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Leaf-cutting ants, seasonal burning and nutrient distribution in Cerrado vegetation

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Abstract Fire and herbivory are known to modify plant community structure. Many studies have suggested that fire ashes may increase soil nutrients in dystrophic soils. Herbivores may also change plant community structure through direct effects of herbivory and affecting nutrient cycling. Leaf-cutting ants were traditionally viewed as herbivores, although their role may be more complex, because their nests affect both chemical and physical soil properties, thus affecting plants indirectly. We investigated the effects of frequent burning and of leaf-cutting ants on the nutrient status of an herbaceous and a shrub species occurring in the Brazilian Cerrado, a habitat that is characterized by natural burnings. The proximity of ant nests resulted in an increase of nutrients in the leaves of both vegetation strata, whereas burning sometimes resulted in a decrease of nutrients. Our results do not lead to a possible positive effect of fire on plant nutrient content. On the other hand, ant nests may represent an important source of nutrients for plants on the nutrient-depleted Cerrado soils and may accelerate vegetation recovery after burning.

Key words: *Atta laevigata*, *Echinolaena inflexa*, nutrient supply, savanna, *Solanum lycocarpum*.

INTRODUCTION

The structure of plant communities is directly affected by biotic and abiotic environmental factors. Fire is one of these environmental factors; it is common in the tropics and has considerable effects on ecosystem structure, species composition and nutrient cycling (Coutinho 1978; Crutzen & Andreae 1990). Fire can act as a mineralizing agent and can increase the short-term availability of nutrients for plant growth (Van de Vijver *et al*. 1999), although long-term productivity is negatively affected through nutrient loss (Kauffman *et al*. 1994). In systems with nutrient-poor soils, such as tropical savannas, the high nutrient concentration in post-burn vegetation is thought to be principally caused by enhanced soil nutrient supply through ashes (Batmanian & Haridasan 1985; Cook 1994).

Fire can also have indirect effects on nutrient cycling through effects on herbivores and soil mesofauna, changing their density, biomass and spatial distribution. Insect herbivores have a trend to concentrate in post-burned areas, and this tendency is likely to be related to a higher nutrient concentration in plant post-fire regrowth (Radho-Toly *et al*. 2001). This indirect effect of fire could create a strong top-down effect of herbivorous insects on plant communities. Unfortunately, few empirical data, to our knowledge, directly tested this assertion (Radho-Toly *et al*. 2001).

The Brazilian Cerrado comprises a complex vegetation mosaic of savannas, grasslands and dry forests with fires occurring every 1–3 years (Eiten 1972). Although plants differ widely in their tolerance to fire and their capacity to recover afterwards, virtually all plants that occur in the Cerrado have evolved to tolerate, survive and sometimes even depend on fire for their reproductive success (Coutinho 1990). Thus, together with seasonal rainfall and low-nutrient soil, frequent burning is probably one of the most important factors for the persistence of the Cerrado in Central Brazil (Coutinho 1990).

Most burnings in the Cerrado are concentrated in the dry season (May to September) and its main effect is the removal of old, dead vegetation, which is replaced by young regrowth. Post-fire regrowth, however, is not fast, so the landscape remains uncovered by vegetation until the start of the rainy season. These vegetation gaps can facilitate establishment by leaf-cutting ants, which prefer open terrain. Disturbed, recently burned areas invariably have high nest densities (Schoereder & Coutinho 1990; Vasconcelos & Cherrett 1995). Like fire, leaf-cutting ants play an important role in the ecosystem; they also affect plant diversity and nutrient cycling (Lugo *et al*. 1973;

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Haines 1978; Moutinho *et al.* 2003; Farji-Brener & Ghermandi 2004). Hence, fire has a direct effect on nutrient cycling through ashes, and an indirect effect through the facilitation of colonization of leaf-cutting ants, whereas leaf-cutting ants directly affect nutrient cycling through herbivory and indirectly by changes in soil properties.

