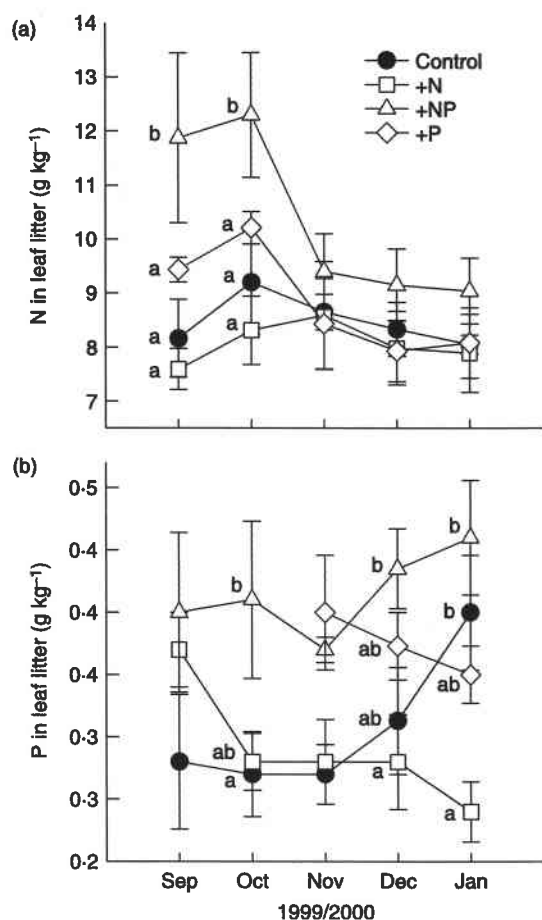


Fig. 6. Nitrogen and phosphorus concentrations in leaf litter collected monthly from September 1999 to January 2000. Different letters indicate significant ( $P < 0.1$ ) differences among treatments within the same month.

Patterns of variation in leaf litter P concentration were more complex. Significantly higher P concentrations in leaf litter were measured in January in the control and in September in the +N plots. Leaf litter from the +NP plots consistently showed the highest P concentrations among treatments, but was significantly higher than the control only in October (Fig. 6b). In January, litter P concentration was significantly lower in the +N plots than in the control. Differences in P concentration in the litter from the +P plots were not significant in spite of the tendency of higher values.

Seasonal and treatment-induced variation in C : N and C : P ratios reflected the variation in N and P concentrations rather than C concentration, which remained nearly constant. Thus, at the end of dry season, lower C : N ratio (September and October) and lower C : P ratio (October) were observed in the leaf litter from the +NP plots than in the control. However, C : N ratio increased throughout the rainy season (October–January) under +NP and +P treatments (see Supplementary Table S2) as well as C : P ratio in the +N plots.

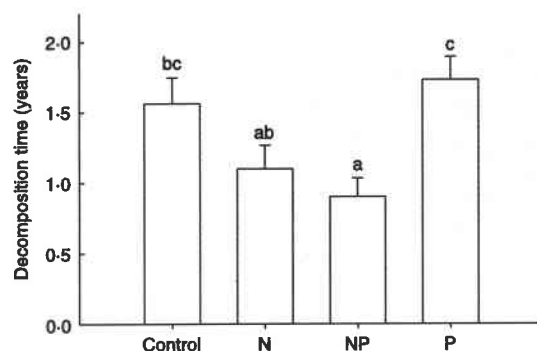


Fig. 7. Decomposition rate of the leaf litter in the control and fertilized plots. Different letters indicate significant ( $P < 0.1$ ) differences among treatments.

The N : P ratio in leaf litter also varied seasonally and among treatments (data not shown). In the control and +NP plots, the highest ratios were observed in September–October (up to 35 for control and 30 for +NP), decreasing to the lowest values in December–January (21 for both treatments) mainly due to a reduction in N concentration. In contrast, leaf litter under the +N treatment showed a significantly lower N : P ratio in September (21), but a significantly higher ratio in January (28) as compared with the control. Variations in P concentration were responsible for this pattern. The leaf litter N : P ratio in the +P plots was lower (around 21) and constant from November to January.

#### LITTER DECOMPOSITION RATE

The estimated decomposition time of leaf litter produced after the first fertilization indicated a reduction of about 42% in the mean time to decompose litter (from 1.6 to 0.9 years) under the +NP treatment (Fig. 7). The addition of N alone also tended to accelerate the litter decomposition rate by 30%, but the increase was not significant in relation to the control. Fertilization with P had no effect on decomposition rates compared with the control.

