

# 4

## The Fire Factor

*Heloisa S. Miranda, Mercedes M. C. Bustamante,  
and Antonio C. Miranda*

FIRE IS A COMMON FEATURE OF THE CERRADOS, AS IT IS FOR MOST savanna ecosystems. Fires set by man or lightning are common and have been for thousands of years. Vicentini (1993), in a paleoclimatic and paleo-vegetational study, has registered the occurrence of fire 32,400 Years Before Present (YBP) in the region of Cromínia (GO); De Oliveira (1992) registered the presence of charcoal particles dated from 13,700 YBP in lake sediments in cerrado of the southeastern Brazil; and Coutinho (1981) has reported the occurrence of charcoal pieces dated from 8,600 YBP from a campo cerrado soil horizon lying at 2 m depth. Although Gidon and Delibrias (1986) date the presence of man in Brazil to 32,000 YBP, according to Prous (1992) and Cooke (1998) there is no evidence of human presence in central Brazil before 12,000–11,000 YBP. Therefore, the particles of charcoal and burned wood dated from 11,000 YBP could, at least in part, be caused by the early inhabitants of the cerrado region (Salgado-Laboriau and Vicentini 1994). The indigenous people of the cerrado region used fire for hunting, stimulation of fruit production, control of undesirable species, and tribal war (Coutinho 1990a; Mistry 1998). Nowadays, the principal cause of fire in the cerrado is agricultural, its purpose either to transform cerrado into crop fields or to manage natural (more open cerrado forms) or planted pasture (Coutinho 1990a; see chapter 5).

Although fire is considered one of the determinants of the cerrado vegetation, the rapid occupation of the cerrado region has changed the natural fire regime (season and frequency of burning) with consequences for the vegetation structure and composition.

In this chapter we present a review of cerrado fire ecology, with emphasis on fuel dynamics, fire behavior, nutrient fluxes, and changes in

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the structure and composition of the vegetation. A review of fire effects on population dynamics of woody plants is presented in chapter 9.

## THE CERRADO FIRES

Cerrado fires, like most savanna fires, are characterized as surface fires, which consume the fine fuel of the herbaceous layer. Luke and McArthur (1978) define fine fuel as live and dead grasses, and leaves and stems with diameter smaller than 6 mm. Depending upon the physiognomic form (chapter 6) and the time since the last fire, the total fine fuel load, up to a height of 2 m, may vary from 0.6 kg/m<sup>2</sup> to 1.2 kg/m<sup>2</sup>. The fine fuel of the herbaceous layer represents 97% of the fuel load for *campo sujo*, 90% for cerrado *sensu stricto*, and 85% for *cerradão* (Miranda 2000; see descriptions of physiognomies in chapter 6). These values are similar to those presented by Castro and Kauffman (1998) for cerrado *sensu stricto*, by San José and Medina (1977) for other South American savannas, and by Kelmann et al. (1987) for African savannas.

The vegetation of the herbaceous layer represents 94% of the fuel consumed during the fires. Most of the fine fuel in the woody layer is not consumed during the fires (see table 4.1). This may be a consequence of the high water content of the live fuel, of the fast rate of spread of the fire front (Kauffman et al. 1994; Miranda et al. 1996a; Castro and Kauffman 1998), and of the height of the flames during the fires. Flame height for savanna fires ranges from 0.8 m to 2.8 m (Frost and Robertson 1987). Castro Neves (unpublished data) determined a reduction of 4% in the canopy cover of a *cerradão* immediately after a prescribed fire. The abscission of the damaged leaves resulted in a reduction of 38% in the canopy cover in the 15 days after the fire, suggesting that most of the live leaves are not consumed but damaged by the hot air flow during the fire.

The fuel consumption in the different physiognomic forms (table 4.1) reflects the difference in fine fuel composition and in fire regime. In the *campo sujo* most of the fine fuel is composed of grasses (live and dead, or dormant) that are not in close contact with the wet soil surface and are well exposed to the wind and solar radiation, quickly losing moisture to the environment.