Most leaf-cutting ant species of the *Atta* genus build and maintain large colonies in Cerrado soils, with nests covering more than 250 m^2 and being several meters deep (Autuori 1947; Coutinho 1984; Hölldobler & Wilson 1990). The excavation of nests by these ants promotes physical and chemical modifications in the soil (Coutinho 1984; Moutinho *et al.* 2003; Verchot *et al.* 2003). Subterraneous chambers containing fungal gardens or garbage are storages of organic matter, where nutrient availability is enhanced and this is accompanied by soil inversion by channel excavation. This picture is valid to most leaf-cutting ant species, although *Atta colombica* and some species of the genus *Acromyrmex* deposit their garbage in soil surface (Farji-Brener & Medina 2000).

Several studies have investigated effects of fire (Kauffman *et al.* 1994; Van de Vijver *et al.* 1999; Moreira 2000) and leaf-cutting ants (Jonkman 1978; Farji-Brener & Illes 2000) on plant communities, but up to now, no studies have investigated these two factors simultaneously. Coutinho (1984) suggested that leaf-cutting ants and fire play an antagonistic role in nutrient cycling in the Cerrado of Brazil. He hypothesized that, owing to the low-nutrient soil, post-fire regrowth of woody plant vegetation may be very difficult if an adequate nutrient supply is not available to roots. Active nests of leaf-cutting ants could act as nutrient sources for woody plants owing to high nest density in burned areas. Thus, fire may favour herbaceous vegetation by ash deposition whereas the presence of active leaf-cutting ants favours woody plants because of the deposition of organic matter (Fig. 1). This hypothesis has not been explicitly tested yet. Coutinho's hypothesis suggests that the nutrient status of herbaceous plants will be increased in burned areas relative to plants in unburned areas, independent of the presence of ant nests. In contrast, a higher nutrient status of woody plants is expected closer to *Atta* nests, and lower nutrient concentrations are expected in woody plants from burned areas.

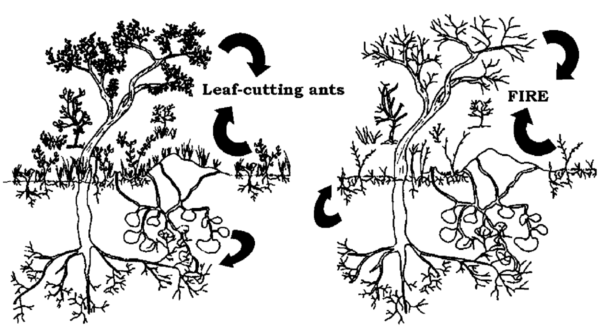

Fig. 1. The hypothetical antagonistic effect of leaf-cutting ants and fire on nutrient cycling in a Cerrado vegetation. Herbaceous plants are thought to benefit from fire ashes in burned areas, whereas leaf-cutting ants are thought to favour woody plants through deposition of organic matter in the nests. Arrows indicate the nutrient direction in the biogeochemical cycle (adapted from Coutinho 1984).

We tested these predictions on the antagonistic effects of leaf-cutting ants and fire on nutrient status of herbs and shrubs, using the ant species *Atta laevigata* F. Smith (1858), the shrub *Solanum lycocarpum* (Solanaceae) and the herbaceous species *Echinolaena inflexa* (Poaceae). These species are indigenous in the Cerrado and the plants are commonly found together on active *A. laevigata* nests mounds.

