Impacts of Cattle, Fire and Wind in Rocky Savannas, Southeastern Brazil

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Abstract: The impacts of cattle (grazing, trampling and dung deposition), fire, and wind upon the rocky savannas (campo rupestre) of Minas Gerais, southeastern Brazil, are briefly evaluated. Peculiar life forms of vascular plants and their adaptations to natural disturbances are analyzed. The Intermediate Disturbance Hypothesis (IDH) is considered consistent with the findings for fire and wind. However, by altering the soil parameters, the presence of cattle brings about continuous and cyclic disturbances with long-lasting negative impacts on vegetation and on the survival of native species. The proportion of fire-adapted vascular plants species in campo rupestre was found to be comparable to those of the Brazilian zonal savannas on latossol (cerrado).

Key words: campo rupestre, ecology, invasive species, management, white-sand savanna

INTRODUCTION

Brazilian rocky savannas (campo rupestre) are a phytogeographic province centered in the Espinhaço mountains in Bahia and Minas Gerais states (Fig. 1), between latitudes 10°–20°35’S and longitudes 40°10’–44°30’W (Giulietti et al. 2007). This extrazonal vegetation complex is inserted mainly within the humid savanna (cerrado) and semiarid savanna (caatinga) biomes (Alves et al. 2007), and typically has exceptionally nutrient-poor soils rich in Fe and Al (Benites et al. 2007), a fire cycle and strong winds. The climate in the studied areas typically has arid winters and rainy summers (Fig. 2).

Following European settlement of Brazil, the campo rupestre vegetation mosaic has been suffering from an increasing number and intensity of disturbances caused by cattle grazing, fire, mineral and wood extraction, road construction, and increasing uncontrolled
Fig. 1: Study sites in the southeastern Brazil (solid round dots) and position of the Serra do Cipó (hollow square)

Fig. 2: Climate diagram of São Joao Del Rey, 6 km west from the Serra de São José. Note that burning of vegetation occurs at the end of the dry season and into the beginning of the rainy season
tourism and human settlement (Giulietti and Menezes 2000; Silva et al. 2003; Viana et al. 2005; Medina and Fernandes 2007).

The main types of disturbance which can be recognized in campo rupestre can be categorized as follows:

1. Severe short-term disturbance followed by relatively rapid vegetation recovery. This includes natural disturbances such as fire with an intermediate frequency and occasional strong winds.
2. Moderate but continuous disturbance which alters the environment in such a manner that total natural recovery, when tangible, would be a long-term process. This includes all impacts of cattle grazing, dung deposition, trampling, and of invasive species.
3. Moderate short-term disturbance with impacts limited to several individuals or populations. This includes selective timber collection and picking of ornamental plants.

Though the cerrado biome, in which most campo rupestre areas form a mosaic, is mostly adapted to natural fire, it has been subjected to two abnormal fire regimes:
– biannual burning by cattle-ranchers at the end of the dry season for the past 3 centuries,
– deliberate exclusion of fire (but with at least two unwanted intense forest fires once every three to five years) in environmental conservation areas over the past 3 decades (França et al. 2007).

Though strong winds are occasional in the campos rupestres, they are a sufficiently common phenomenon which determines the maximum height of trees in white-sand vegetation.

Cattle grazing and the associated impacts in campo rupestre are not uniform throughout the range of this vegetation type. Consequently, in any campo rupestre range, a mosaic of severely grazed areas alternates with relatively well preserved species-rich localities.

The regeneration potential of vegetation represents a crucial factor for its conservation and management (Medina and Fernandes 2007). The intermediate disturbance hypothesis (IDH, viz. Connell 1978; Huston 1979) predicts that species diversity will be maximized at intermediate disturbance frequencies and severities which minimize species losses due to competitive exclusion and direct disturbance effects, while maintaining opportunities for establishment of new species (Peterson and Reich 2008). We assumed that because they grow slowly and resist extreme nutrient poverty of the soil, most campo rupestre vascular plant species are r-strategists adapted to cyclic natural stress factors, but vulnerable to disturbances.

Campo rupestre is a vegetation complex with extreme environmental heterogeneity (Conceição and Pirani 2005, 2007). Disturbances and environmental heterogeneity are two factors thought to influence plant species diversity, but their effects are still poorly understood in many ecosystems (Peterson and Reich 2008).

In this paper we confronted the IDH with twenty years of field research of the effects of fire, wind, cattle-grazing, extraction of firewood and ornamental plant collecting in several campo rupestre sites in Minas Gerais, Brazil, and provide a preliminary evaluation of the impacts.
METHODS

On many field studies spanning the last two decades, we monitored changes of floristic composition in permanent and non-permanent plots, sampling vegetation and synecological data, dug soil profiles, recorded the effects of fire, wind and cattle on vegetation and soils of the campo rupestre vegetation complex in seven localities (Tab. 1), of which the Serra da Chapada, Serra do Ouro Branco and Serra Bico de Pedra are located at the southern limit of the Espinhaço mountain chain and the remaining sites are over 100 km southwest (Fig. 1). A floristic survey was conducted in the Serra de São José range in Minas Gerais, and complemented by many collections and observations in the remaining localities.