In the denser forms of cerrado (i.e., *cerradão*) the composition of the fine fuel reflects the fire regime much more than the open form, with the dead leaves of the litter layer representing most of the fuel load after long periods of protection from fire. In this case the dead fuel is in close contact with the soil surface. The microclimate may affect the rate of fuel moisture

**Table 4.1** Range of Fine Fuel Load and Fuel Consumption During Prescribed Fires in the Cerrado Vegetation at the Reserva Ecológica do IBGE, Brasília, DF

	<i>Campo sujo</i>	<i>Cerrado sensu stricto</i>	<i>Cerradão</i>
Before fire (kg/m <sup>2</sup> )			
Herbaceous layer	0.64–0.96	0.59–1.11	0.50–0.75
Woody layer	0.03–0.03	0.06–0.14	0.08–0.14
Total	0.67–0.99	0.65–1.25	0.58–0.89
Dead fuel (%)	69–75	76–61	50–69
Live fuel (%)	31–25	24–39	50–31
After fire (kg/m <sup>2</sup> )			
Herbaceous layer	0.05–0.06	0.09–0.00	0.08–0.04
Woody layer	0.01–0.01	0.06–0.04	0.06–0.14
Total	0.06–0.07	0.15–0.04	0.14–0.18
Fuel consumption (%)	91–93	77–97	75–76

Source: H. S. Miranda, unpublished data.

Note: See chapter 6 for descriptions of cerrado physiognomies.

loss due to shading of the fine fuel by the trees and shrubs, leaving patches of vegetation unburned (Miranda et al. 1993; Kauffman et al. 1994).

As the fire front advances, air temperatures rise sharply. Miranda et al. (1993, 1996a), in studies of vertical distribution of temperatures (1 cm, 60 cm and 160 cm height) during cerrado fires, have registered maximum values in the range of 85°C to 840°C (regardless of the physiognomic form), with the highest temperatures occurring most of the time at 60 cm above ground. The range of temperatures reported is similar to that of savanna fires, where a considerable range of temperatures has been recorded, from 70–800°C at ground level, or just above it, to 200–800°C at about 1 m (Frost and Robertson 1987). The great variability in the temperature may reflect the varying compositions and spatial distributions of the fine fuel; fuel water content; days since last rain; and weather conditions at the moment of the fire (Miranda et al. 1993). The duration of temperatures above 60°C varied from 90 to 270 seconds at 1 cm height, from 90 to 200 seconds at 60 cm height, and from 20 to 70 seconds at 160 cm height. Although 60°C is considered the lethal temperature for plant tissue, Kayll (1968) has shown that lethal temperature varies in relation to the exposure time, with leaves withstanding 49°C for 2 hours, 60°C for 31 seconds, or 64°C for 3 seconds. The duration of temperatures above 60°C in cerrado fires was long enough to kill the leaves exposed to the hot air flow.

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Wright (1970) shows that the death of plant tissue depends primarily on moisture content and is an exponential function of temperature and time. Consequently, the heat tolerance of a tree (the ability of a tree's organs to withstand high temperatures) along with its fire resistance (mainly determined by its size, bark thickness, and foliage distribution) may vary with season as a result of the seasonal changes in plant water content. Guedes (1993) and Rocha e Silva and Miranda (1996) have shown that the short duration of the heat pulse and the good insulating effect of thick bark, characteristic of the cerrado trees, provide protection to the cambium so that the increase in cambium temperature during the fires is small. These authors determined a minimum bark thickness of 6–8 mm for effective protection of the cambium tissue. However, in the lower branches, where bark is not thick enough to produce an effective insulation, the cambium may reach high temperatures, remaining over 60°C long enough to cause the death of the cambium tissue, and consequently the death of the branches, altering the structure of the tree canopy.

As a consequence of the short time of residence of the fire front, the increase in soil temperature is small. At 1 cm depth the highest temperatures range from 29°C to 55°C. Soil temperature changes are negligible at and below 5 cm depth, with a maximum increase of 3°C regardless of the physiognomic form of cerrado being burned. The maximum temperatures are registered 10 min after the fire at 1 cm depth and after 4 h at 10 cm depth (Coutinho 1978; Castro Neves and Miranda 1996). The rise in soil temperature during cerrado fires may have little effect on soil organic matter, microbial population, and buried seeds, and also is likely to have little effect on the loss of nutrients from the soil pool.