METHODS

Study site

The study was conducted at the Ecological Reserve of Brazilian Institute of Geography and Statistics (RECOR-IBGE) in Brasília, DF, Brazil (15°51′41″S; 47°51′02″W) within the experimental area of a large fire project. This reserve is 1375 ha large within a slightly hilly landscape (1130–1160 m a.s.l.). The mean annual rainfall is 1478 mm with a well-defined dry season from May to September and a mean annual temperature around 21°C (12–29.3°C). The native vegetation includes the common physiognomic forms of Cerrado of the central Brazilian region: *cerradão* (70–90% canopy cover); *Cerrado denso* (50–70% canopy cover); cerrado *sensu strictu* (20–50% canopy cover); *campo sujo* (<5% canopy cover) and *campo limpo* (grassland) (Ribeiro & Walter 1998). The dominant soil type is a deep well-drained red latosol (oxysol), with high clay content, mostly kaolinite and low cation exchange capacity with moderate acidity (pH range: 4.5–6.2). It is derived from Tertiary lateritic deposits (EMBRAPA 1999). In this soil, Ca is a limiting factor for plant growth (Ritchey *et al.* 1980). The fire project consisted of 30 plots of 4–10 ha, distributed in several Cerrado physiognomies (from grasslands to cerradão woodland) and subjected to different fire regimes or left unburned. In this study the samples were taken from a burned and an unburned plot both 10 ha in a unique vegetation type.

The leaf-cutting ant *A. laevigata* is very common in the study area with large active and abandoned nests. The plots, including active *A. laevigata* nest mounds, are commonly covered with *E. inflexa* grass and *S. lycocarpum* shrubs.

Experimental design

The possible antagonistic effect of fire and *A. laevigata* nests on plant nutrient status was tested using a burned and an unburned plot of 200 × 500 m (10 ha) in a *Cerrado denso* vegetation type. These plots were chosen for sampling because, among those 30 plots in the fire project, they presented the best sampling conditions, such as relatively large ant colonies covered with both *E. inflexa* and *S. lycocarpum* and higher densities of these plant species in non-nest areas than other plots. The plots were surveyed from March to April 2004 for mature *A. laevigata* nests (>4 m^2), both at the margin of the plot and inside it. The nests were classified as either active or abandoned: active nests were considered those with ants present (most cases), recently cut leaves dropped on the nest-mound, well-maintained foraging trails, or recent signs of soil disturbance. To avoid great physical and chemical differences among ant nests and subsequent differences on foliar content in plants, only active mature nests were sampled. Thus, the number of replications (ant nests) in each plot was limited but it was compensated by higher homogeneity of the samples. The burned plot had been subjected to prescribed fires every 2 years since 1992. The unburned plot (control) was protected from fire since 1974 (Miranda *et al.* 1993). Plants from four environments were used: plants on five *A. laevigata* nests in the burned and unburned plots and plants from five points at a minimum distance of 25 m from ant nests in the burned and unburned plots. A total of 100 apical leaves from 20 *S. lycocarpum* shrubs (five leaves per plant, five plants per treatment) and 100 entire *E. inflexa* plants (five plants per treatment) were collected. Samples of shrubs were collected in July 2004 (dry season), 2 months after the last prescribed fire. Herbs were collected in October 2004, when post-fire herbs recovery was reached. Leaf samples were dried at 70°C. Prior to chemical analyses plant material was digested using the micro-Kjeldahl method (Silva 1999). N and P concentrations were analysed colourimetrically with a continuous flow analyser and the concentrations of K, Ca, Mg, Al, S, Zn, Fe, Mn, Cu, B were analysed with an Atomic Absorption Spectrophotometer (Silva 1999).

The effect of burning and leaf-cutting ants on plant status was tested using multivariate analyses of variance (MANOVA) with all measured nutrients as dependent variables and the presence of ant nests and fire as fixed independent variables. In case of significant effects in the multivariate test, univariate *F*-tests (ANOVA) were used to identify the specific dependent variables that were significant in the general model. Non-significant factor levels were lumped together using *a posteriori* contrasts (Crawley 2002).