#### Discussion

##### EFFECTS OF FERTILIZATION TREATMENTS ON FOLIAR NUTRIENT CONCENTRATION, AND RESORPTION EFFICIENCY AND PROFICIENCY

Previous studies in Cerrado ecosystems indicated a very conservative N cycle (Bustamante *et al.* 2006). On the other hand, some evidence suggests that Cerrado ecosystems are also severely limited by P as indicated by the very low concentrations of available P in soil (Resende 2001) and the higher nutrient-use efficiency value at ecosystem level for P (4373) than for N (137) (Nardoto *et al.* 2006).

In the present study, +N and +NP fertilization treatments increased the plant availability of N. The higher

$\text{NH}_4^+$  availability at the end of the dry season, also observed by Nardoto & Bustamante (2003) and Liliencron *et al.* (2003) in Cerrado ecosystems, was probably a consequence of the restricted diffusion of ions in the thin water films and the low biological activity in the dry soils (Stark & Firestone 1995; Austin *et al.* 2004). Available P in the 0–5 cm depth increased significantly and to a larger extent under the +NP treatment than under the +P treatment. Low soil pH values may have prevented a higher increase in P availability due to the sorption of available P by clay and Fe–Al oxides. However, considering the very low availability of P and N in these soils, the observed increase in P and mineral N concentrations may influence plant nutrition and soil processes.

In spite of the increased availability of N and P, fertilization did not significantly increase foliar N and P concentrations (contrarily to hypothesis 1), with the exception of *B. salicifolius*, which exhibited higher P concentration in the +P plots. The absence of a general response of foliar nutrient concentration to nutrient availability could be related to the high species diversity in Cerrado biome, to a time-dependent response to treatments (Güsewell *et al.* 2003), changes in biomass allocation with a dilution of nutrient due to higher leaf production or to retention of nutrients in the below-ground system (Güsewell *et al.* 2003).

Resorption efficiency values were similar to those recorded in another Cerrado *stricto sensu* area (15% and 37% for N and between 40% and 70% for P) by Nardoto *et al.* (2006) and in Venezuelan Savannas (50% for N and 60% for P) recorded by Medina (1984). The higher P than N resorption in Cerrado woody plant species is an additional indication of stronger P limitation. Güsewell (2005) indicated that the type of nutritional limitation (N or P) can induce different responses in terms of NRE and that high resorption efficiency is more beneficial under P limitation through a high P retention by plants. NRE is an important nutrient-conserving strategy in dystrophic systems, but a strict correlation of NRE and nutrient availability is not ubiquitous. In the present study, +NP treatment decreased N resorption efficiency significantly in two brevideciduous species (*Q. parviflora* and *B. salicifolius*). The addition of P alone did not induce changes in P resorption efficiency. Thus, differential responses for resorption efficiency of the five species provided only partial support for hypothesis 2.

According to van Heerwaarden *et al.* (2003), resorption proficiency seems to be more responsive to nutrient availability than resorption efficiency. In the present study, resorption efficiency and proficiency tended to be strongly related for P, as species that responded with a reduction in P resorption proficiency tended to present lower resorption efficiency while reduction of N resorption efficiency and proficiency were found together only for *B. salicifolius*.

Killingbeck (1996) suggested ranges of N and P concentrations in senesced leaves as indicators of complete

and incomplete resorptions. Complete resorption is equal to high resorption proficiency while incomplete resorption means low resorption proficiency. The observed increase in the P concentration in senesced leaves under +NP treatment in *C. brasiliense*, *B. salicifolius* and *S. macrocarpa* surpassed the limit of 0.04% for evergreen and 0.05% for deciduous species proposed by Killingbeck (1996), indicating an intermediate P resorption. However, in all other treatments, P concentration in senesced leaves was below these limits, indicating a highly efficient and complete P resorption. On the other hand, in general, N concentrations in senesced leaves were slightly over the limit of 0.7%, indicating intermediate or incomplete resorption efficiencies. These results again support the idea of a stronger P than N limitation in the Cerrado and that the combined addition of N and P might induce changes in the controls of resorption in some Cerrado species.

The foliar N : P ratios in three of the five species studied were above 16, a threshold which indicates plants to be more P than N limited (Aerts & Chapin 2000). In contrast, two species showed N : P ratios below 14, indicating N limitation. The analysis of only five species revealed no clear pattern of leaf N to P concentration in Cerrado woody species, which would be expected to some extent, considering the high diversity of species, variation in leaf life span and resource availability in the soil. Townsend *et al.* (2007) analyzed a large data set on N and P foliar concentrations in tropical rain forests and concluded that the dominant influence on N : P ratios in the tropics is interspecific variability and that the N : P stoichiometry of tropical forests is not well constrained.