The reduction of the vegetation cover and the deposition of an ash layer over the soil surface result in a postfire alteration in soil microclimate. Castro Neves and Miranda (1996) found that the albedo ( $\rho$ ) between 10:00 A.M. and 2:30 P.M. is reduced from 0.11 to 0.03 after a *campo sujo* fire, where 94% of the vegetation was consumed. This decrease in  $\rho$  represents a 10% increase in the energy absorbed. One month after the fire,  $\rho$  returned to 54% of the prefire value. Soil heat flux ( $G$ ) changed from 55 W/m<sup>2</sup> before the fire to 75 W/m<sup>2</sup> after the fire, representing 7% of the incident solar radiation (Castro Neves and Miranda 1996). The alteration in  $\rho$  and  $G$  results in an increase in the amplitude of soil temperature after the fire on the order of 30°C at 1 cm depth, and 10°C at 5 cm depth, with no alteration at 10 cm depth (Dias 1994; Castro Neves and Miranda 1996). Although these alterations in soil microclimate may have some effect on plant colonization and soil microorganisms (Frost and Robertson 1987), they are of short duration as a

consequence of the fast recovery of the vegetation of the herbaceous layer. Andrade (1998) has shown that 80% of the fuel load of the herbaceous layer of a *campo sujo* is recovered one year after a fire. Neto et al. (1998) have determined that after 2 years the biomass of the herbaceous layer of *campo sujo* has completely recovered from fire.

Bustamante et al. (1998) showed that soil water content (0–10 cm depth) was lower in a burned cerrado *sensu stricto* area than in an adjacent unburned area. The difference in soil water content between the two areas lasted for 15 months, probably as a consequence of plant cover removal and alteration of the vegetation composition. The frequent fires in the area reduced the woody plant density, favoring the recolonization of grasses that used water of the superficial soil layer.

## NUTRIENT CYCLING

Nutrient cycling is a very important aspect of fire ecology, especially in the cerrado region where the native vegetation presents a low nutrient content (Haridasan 2000), with low decomposition rate of the litter (Silva 1983), and the soils are poor (see chapter 2). As a consequence of the many different physiognomic forms, floristic composition, soil characteristics, differences in fire regime, and differences in the sampling methods used, there is a great variability in the data regarding the nutrient content of the cerrado vegetation (André-Alvarez 1979; Batmanian 1983; Pivello and Coutinho 1992; Kauffman et al. 1994; Castro 1996).

During a fire the nutrients may be lost by volatilization or as particles deposited in the soil as ash, or remain in the unburned vegetation. The studies of loss of nutrients from the cerrado vegetation during fires suggest that the loss is greatest in *campo limpo* and declines along the gradient from *campo sujo* to *cerradão* (see table 4.2; chapter 6). Silva (1990) studied the partition of biomass and nutrients in the tree layer of a cerrado *sensu stricto*. The woody components of the vegetation are the major pool of nutrients (see table 4.3). In general, the large woody parts of the vegetation do not burn during cerrado fires. The nutrient stock in the leaves of cerrado trees (Silva 1990) is smaller than the stock of the green vegetation of the herbaceous layer (Batmanian 1983, see table 4.4). The difference in nutrient stock and the higher fuel consumption during fires in more open areas of cerrado may explain the decline in nutrient loss with the increase in the density of woody plants.

In general 300 to 400 kg/ha of ash are deposited on the soil surface after a cerrado fire (Coutinho 1990b). Some of the nutrients deposited in

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**Table 4.2** Loss of Nutrients from Vegetation During Fires in Different Physiognomic Forms of Cerrado

Physiognomy	Loss of nutrients (%)						Source
	N	P	K	Ca	Mg	S	
<i>Campo limpo</i>	97	50	60	58	—	16	Kauffman et al. (1994)
<i>Campo limpo</i>	85	—	—	—	—	88	Castro (1996)
<i>Campo limpo</i>	82	72	50	40	—	17	Kauffman et al. (1994)
<i>Campo sujo</i>	81	—	—	—	—	51	Castro (1996)
<i>Campo cerrado</i>	93–97	45–61	29–62	22–71	19–62	43–81	Pivello and Coutinho (1992)
<i>Campo cerrado</i>	66	47	53	67	—	35	Kauffman et al. (1994)
<i>Cerrado sensu stricto</i>	49	47	46	60	—	34	Kauffman et al. (1994)
<i>Cerrado sensu stricto</i>	25	—	—	—	—	44	Castro (1996)
<i>Cerradão</i>	18	—	—	—	—	30	Castro (1996)

Note: See chapter 6 for descriptions of cerrado physiognomies.