RESULTS

Leaf-cutting ants contributed to the significant overall effect of foliar nutrient both for the shrub (MANOVA, Wilks' lambda = 0.082, $F = 5.08$, d.f. = 12, $P = 0.042$) and the herb (Wilks' lambda = 0.065, $F = 6.0$, d.f. = 12, $P = 0.03$). There was no significant effect of burning or interaction between ants and burning on nutrient contents for the shrub (MANOVA, Wilks' lambda = 0.28, $F = 1.27$, d.f. = 12, $P = 0.4$) or for the herb (MANOVA, Wilks' lambda = 0.15, $F = 2.81$, d.f. = 12, $P = 0.063$). This means that ant nests had a significant effect on nutrient status of the plants whereas burning did not or at least was not evident.

For the shrub species, the proximity of leaf-cutting ant nests resulted in an increase of foliar concentrations of phosphorus ($F_{1,18} = 9.2$, $P = 0.0076$) and copper ($F_{1,18} = 11.7$, $P = 0.003$) in the unburned plot as well as of sulphur ($F_{1,18} = 11.9$, $P = 0.003$) and zinc ($F_{1,18} = 26.0$, $P < 0.001$) in both plots (Fig. 2). In addition, ant nests in the burned plot led to positive effect on the foliar concentrations of manganese ($F_{1,18} = 13.3$, $P = 0.002$) and aluminium ($F_{1,18} = 16.3$, $P < 0.001$, Fig. 2). Burning did not directly affect any of the compounds analysed; however, the concentration of phosphorus and copper in plants from nests in the burned plot was lower than those plants from nests in the unburned plot. This suggests that fire had a negative effect on foliar concentrations of these nutrients (Fig. 2). In contrast, burning increased manganese and aluminium concentrations of plants close to ant nests (Fig. 2). There was no significant difference in foliar concentrations of nitrogen ($F_{3,16} = 1.6$, $P = 0.23$), potassium ($F_{3,16} = 2.3$, $P = 0.11$), calcium ($F_{3,16} = 0.8$, $P = 0.49$), magnesium ($F_{3,16} = 0.08$, $P = 0.97$), iron ($F_{3,16} = 2.3$, $P = 0.11$) and boron ($F_{3,16} = 1.5$, $P = 0.25$) (Fig. 2).

Concentrations of some nutrients in leaves of herbs were also differently affected by ants and burning (Fig. 3). Ant nests and burning increased foliar nitrogen ($F_{1,18} = 7.6$, $P = 0.013$), phosphorus ($F_{1,18} = 4.2$, $P = 0.34$) and potassium ($F_{3,16} = 9.8$, $P < 0.01$) concentrations. Plants near ant nests had higher potassium concentrations compared with plants away from nests ($F_{1,18} = 6.0$, $P = 0.02$, Fig. 3). Plants from the burned plot were lower in zinc than plants from the unburned plot ($F_{1,18} = 5.8$, $P = 0.026$). There was a higher concentration of calcium in plants from ant nests in the unburned plot than in other environments ($F_{1,18} = 11.6$, $P = 0.003$). In addition, boron was only found in plants from ant nests ($F_{1,18} = 36.2$, $P < 0.001$, Fig. 3). The combined effect of ants and burning resulted in higher amounts of potassium but lower levels of zinc, calcium and boron (Fig. 3). There was no significant difference in nutrient status of herbs for magnesium ($F_{3,16} = 2.7$, $P = 0.08$),