Besides being taxonomically diverse, Cerrado woody plants exhibit a broad continuum of phenological patterns from evergreens that flush new leaves continuously throughout most of the year to brevideciduous and deciduous species that flush by the end of the dry season (Franco *et al.* 2005). A longer leaf life span and lower SLA are also strategies that minimize the cost of leaf construction in dystrophic environments. Franco *et al.* (2005) comparing evergreen and deciduous Cerrado species found that the production of new leaves with high N and P concentrations allowed deciduous species to achieve higher water-use efficiency and potentially higher photosynthetic rates than evergreen trees at the end of the drought period and during the onset of the rainy season. For the Cerrado, it is an open question whether selection has promoted different mechanisms and controls in response to nutrient availability in these different phenological types in terms of NRE/nutrient resorption proficiency and leaf life span. In spite of the low number of species analyzed in each group (two evergreen and three deciduous) in the present study, it is interesting to note that evergreen species did not respond to the treatments at all in terms of N and P resorption efficiencies while brevideciduous species presented lower N resorption efficiency under

the +NP treatment, possibly indicating a more responsive control of resorption in this group. Milla *et al.* (2005) compared species that shed leaves gradually throughout the year with those that shed leaves during a short period in Mediterranean systems and concluded that the leaf shedding pattern *per se* influences nutrient resorption irrespective of additional environmental controls.

#### EFFECTS OF FERTILIZATION TREATMENTS ON LITTERFALL AND DECOMPOSITION RATE

In contrast to the species level, a general trend was observed at community level regarding litter quality and decomposition rate. Woody plants in the +NP plots did shed leaves richer in N and to a lesser extent in P compared to leaf litter from the control plots, consistent with the hypotheses 2 and 3 that fertilization would decrease leaf NRE and nutrient resorption proficiency and result in litter with lower C : N and C : P ratios. This suggests that the reduction in N resorption efficiency and/or proficiency observed in some of the five study species might be a common response of a larger number of species to the +NP treatment and could be related to the proportion of brevideciduous to evergreen species in the community.

Leaf litter in the +NP plots presented higher N and lower C : N ratios at the end of the dry season possibly as a result of incomplete nutrient resorption. The release of leaf litter with a lower C : N ratio in the +NP plots coincided with the highest peak of litterfall, which could significantly influence nutrient cycling. The decrease in N concentration in litterfall in the subsequent months would indicate delayed nutrient resorption processes in leaves under the +NP treatment.

The N : P ratio in leaf litter also showed differences between treatments and season. A wide range of critical N : P ratios for decomposition has been reported in the literature. Güsewell & Verhoeven (2006) indicated 25 for graminoid litter, while 10–16 for temperate and tropical litter was indicated by Aerts (1997). The values in the present work ranged from 21 to 35 with lower and less variable values in the +P plots. The observed seasonal variation in litter N : P ratio alters N and P limitations for decomposition along the season and might be related to changes in nutrient resorption, plant growth and biomass allocation with increasing water availability from October to February.

The rapid response of litter quality to fertilization was reflected in a 42% faster decomposition time measured in the +NP plots relative to the control, confirming our hypotheses that fertilization would result in litter with lower C : N and C : P ratios causing it to decompose faster.

#### Conclusions

At community level, responses to changes in N and P availability were more consistent than at the species

level as indicated by the enhanced litter quality and consequently faster litter decomposition rate in the +NP treatment. An increase in leaf N and P concentrations, and reduction in NRE and nutrient resorption proficiency might explain the higher litter quality, although at species level, a general trend was not observed. The lack of a clear-cut response of the five woody species to fertilization treatments is probably related to the high species richness and consequent interspecific variation in leaf phenology. Cerrado woody species exhibited variable responses to N and P fertilizations in terms of nutrient concentrations and resorption efficiency and proficiency to N and P fertilizations, suggesting large differences in terms of nutrient limitations, metabolic requirements and uptake ability in the woody layer and in the capacity to cope with the low nutrient availability that is typical of Cerrado soils. Results regarding N and P resorptions suggest different levels of regulation for these two limiting elements and a higher limitation by P than by N. In spite of the different responses at species level, the Cerrado woody vegetation was generally more responsive to the combined addition of N and P, and less or even unresponsive to fertilization with N or P alone over the time span of this study.