Tab. 1: Location (in decimal degrees from N to S), altitude ranges (m a.s.l.), and impacts of the surveyed localities: Lat. = south latitude, Long. = west longitude, G = grazing damage to native vegetation, T = erosion induced by trampling, D = invasive species due to dung-deposition, Wo = Firewood collecting, Or = Ornamental plant collecting. Estimated impact intensities of each factor: 0 = nil, 1 = intermediate, 2 = severe, ? = undetected

<table>
<thead>
<tr>
<th>Serra (Mountain)</th>
<th>Lat.</th>
<th>Long.</th>
<th>Alt. m a.s.l.</th>
<th>Impact intensities</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Fire</td>
</tr>
<tr>
<td>Serra Bico de Pedra</td>
<td>–20.474</td>
<td>43.595</td>
<td>1071–1236</td>
<td>1</td>
</tr>
<tr>
<td>Serra da Chapada</td>
<td>–20.471</td>
<td>43.588</td>
<td>1276–1286</td>
<td>1</td>
</tr>
<tr>
<td>Serra do Ouro Branco</td>
<td>–20.490</td>
<td>43.695</td>
<td>1420–1529</td>
<td>1</td>
</tr>
<tr>
<td>Serra de São José</td>
<td>–21.086</td>
<td>44.169</td>
<td>1175</td>
<td>1</td>
</tr>
<tr>
<td>Serra do Lenheiro</td>
<td>–21.131</td>
<td>44.306</td>
<td>990–1194</td>
<td>1</td>
</tr>
<tr>
<td>Serra do Ouro Grosso</td>
<td>–21.307</td>
<td>44.638</td>
<td>950–992</td>
<td>1</td>
</tr>
<tr>
<td>Serra de Carrancas</td>
<td>–21.440</td>
<td>44.707</td>
<td>1260–1302</td>
<td>2</td>
</tr>
</tbody>
</table>

Nomenclature of all species follows the Missouri Botanical Garden’s Vast nomenclatural database Tropicos.org (2008). For all sampled vascular plants, peculiar life forms, morphological adaptations, and post-fire recovery strategies were recorded during the field investigations. As each species can assume more than one life form, those attributed herein refer to the predominant life form of adult individuals. Hemiparasites on trees were classified as epiphytes. For comparison with life form spectra from the cerrado biome (Batalha and Martins 2004; Gottsberger and Silberbauer-Gottsberger 2006), only the main life forms with available data were used.

The relative frequency of disturbances in each site was compiled from field observations, reports by local inhabitants and from fire data provided by the Instituto Estadual de Florestas (IEF). For vegetation of each locality, impact of fire, wind, and the effects of cattle (trampling, grazing and dung deposition) were estimated as nil, severe or intermediate (Tab. 1). The constancy and cover of the invasive African molasses grass (*Melinis minutiflora*) on rock outcrops was compared to that in crevices among outcrops.
and in colluvial white-sand savannas, since these substrate types harbor the three main vegetation physiognomies of campo rupestre (Alves and Kolbek, in prep.) Data on the constancy and cover of selected life-forms and taxa were extracted from vegetation relevés (Braun-Blanquet 1932). We estimated impact intensities as nil, intermediate (when native vegetation was still relatively intact, low cover of invasive species, effects of fire and wind were not severely visible) and severe (high cover of invasive species, long-lasting impacts of fire etc.).

RESULTS

Vegetation in the studied localities is burned by cattle-ranchers approximately once every second year during the end of the dry season (Fig. 2). The most notorious fire-spreading plant in the studied campo rupestre sites is the invasive grass Melinis minutiflora. This C4 species was initially introduced as a forage plant for cattle, but soon became an aggressive weed. Hence this species has an effect on both the impacts of cattle and fire. The relative importance of M. minutiflora in the three main habitat types of the studied campo rupestre sites is in Tab. 2.