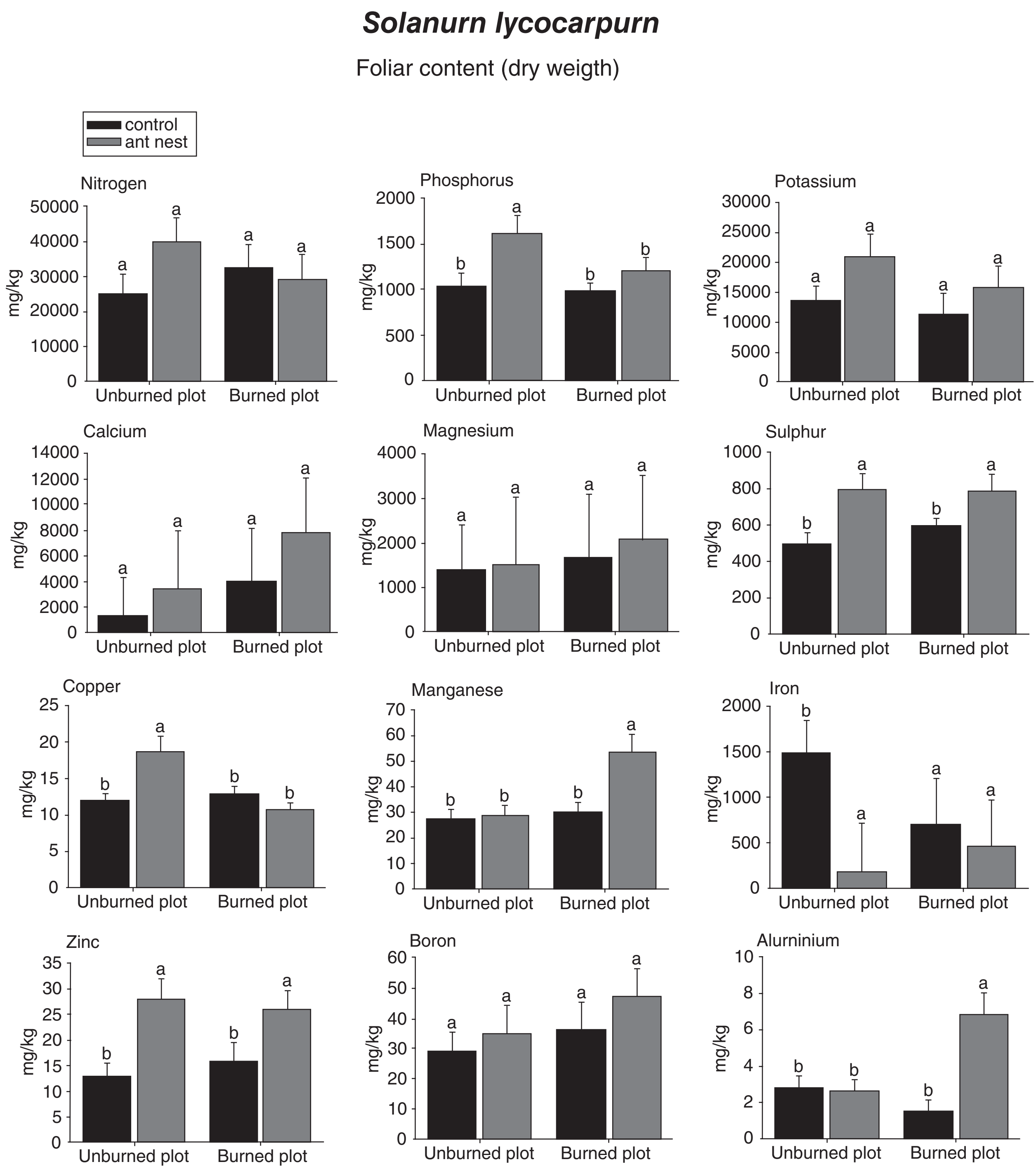

Fig. 2. Foliar contents of the shrub *Solanum lycocarpum* (Solanaceae) in four different environments: plants on five ant (*Atta laevigata*) nests in a burned and unburned plot (light bars) and plants from five points at a minimum distance of 25 m from the ant nests in the same plots (black bars). Different letters above bars indicate a significant difference ($\alpha = 5\%$, ANOVA with *a posteriori* contrast). Values are mean + SE.