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#### References

- Aerts, R. (1997) Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: a triangular relationship. *Oikos*, **79**, 439–449.
- Aerts, R. & Chapin, F.S. (2000) The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. *Advances in Ecological Research*, **30**, 1–67.
- Aerts, R., de Caluwe, H. & Beltman, B. (2003) Is the relation between nutrient supply and biodiversity co-determined by type of nutrient limitation? *Oikos*, **101**, 489–498.
- Austin, A.T., Yahdjian, L., Stark, J.M., Belnap, J., Porporato, A., Norton, U., Ravetta, D.A. & Schaeffer, S.M. (2004) Water pulses and biogeochemical cycles in arid and semi-arid ecosystems. *Oecologia*, **141**, 221–235.
- Barger, N.N., D'Antonio, C.M., Ghneim, T., Brink, K. & Cuevas, E. (2002) Nutrient limitation to primary productivity in a secondary savanna in Venezuela. *Biotropica*, **34**, 493–501.
- Bucci, S.J., Scholz, F.G., Goldstein, G., Meinzer, F.C., Franco, A.C., Campanello, P.I., Villalobos-Vega, R., Bustamante, M.M.C. & Miralles-Wilhelm, F. (2006) Nutrient availability constrains the hydraulic architecture and water relations of savanna trees. *Plant, Cell and Environment*, **29**, 2153–2167.
- Bustamante, M.M.C., Medina, E., Asner, G.P., Nardoto, G.B. & Garcia-Montiel, D.C. (2006) Nitrogen cycling in