the soil are quickly absorbed. Cavalcanti (1978) observed that, immediately after a fire, there was an increase in the concentration of nutrients to a depth of 5 cm, with a significant reduction in the next 3 months. The author observed little alteration in nutrient concentration at greater depths. After a fire in cerrado *sensu stricto*, Batmanian (1983) measured an increase in the concentration of K, Na, Ca and Mg to a depth of 60 cm; no alteration in the concentrations of N and P was observed. The high concentrations of K, Na, Ca, and Mg lasted for 3 months. Batmanian (1983) and Cavalcanti (1978) suggest that most of the nutrients liberated during the fires are absorbed by the superficial roots of the plants of the herbaceous layer. In fact, Dunin et al. (1997), in a study comparing the evapotranspiration of a burned *campo sujo* (3 months after the fire) with an unburned *campo sujo* (1 year since last fire), concluded that almost all the water used by the vegetation of the burned area is removed from the first 1.5 m of the soil. According to Coutinho (1990a), this is the region where the alteration of postfire nutrient concentration has been observed and where the greatest concentration of fine roots is found (Castro 1996).

**Table 4.3** Partition of Above-Ground Biomass and Nutrients in Different Components of the Tree Layer of Cerrado *Sensu Stricto*

	<i>Partition of biomass and nutrients</i>					
	<i>Trunk</i>	<i>Branches</i>	<i>Stems</i>	<i>Leaves</i>	<i>Fruits</i>	<i>Total (kg/ha)</i>
Biomass (kg/ha)	6591	4280	9416	1049	64	21,400
Biomass (%)	30.8	20.0	44.0	4.9	0.3	
Nutrient (kg/ha)						
P	1.3	0.8	1.3	0.8	0.3	4.5
K	6.7	4.8	8.9	6.0	3.3	29.7
Ca	6.5	3.7	9.3	2.9	0.5	22.9
Mg	3.6	1.9	4.0	1.2	0.3	11.0
Al	4.9	2.9	5.9	2.0	0.4	

Source: Silva 1990.

Note: Values represent the mean for 35 woody species and a tree density of 1333 trees/ha.

As discussed before, the rise in soil temperature is small during cerrado fires and is restricted to the first centimeters. Therefore, it may have little effect on the loss of nutrients from the soil pool. Raison (1979) reported a loss of 25% of N in the soil after 2 h at 200°C. No alteration in the N concentration in the 0–20 cm soil layer was recorded by Kauffman et al. (1994) and Kozovits et al. (1996). Further studies of N and S concentration, to a depth of 2 m (Castro 1996), likewise showed no change after cerrado fires. Similar results were reported by Montes and San José (1993) for another neotropical savanna. The loss of nutrients in

**Table 4.4** Nutrient Content of the Herbaceous Layer During the Wet and Dry Seasons in an Unburned Cerrado *Sensu Stricto*

<i>Nutrient</i>	<i>Nutrient content (kg/ha)</i>			
	<i>Grasses</i>		<i>Nongrasses</i>	
	<i>Wet season</i>	<i>Dry season</i>	<i>Wet season</i>	<i>Dry season</i>
P	0.9	0.6	0.5	0.3
K	5.9	3.8	6.0	2.5
Ca	0.5	0.5	2.5	1.8
Mg	0.9	1.2	1.1	0.7
Al	3.7	3.0	0.6	0.5

Source: Batmanian 1983.

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the system pool (vegetation + soil) is therefore a consequence of the burning of the above-ground biomass representing 3.8% of the system pool (Kauffman et al. 1994).

During cerrado fires the maximum temperatures are around 800°C (Miranda et al. 1993, 1996a), and most of the nutrients are lost by volatilization. Considering that Ca and Mg have high volatilization temperatures, 1240°C and 1107°C, respectively (Wright and Bailey 1982), Coutinho (1990a) assumes that they are lost by particle transport. Kauffman et al. (1994) estimated that about 33% of N, 22% of P and 74% of S are lost by volatilization during cerrado fires. Castro (1996) presented similar values for N (35%) and S (91%).