sulphur ($F_{3,16} = 1.2$, $P = 0.33$), manganese ($F_{3,16} = 0.6$, $P = 0.65$), copper ($F_{3,16} = 1.4$, $P = 0.29$), iron ($F_{3,16} = 2.40$, $P = 0.11$) and aluminium ($F_{3,16} = 0.9$, $P = 0.44$) (Fig. 3). Hence, there is no antagonistic effect of burning and leaf-cutting ants on nutrient status of both plant species. Our results were not as predicted by Coutinho (1984), who expected an increased nutrient concentration in leaves of herbs and

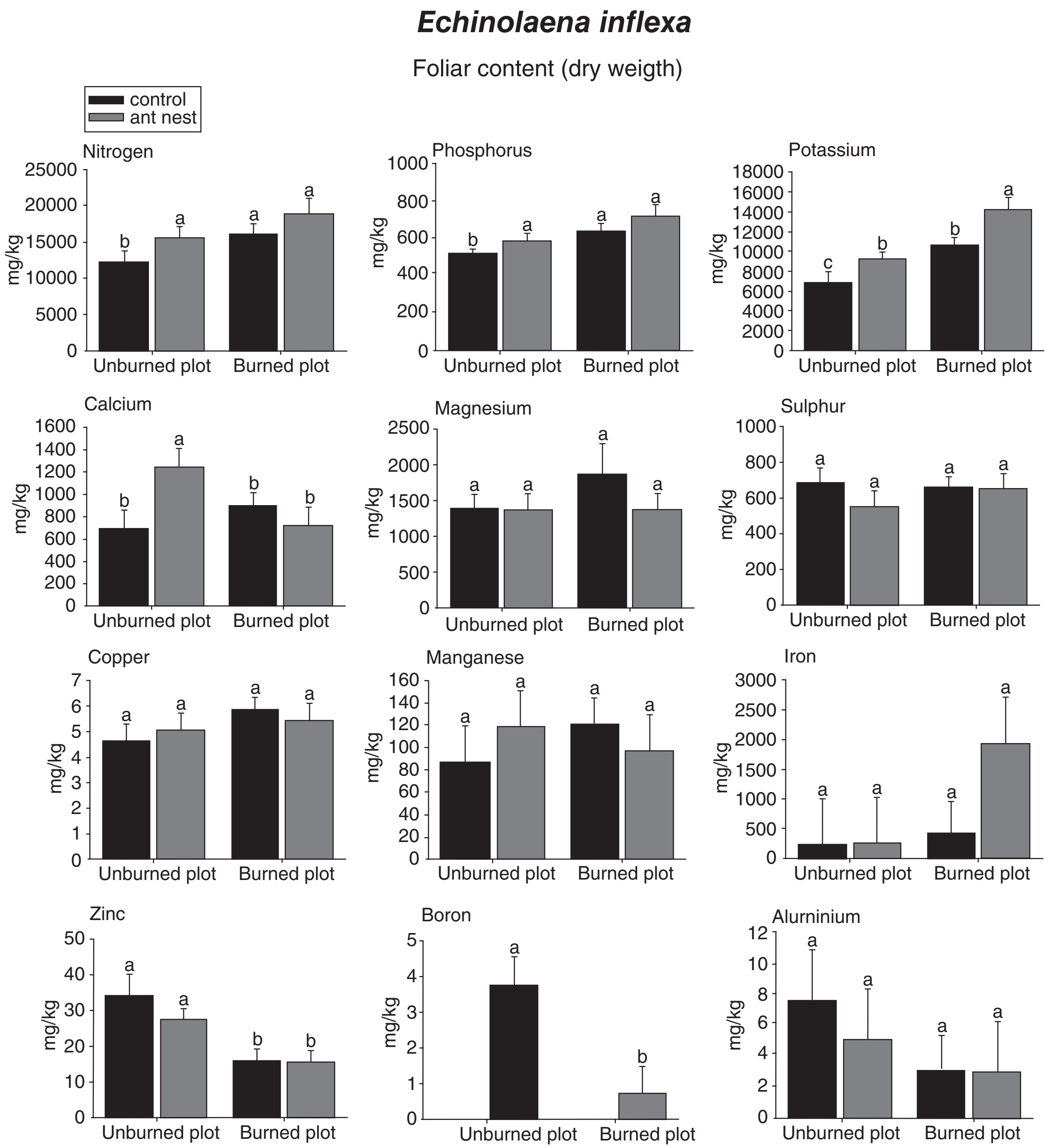

Fig. 3. Foliar contents of the herb *Echinolaena inflexa* (Poaceae) in four different environments: plants on five ant (*Atta laevigata*) nests in a burned and unburned plot (light bars) and plants from five points at a minimum distance of 25 m from the ant nests in the same plots (black bars). Different letters above bars indicate a significant difference ($\alpha = 5\%$, ANOVA with *a posteriori* contrast). Values are mean + SE.

a decreased amount of nutrients in the shrubs leaves caused by burning. Instead, in general, the proximity of ant nests resulted in a nutrient increase for both vegetation types and burning had no effects of plant nutrient status (Figs 2,3).

DISCUSSION

We measured the impact of leaf-cutting ants and burning on plant nutritional contents in the Cerrado and we found that leaf-cutting ant nests might have an impact on Cerrado physiognomy, functioning and structure by increasing both macronutrient and micronutrient availability to herbaceous and shrub species, even in the presence of burning. Fire, however, did not affect macronutrient concentrations in the plants studied and had a negative effect on micronutrient contents of herbs. Hence, the hypothesis proposed by Coutinho (1984) that fire ashes could benefit herbs by increasing nutrients was not confirmed. These results, however, should be viewed with caution, because only one herb and one shrub species were used. Although there was great plant diversity in our study site (Moreira 2000), there were few plant species that were found growing from the nest mounds and only *E. inflexa* and *S. lycocarpum* were found together in all ant nests sampled.