- tropical and temperate savannas. *Biogeochemistry*, **79**, 209–237.
- Caldas, L.S., Bravo, C., Piccolo, H. & Faria, C.R.S.M. (1992) Measurement of leaf area with a hand-scanner linked to a microcomputer. *Revista Brasileira de Fisiologia Vegetal*, **4**, 7–20.
- Cordell, S., Goldstein, G., Meinzer, F.C. & Vitousek, P.M. (2001a) Morphological and physiological adjustment to N and P fertilization in nutrient-limited *Metrosideros polymorpha* canopy trees in Hawaii. *Tree Physiology*, **21**, 43–50.
- Cordell, S., Goldstein, G., Meinzer, F.C. & Vitousek, P.M. (2001b) Regulation of leaf life-span and nutrient-use efficiency of *Metrosideros polymorpha* trees at two extremes of a long chronosequence in Hawaii. *Oecologia*, **127**, 198–206.
- Eiten, G. (1994) Vegetação do cerrado. *Cerrado: Caracterização, Ocupação e Perspectivas* (ed. M.N. Pinto), pp. 17–73. Editora Universidade de Brasília, Brasília.
- Embrapa (1998) *Manual de Métodos de Análises Químicas Para Avaliação da Fertilidade do Solo*. Embrapa, Brasília.
- Filoso, S., Martinelli, L.A., Howarth, R.W., Boyer, E.W. & Dentener, F. (2006) Human activities changing the nitrogen cycle in Brazil. *Biogeochemistry*, **79**, 61–89.
- Franco, A.C., Bustamante, M.M.C., Caldas, L.S., Goldstein, G., Meinzer, F.C., Kozovits, A.R., Rundel, P.W. & Coradin, V.T.R. (2005) Leaf functional traits of Neotropical savanna trees in relation to seasonal water deficit. *Trees*, **19**, 326–335.
- Galloway, J.N., Dentener, F.J., Capone, D.G., Boyer, E.W., Howarth, R.W., Seitzinger, S.P., Asner, G.P., Cleveland, C., Green, P., Holland, E., Karl, D.M., Michaels, A.F., Porter, J.H., Townsend, A. & Vorösmarty, C. (2004) Nitrogen cycles: past and future. *Biogeochemistry*, **70**, 153–226.
- García-Miragaya, J., San José, J.J. & Hernández, J.I. (1983) Effect of added nitrogen, phosphorus and potassium on above-ground biomass production and nutrient control of *Trachypogon* savanna grasses. *Journal of Tropical Ecology*, **24**, 33–42.
- Güsewell, S. (2005) Nutrient resorption of wetland graminoids is related to the type of nutrient limitation. *Functional Ecology*, **19**, 344–354.
- Güsewell, S. & Verhoeven, J.T.A. (2006) Litter N : P ratios indicate whether N or P limits decomposability of graminoid leaf litter. *Plant and Soil*, **287**, 131–143.
- Güsewell, S., Bollens, U., Ryser, P. & Klötzli, F. (2003) Contrasting effects of nitrogen, phosphorus and water regime on first-and second-year growth of 16 wetland species. *Functional Ecology*, **17**, 754–765.
- Haridasan, M. (2001) Nutrient cycling as a function of landscape and biotic characteristics in the cerrados of Central Brazil. *The Biochemistry of the Amazon Basin* (eds M.E. McClain, R.L. Victoria & J.R. Richey), pp. 68–83. Oxford University Press, New York.
- van Heerwaarden, L.M., Toet, S. & Aerts, R. (2003) Current measures of nutrient resorption efficiency lead to a substantial underestimation of real resorption efficiency: facts and solutions. *Oikos*, **101**, 664–668.
- Killingbeck, K.T. (1996) Nutrients in senesced leaves: keys to the search for potential resorption and resorption proficiency. *Ecology*, **77**, 1716–1727.
- Lavelle, P., Blanchart, E., Martin, A. & Martin, S. (1993) A hierarchical model for decomposition in terrestrial ecosystems: application to soils of the humid tropics. *Biotropica*, **25**, 130–150.
- Lilienfein, J., Wilcke, W., Vilela, L., Ayarza, M.A., Lima, S.C. & Zech, W. (2003) Soil fertility under native Cerrado and pasture in the Brazilian savanna. *Soil Science Society of America Journal*, **67**, 1195–1205.
- Medina, E. (1984) Nutrient balance and physiological processes at leaf level. *Physiological Ecology of Plants of the Wet Tropics* (eds E. Medina, H.A. Mooney & C. Vázquez-Yanes), pp. 139–154. Dr. W. Junk Publications, The Hague.
- Meier, M. (1991) Nitratbestimmung in Boden-Proben (N-min-Methode). *LaborPraxis*, pp. 244–247. Berlin.
- Milla, R., Castro-Díez, P., Maestro-Martínez, M. & Montserrat-Martí, G. (2005) Does the gradualness of leaf shedding govern nutrient resorption from senescing leaves in Mediterranean woody plants? *Plant and Soil*, **278**, 303–313.
- Nardoto, G.B. & Bustamante, M.M.C. (2003) Effects of fire on soil nitrogen dynamics and microbial biomass in savannas of Central Brazil. *Pesquisa Agropecuária Brasileira*, **38**, 955–962.
- Nardoto, G.B., Bustamante, M.M.C., Pinto, A.S. & Klink, C.A. (2006) Nutrient use efficiency at ecosystem and species level in savanna areas of Central Brazil and impacts of fire. *Journal of Tropical Ecology*, **22**, 1–11.
- Oliveira, S. (1986) Método simplificado para determinação de nitrogênio em plantas. *Ciência e Cultura*, **38**, 178–180.
- Peterman, R. (1990) The importance of reporting statistical power: the forest decline and acidic deposition example. *Ecology*, **71**, 2024–2027.
- Resende, J. (2001) *A ciclagem de nutrientes em áreas de Cerrado e a influência de queimadas controladas*. PhD thesis, University of Brasília, Brasília-Brazil.
- Solbrig, O.T. (1996) The diversity of the savanna ecosystem. *Biodiversity and Savanna Ecosystem Processes* (eds T. O. Solbrig, E. Medina & J. A. Silva), pp. 1–27. Springer-Verlag, Heidelberg.
- Stark, J.M. & Firestone, M.K. (1995) Mechanisms for soil moisture effect on activity of nitrifying bacteria. *Applied Environmental Microbiology*, **61**, 218–221.
- Townsend, A.R., Cleveland, C.C., Asner, G.P. & Bustamante, M.M.C. (2007) Controls over foliar N:P ratios in tropical rain forests. *Ecology*, **88**, 107–118.
- Vitousek, P.M. (1998) Foliar and litter nutrients, nutrient resorption, and decomposition in Hawaiian *Metrosideros polymorpha*. *Ecosystems*, **1**, 401–407.

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## Supplementary material

The following supplementary materials are available for this article:

**Table S1.** Results of the Tukey's studentized range test for leaf litter, ammonium and nitrate concentrations in soil (0–5 cm)

**Table S2.** Results of the Tukey's studentized range test for nitrogen and phosphorus concentrations and C-related ratios in leaf litter

This material is available as part of the online article from: <http://www.blackwell-synergy.com/doi/full/10.1111/j.1365-2435.2007.01325.x>  
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