Although a large proportion of the nutrients is lost from a determined area during a fire, some will return to the ecosystem as dry or wet deposition. Coutinho (1979) reported that for a cerrado area there is an annual total deposition of 2.5 kg/ha of K, 3.4 kg/ha of Na, 5.6 kg/ha of Ca, 0.9 kg/ha of Mg, and 2.8 kg/ha of PO<sub>4</sub>. Considering Coutinho's (1979) data on the input of nutrients, Pivello and Coutinho (1992) estimated that the replacement time for P and S lost during burning was far less than 1 year; in the range of 1 to 3.4 years for Ca; 1.6 to 4.1 years for K; and 1 to 5.3 years for Mg. They concluded that an interval of 3 years between burnings was initially considered adequate to stimulate the recycling of the elements retained in the dead plant material and to avoid a critical nutrient impoverishment in the ecosystem. The time interval between burnings suggested by Pivello and Coutinho (1992) was confirmed by Kauffman et al. (1994).

In addition to the return of nutrients through dry and wet deposition, one has also to consider the transfer of nutrients through the decomposition of the scorched leaves that are prematurely dropped after the fire. Silva (1983) determined that in the litter accumulated during 1 year in a cerrado *sensu stricto* area there is 4.8 kg/ha of K, 3.6 kg/ha of Ca, 3.0 kg/ha of Mg, and 0.8 kg/ha of P, and that after 300 days of decomposition there is a reduction of 70%, 55%, and 35% in the initial concentrations of K, Mg, and Ca, respectively. Considering that senescent leaves have a lower nutrient concentration than mature green leaves, the premature drop of scorched leaves may play an important role in the recycling of nutrients caused by fires, even considering the low decomposition rate for the cerrado litter.

Alterations in the carbon cycle have also been observed for cerrado areas submitted to prescribed fires. Burned areas present higher soil CO<sub>2</sub> fluxes than unburned areas, and this effect lasts several months after the fire (Poth et al. 1995). The higher fluxes might be due to the increase of



soil organic matter availability in response to the increase of soil pH. The CO<sub>2</sub> fluxes to the atmosphere over *campo sujo* areas under different fire regimes were also studied (Santos 1999; Silva 1999). From June to August the *campo sujo* fixed more CO<sub>2</sub> than was released through respiration. Maximum assimilation rates varied from 2.5 to 0.03 μmol CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup>. In September the *campo sujo* became a source of CO<sub>2</sub> to the atmosphere, with a maximum emission rate of 1.5 μmol CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup>. A prescribed fire in late September resulted in an increase of the CO<sub>2</sub> emission to 4.0 μmol CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup>. In November and December the *campo sujo* again became a sink for CO<sub>2</sub>, with the assimilation rate increasing to 15.0 μmol CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup>. During the seven months of measurements the *campo sujo* accumulated 0.55 t C ha<sup>-1</sup> (25% of the amount of carbon accumulated in one year by the cerrado *sensu stricto* as determined by Miranda et al. 1996b, 1997).

Burned areas are also a source of trace gases to the atmosphere. Poth et al. (1995) measured soil fluxes of NO, N<sub>2</sub>O and CH<sub>4</sub> from cerrado sites that had been burned within the previous 2 days, 30 days, and 1 year, and from a control site last burned in 1976. NO and N<sub>2</sub>O fluxes responded to fire with the highest fluxes observed from newly burned sites after addition of water. NO fluxes immediately after burning are among the highest observed for any ecosystem studied to date. However, these rates declined with time after burning, returning to control levels 1 year after the fire. The authors concluded that cerrado is a minor source of N<sub>2</sub>O and a sink of atmospheric CH<sub>4</sub>.

## FIRE EFFECTS ON THE VEGETATION

The flora of the herbaceous/undershrub stratum is highly resistant to fire (Coutinho 1990a). Some plants are annuals, growing in the rainy season, and many species exhibit subterranean organs such as rizomes, bulbs, and xylopodia (Rawitscher and Rachid 1946; chapter 7) that are well insulated by soil. A few days after the fire, the organs sprout with full vigor (Coutinho 1990a).

Many plant species appear to depend upon fire for sexual reproduction. Intense flowering can be observed a few days or weeks after cerrado fires for many species of the herbaceous layer. Oliveira et al. (1996) observed 44 species of terrestrial orchids flowering after fires in areas of cerrado *sensu stricto*, *campo sujo*, and *campo limpo*, with some of the species flowering in the first two weeks after fire. Intense flowering of *Habenaria armata* was observed just after an accidental fire, while in the