Several studies have been carried out with *A. colombica* and some *Acromyrmex* species which deposit their refuse on the soil surface (Haines 1978; Farji-Brener & Medina 2000; Farji-Brener & Ghermandi 2004). The effects of nutrient-rich organic refuse produced by these leaf-cutting ant species are easier to detect than those of deposits deep in the ground, typical for leaf-cutting ants species in Cerrado habitats (Coutinho 1984). Therefore, it was necessary to look for indirect evidence of the nutrient enrichment of patches, such as foliar nutrient-contents in plants near ant nests. However, nests of leaf-cutting ants affect the plant community differently when they are active or abandoned (Garrettson *et al.* 1998; Farji-Brener & Illes 2000). Active ant nests provide high nutrient availability to the adjacent plants and facilitate root establishment (Moutinho *et al.* 2003) but support reduced diversity and abundance of plants when compared with non-nest areas or abandoned ant nests (Garrettson *et al.* 1998). Hence, the study of active ant nests presents some sampling limitations. These limitations may be compensated by studying nests from different regions or physiognomies, such as savannas, grasslands, Cerrado *sensu strictu*, cerradão and forests. It is evident from this study that any higher nutrient concentration in the soil through biomass mineralization by fire ashes, as found in previous studies (Coutinho 1984; Cook 1994), did not lead to higher assimilation of nutrients in plants. Most eutrophic savannas have an N/P ratio of plant material ranging between 6 and 7 (Van de Vijver *et al.* 1999). In our study the N/P ratio was between 22 and 33 for herbs and shrubs. This indicates that, as in many other Cerrado systems, phosphorus is a limiting nutrient in our study area. Van de Vijver *et al.* (1999) suggested there should be increased nutrients in the soil from fire ashes in dystrophic soils, like those of the Brazilian Cerrado. Our results, however, did not confirm this hypothesis, suggesting that any nutrients from ashes are not assimilated by the vegetation we tested, at least not in the period of 60–120 days after burning.