Tab. 2: Cover and constancy of Melinis minutiflora in 308 phytocoenological relevés obtained in three distinct campo rupestre habitats from the studied localities

<table>
<thead>
<tr>
<th></th>
<th>White sand savanna</th>
<th>Rock outcrops</th>
<th>Large crevices and scree</th>
</tr>
</thead>
<tbody>
<tr>
<td>Area analyzed (m²)</td>
<td>4812</td>
<td>6192</td>
<td>1467</td>
</tr>
<tr>
<td>Cover area (m²)</td>
<td>64</td>
<td>353.9</td>
<td>2.4</td>
</tr>
<tr>
<td>Cover (%)</td>
<td>4.4</td>
<td>8.3</td>
<td>1.8</td>
</tr>
<tr>
<td>Total relevés</td>
<td>19</td>
<td>186</td>
<td>103</td>
</tr>
<tr>
<td>Constancy (%)</td>
<td>89</td>
<td>60</td>
<td>14</td>
</tr>
</tbody>
</table>

Some rather unusual life forms are present in the campo rupestre complex. A caudex covered by leaf sheaths is an efficient protection against heat-damage from fire. This feature is common to shrubby Velloziaceae, in the Serra de São José this is true for Vellozia kolbekii and V. crassicaulis, but most campo rupestre sites have their own endemic and vicarious species with similar adaptations. Among the Cyperaceae, caudices do not have a central stem protected by sheath layers, but instead, they are formed by intertwined leaf sheaths and adventive roots. In Bulbostylis paradoxa, such peculiar caudices can be only a few decimeters tall (Gottsberger and Silberbauer-Gottsberger 2006). In Machaerina ensifolia they can exceed 1 m, hence individuals of can be about 2 m tall. Several campo rupestre species of Paepalanthus (Eriocaulaceae) are perennial plants with a caulirosulate habit (sensu Hedberg 1964): the caudex can have up to 30 cm in P. planifolius and 15 cm in P. plantagineus. In all aforementioned species the observed caudices were found blackened by previous fires.

The proportion of plant species which require fire and those with special adaptations to withstand fire in the campos rupestres indicates that, as occurs with the cerrado, this
particular ecosystem is also well adapted to a natural fire regime (Tab. 3). Several plants that grow in campo rupestre seem to require fire in order to flower (for ex. many *Vellozia* spp. and *Bulbostylis paradoxa*) while the plants which have lignotubers or analogous organs just under the soil surface benefit from fire because they can grow new aerial rosettes, stems or branches long before other plant life forms can recover (viz. Coutinho 1977; Marchioretto et al. 2005). Field measurements of soil temperatures at various depths indicated that the sandy soil typical of campo rupestre acts as a thermal insulator, which may increase the chances of survival of the seed bank during fire.

**Tab. 3:** Adaptations to fire and eventually wind detected among 1137 terrestrial vascular plant taxa in the Sã o José range in Minas Gerais

<table>
<thead>
<tr>
<th>Adaptation type</th>
<th>Examples of taxa</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lignotubers with annually renewed aerial branches</td>
<td><em>Aspilia foliacea</em>, <em>Camarea affinis</em>, <em>C. ericoides</em>, <em>Cuphea ericoides</em>, <em>Declieuxia aspalathoides</em>, <em>D. cordigera</em>, <em>Stachytarpheta reticulata</em>, <em>S. sellowiana</em></td>
</tr>
<tr>
<td>Underground trees and shrubs</td>
<td><em>Alibertia concolor</em>, <em>Andira vermifuga</em>, <em>Jacaranda decurrens</em>, <em>Vellozia crinita</em></td>
</tr>
<tr>
<td>Herbaceous geophytes</td>
<td><em>Hippeastrum morelianum</em>, <em>Klotzschia brasiliensis</em>, <em>Sisirynchium vaginatum</em>, <em>Trimezia juncifolia</em></td>
</tr>
<tr>
<td>Stem densely covered by leaf sheaths or thick layer of corky bark</td>
<td><em>Bulbostylis paradoxa</em>, <em>Kielmeyera coriacea</em>, <em>Lafoensia pacari</em>, <em>Erythroxylum tortuosum</em>, <em>Vellozia</em> sp. div.</td>
</tr>
<tr>
<td>Leaves congested at apices of branches, hence above flames in taller individuals</td>
<td><em>Erythroxylum tortuosum</em>, <em>Kielmeyera coriacea</em>, <em>Lychnophora blanchetii</em>, <em>L. passerina</em>, <em>Palicourea rigida</em>, <em>Vellozia</em> sp. div.</td>
</tr>
<tr>
<td>Therophytes completing reproductive cycle in rainy season</td>
<td><em>Genlisea</em> sp. div., <em>Utricularia</em> sp. div., <em>Schultesia gracilis</em>, <em>Siphanthera arenaria</em>, <em>Syngonanthus gracilis</em>, <em>S. niveus</em></td>
</tr>
<tr>
<td>Lithophytes growing far from adjacent fire-spreading vegetation</td>
<td><em>Bifrenaria tyrianthina</em>, <em>Bulbophyllum ipanemensis</em>, <em>Hatiora salicornioides</em>, <em>Prosthechea vespa</em>, <em>Sophronitis caulescens</em>, <em>Tillandsia gardneri</em>, <em>T. streptocarpa</em></td>
</tr>
<tr>
<td>Flowering or seed germination triggered by fire</td>
<td><em>Bulbostylis paradoxa</em>, <em>Erythroxylum tortuosum</em>, <em>Cuphea ericoides</em>, <em>C. thymoides</em>, <em>Gomphrena</em> sp. div., <em>Lychnophora blanchetii</em>, <em>L. passerina</em></td>
</tr>
<tr>
<td>Growing in fissures but mechanically stabilized by outcrops</td>
<td><em>Clusia arrudea</em>, <em>Copaifera langsfordii</em>, <em>Dyssochroma longiflora</em>, <em>Eremanthus crotonoides</em>, <em>E. erythropappus</em>, <em>Myrcia mutabilis</em>, <em>Podocarpus lambertii</em>, <em>Vellozia kolbekii</em></td>
</tr>
</tbody>
</table>