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four preceding years, when the vegetation was protected, no flowering individuals could be observed. Coutinho (1976) observed that a great number of species depend on fire to flower, responding with intense flowering to burns occurring any season of the year. In experiments with four species of the herbaceous/undershrub stratum (*Lantana montevidensis*, *Stylosanthes capitata*, *Vernonia grandiflora* and *Wedelia glauca*), Coutinho (1976) showed that burning, cutting the plants close to the soil, exposing them to a period of drought, or causing the death of their epigeous parts all resulted in a high percentage of flowering. He concluded that the effect of fire on the induction of flowering is not a result of thermal action or fertilization by the ashes. In a comparative study on the effects of fire and clipping on the flowering of 50 species of the flora of the herbaceous layer of a *campo sujo*, Cesar (1980) concluded that, for most of the species studied, flowering was independent of the season of burning and resulted in a similar phenological response in both treatments. Fire-induced flowering has been frequently reported, especially for grasses and geophytic lilies and orchids (Gill 1981). The causes of intense flowering may be related both to the increase in productivity after fire and to the damage caused by fire to the above-ground plant parts, possibly stimulating the production of flower primordia (Whelan 1995).

Regeneration after fire for savanna vegetation through germination of soil stored seeds has been reviewed by Frost and Robertson (1987), but few studies report on seed dispersal in relation to fire (Whelan 1986). For the herbaceous vegetation of cerrado, Coutinho (1977) observed that *Anemopaegma arvense*, *Jacaranda decurrens*, *Gomphrena macrocephala* and *Nautonia nummularia* dispersed their seeds shortly after fire. This suggests that fire may be beneficial to such species, since it promotes or facilitates the dispersal of their anemocoric seeds. Seed germination of *Echinolaena inflexa* (a C3 grass common in all cerrado forms) was higher after a mid-dry season quadrennial fire in a *campo sujo* than in an area protected from fire for 21 years. However, recolonization by vegetative growth was higher than by seeds in both areas (Miranda 1996). After the fire, the density of *E. inflexa* was twice the density determined for the unburned area. Parron (1992) observed no difference in the density of *E. inflexa* in a *campo sujo* burned annually for 3 years, at the beginning of the dry season, and an adjacent area protected from fire for 3 years. These results may reflect the interaction between fire regime and the reproductive strategies of *E. inflexa*. San José and Farinas (1991), in a long-term monitoring of density and species composition in a *Trachypogon* savanna, showed that the dominant species, *Trachypogon plumosus*, was replaced by *Axonopus canescens* when fire was suppressed. The alteration in

species density was associated with differences in reproductive strategies: *T. plumosus* presented vegetative reproduction; *A. canescens*, sexual reproduction. For *A. canescens*, fire suppression may increase the probability of seedling survival.

Most of the woody species of the cerrado present strong suberization of the trunk and branches, resulting in an effective thermal insulation of the internal living tissues of those organs during fires. Nevertheless, plants differ greatly in their tolerance to fire and in their capacity to recover subsequently.

Most of the work on the response of savanna woody vegetation to fire is related to mortality, regeneration through seedlings, or resprouting from epicormic meristems or lignotubers (Frost and Robertson 1987). Landim and Hay (1996) reported that fire damaged 79% of the fruits of *Kielmeyera coriacea*, irrespective of tree height (1 to 3 m), but there were no differences in flower and bud initiation in the next reproductive period. Hoffmann (1998) observed that fruits and seeds of *Miconia albicans*, *Myrsine guianensis*, *Roupala montana*, *Periandra mediterranea*, *Rourea induta*, and *Piptocarpha rotundifolia* were damaged by a late dry season biennial fire, with a negative impact on sexual reproduction. All species but *P. rotundifolia* exhibited overall reductions in seed production in the years following fire (see chapter 9). An increase in the reproductive success for *Byrsonima crassa* after a mid-dry-season fire was reported by Silva et al. (1996).

Although most of the cerrado trees are well insulated by thick bark, the small individuals may not have produced an effective insulation between fires, being more susceptible to the effects of the high temperature of the flames (Guedes 1993). Consequently, frequent fires reduce the density of woody vegetation through the mortality of the smaller individuals (Frost and Robertson 1987) and through the alteration of the regeneration rate of the woody species (Hoffmann 1998; Matos 1994; Miyanish and Kellman 1986).