It has been reported that excessive concentrations of aluminium in plants would reduce the uptake of calcium, phosphorus, manganese, zinc and iron (Foy 1974). Our results, however, shrubs with higher aluminium concentrations from ant nests in the burned plot extracted other cations, such as phosphorus, sulphur, manganese or zinc more efficiently. Plants from ant nests in the burned plot had higher concentrations of these nutrients than shrubs from the burned or control plots (Fig. 2). This suggests that shrubs and woody plants can overcome the possible deleterious effects of aluminium on the uptake and transport of these elements. Alternatively, aluminium in the soil may have had a positive effect on uptake of other nutrients (Hackett 1962). Haridasan (1982) also found a positive correlation among foliar aluminium concentrations with levels of calcium, magnesium and zinc in plants from a Brazilian Cerrado near our study site.

Farji-Brener and Silva (1995) found a higher soil concentration of calcium in ant nests of *A. laevigata* than in adjacent soil, in a Venezuelan savanna. The higher calcium content in the herbs from unburned nests in our study indicates that *A. laevigata* nests act in the biogeochemical cycling of nutrients, promoting plant growth by increase of both soil fertility and foliar nutrient content. The importance of *A. laevigata* on Cerrado vegetation is high if we consider that (i) P and Ca are limiting factors in these soils (Ritchey *et al.* 1980); (ii) the nest durability and persistence (estimates range from 10 to 20 years) even after death of the colony allows the plant community to exploit each 'ant oasis' for long time (Coutinho 1984); and (iii) there is a relatively high turnover rate of leaf-cutting ant nests (Perfecto & Vandermeer 1993). Perfecto and Vandermeer (1993) estimated the size and turnover rate of *A. cephalotes* nests in a tropical forest and suggested that the ant nests could occupy the equivalent of the entire forest area every 200–300 years. The total area covered by nest mounds in our study site was considerable (0.55% in unburned plot and 1.1% in the burned plot). Considering the total area covered by leaf-cutting ants in many Neotropical environments, the positive effects of their nests could have far-reaching impacts on the plant community of Cerrado.

The factors responsible for higher foliar nutrient concentrations in plants from ant nests are not yet fully understood. Schoereder and Howse (1998) analysed the effect of nest distance on foliar content in various woody species of the Cerrado and did not find a positive effect of nest on plants close to the nests. These authors, however, did not consider variation in nutrient content among plant species (Haridasan 1982; Malavolta *et al.* 1997); hence, variation among plant species could have masked any positive effects of ant nests. This hypothesis was confirmed because in our study *S. lycocarpum* and *E. inflexa* also varied in levels of essential nutrients (Figs 2,3). An alternative explanation for higher foliar nutrient concentrations in plants is that, together with organic matter accumulation, ant nests promote a reorganization of soil microaggregates, facilitating soil solution assimilation by roots (rhyzosphere). It would therefore be interesting to assess whether root density inside *Atta* nests is higher and if there are differences in soil microstructure in ant nests compared with adjacent soil.

In conclusion, it is possible that leaf-cutting ants play an important role in biogeochemical cycling in the Cerrado ecosystem through concentrating nutrients in plants near the nests. In contrast, burning did not result in any significant increase in the accumulation of nutrients by the studied plants, nor did it result in any significant losses. Therefore, leaf-cutting ants are important actors in ecosystem processes and possibly affect plant species composition, at least on a local scale. The low concentration of nutrients in control plots and high nutrient concentration in plants near ant nests suggest that plants of Cerrado are adapted to the low-soil fertility and seasonal burning but they can respond to higher nutrient soil conditions promoted by leaf-cutting ant nests. Nests of *A. laevigata* should accelerate vegetation recovery after burning and could affect the plant structure in Cerrado ecosystem if the balance between its negative effect via herbivory and its positive effect via the enrichment of soil nutrients is positive.

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