In a study of the effects of a biennial fire regime on the regeneration of *Blepharocalyx salicifolius* in cerrado *sensu stricto*, Matos (1994) found twice the number of individuals (seedlings and juveniles) in an area protected from fire for 18 years than in an area that was burned biennially. The mortality caused by the biennial fires was greater than 90% for seedlings and less than 50% for juveniles. The author estimated that the critical size for survival and resprout after fire was 50 cm in height with 0.6 cm in basal diameter. Hoffmann (1998), investigating the postburn reproduction of woody plants in areas subjected to biennial fires, observed that fire caused a high mortality in seedlings of *Miconia albicans* (100%), *Myrsine*

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*guianensis* (86%), *Roupala montana* (64%), *Periandra mediterranea* (50%), and *Rourea induta* (33%). Root suckers of *M. guianensis*, *R. montana*, and *R. induta* had a higher survival rate, perhaps a consequence of their stem diameters (1.7 mm to 2.4 mm, two to four times greater than the seedlings) and connection with the mother plant (chapter 9).

The effect of two annual fires on small individuals (from 20 cm to 100 cm in height and diameter greater than 1.5 cm, at 30 cm from the soil) was investigated by Armando (1994) for nine woody species: *Aspidosperma dasycarpon*, *Blepharocalyx salicifolius*, *Caryocar brasiliense*, *Dalbergia miscolobium*, *Hymenaea stigonocarpa*, *Stryphnodendron adstringens*, *Sclerolobium paniculatum*, *Siphoneugena densiflora*, and *Virola sebifera*. The two consecutive fires resulted in a reduction of 10 cm in the mean height of the plant community and in a mortality of 4%. Only four species presented reduction in the number of individuals: *D. miscolobium* (12%), *S. adstringens* (14%), *S. densiflora* (14%), and *S. paniculatum* (15%).

Sato (1996) determined that, for woody vegetation submitted to a biennial fire regime in the middle of the dry season, after 18 years of protection, the highest mortality rate occurred among the individuals with height between 0.3 m and 2.0 m. After the first fire they accounted for 40% of the mortality, and for 72% after the second fire. Ramos (1990) observed that young trees and shrubs up to 128 cm tall, and with diameter smaller than 3 cm (measured at 30 cm above ground), are seriously damaged by biennial fires.

Mortality rates related to fire season have been reported by Sato and Miranda (1996) and Sato et al. (1998) for cerrado vegetation. The authors considered only the individuals with stem diameter equal to or greater than 5.0 cm, at 30 cm from soil surface. After 18 years of protection from fire, three biennial fires at the middle of the dry season resulted in mortality rates of 12%, 6%, and 12%, with a final total reduction in the number of individuals of 27% after the third fire. In an experimental plot burned at the end of the dry season, the mortality rates were 12%, 13%, and 19%, with a reduction of 38% in the number of individuals. Williams (1995) presents similar values for mortality of tropical savanna trees in Australia, and higher rates are presented by Rutherford (1981) and Frost and Robertson (1987) for species of African savanna. Most of the trees that died in the second fire ( $\approx 60\%$ ) had suffered top kill during the first fire after a long period of protection. Some of the mortality following the second and third fires may be an indirect effect of fire. Cardinot (1998), studying the sprouting of *Kielmeyera coriacea* and *Roupala montana* after fires, in the same experimental plots, reported that the mortality of some

trees is a consequence of herbivory and nutrient shortage. The higher mortality rates for late dry season fires may be related to the phenology of many species of the cerrado vegetation that launch new leaves, flowers, and fruits during the dry season (Bucci 1997).

Similar results have been reported by Rocha e Silva (1999) for *campo sujo*. After protection from fire for 18 years, three biennial fires, at the middle of the dry season, resulted in tree and shrub mortality rates of 5%, 8% and 10%, reducing the number of individuals by 20%. In an experimental plot burned for four years at the middle of the dry season, mortality rates were 10% and 12%, with a reduction of 20% of the number of individuals, suggesting that two quadrennial burns produce the same mortality as three biennial burns. Of the 30 woody species present in the experimental plots, only 7 did not suffer alteration in the number of individuals after the fires: *Byrsonima verbascifolia*, *Caryocar brasiliensis*, *Eremanthus mollis*, *Eriotheca pubescens*, *Qualea parviflora*, *Syagrus comosa*, and *Syagrus flexuosa*.

The alteration in the regeneration rates of woody species and the high mortality rate determined in these studies suggest that the biennial fire regime is changing the physiognomies of cerrado *sensu stricto* and *campo sujo* to an even more open form, with grasses as the major component of the herbaceous layer. This alteration, in turn, favors the occurrence of more intense and frequent fires.

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