With a frequency of about once every three years, fires are apparently beneficial to shrubby *Vellozia* populations in campo rupestre. On a single day in August, 1989, 13 distinct smokestacks from burning vegetation were visible on the horizon from the summit of the
São José range. While the effect of more frequent fires is difficult to predict, their intermediate intensity does not harm most native plant species (Fig. 3a). If fire is avoided for several consecutive years, the buildup of organic matter (fuel) eventually increases fire severity, resulting in serious mortality rates (Fig. 3b).

**Fig. 3:** Populations of *Vellozia kolbekii* São José range affected by fire: a – surviving population in locality with a 2–3 year fire cycle (2006), b – stand almost entirely killed by intense fire in an area which remained unburned for at least ten years (2004)
The sandy soil proved to be an efficient thermal insulator: temperatures measured in a depth of 1 cm at midday were over 6 °C lower than those on the surface, and nine degrees lower at a depth of 25 cm. This insulation may be vital for the survival of dormant buds on lignotubers, bulbs of geophytes and for seeds of therophytes during fire.

Thickened corky bark as in *Kielmeyera coriacea* (Fig. 4a) or exfoliating bark as in *Lafoensia pacari* (Fig. 4b) can provide trees with some protection against fire. However, the proportion of plant species with lignotubers in campo rupestre can be considerable.

**Fig. 4:** Examples of adaptations against fire: a – corky bark of *Kielmeyera coriacea*, b – exfoliating bark of *Lafoensia pacari*, c – lignotuber of *Camarea ericoides*, d – *Paepalanthus planifolius* with the basal leaves of the rosette killed by fire and new leaves sprouting from the center
Of 1137 vascular plant species found to date in the campo rupestre of the São José range (Alves and Kolbek, in prep.), 426 species (37.5% of the flora) are woody species with lignotubers (Fig. 4c), and a further 70 species (6.1%) are geophytes with bulbs, corms, rhizomes or tubers. Not every species encountered in the range was uprooted; hence the real percentage is probably even higher. The most underground organs were among the Asteraceae (94 species), Melastomataceae and the Leguminosae (each with 33), Orchidaceae (30), Apocynaceae (including Asclepiadoideae, with 26), Lamiaceae (21), Malpighiaceae (16), Euphorbiaceae (15), and Rubiaceae (13). The remaining families had less than ten species with thickened underground organs.

For comparison, in 1 hectare of cerrado, Gottsberger and Silberbauer-Gottsberger (2006) found 94 species with lignotubers representing 31.2% of the flora. Species with lignotubers may be originated by the stem, root or both, have varying degrees of lignification, their above-ground organs may be woody or herbaceous, erect, prostrate or winding, annual or lasting at least until the next fire (Gottsberger and Silberbauer-Gottsberger 2006). For simplicity, we chose not to distinguish these categories herein. The importance of lignotubers for the survival in ecosystems with fire is notorious from the fact that several campo rupestre species of Melastomataceae develop these thickened organs in seedling stage (for instance *Leandra pennipilis*, *Miconia sellowiana*, *Svitramia pulchra* and *Tibouchina heteromalla*).

Underground trees are a notorious life-form. While in the aforementioned cerrado plot, Gottsberger and Silberbauer-Gottsberger (2006) observed them in *Andira humilis* (Fabaceae), we have found the most notorious cases in *Jacaranda decurrens* (Bignoniacaeae) in the Ouro Grosso range, *Alibertia concolor* (Rubiaceae) and *Andira vermifuga* (Fabaceae) in the Serra de São José. Curiously enough, in the cerrado plot, the same authors observed lignotubers in *Jacaranda decurrens*, but not subterranean trees. *Vellozia crinita* is exceptionally difficult to classify using the aforementioned criteria. Though it has repent caudices covered by leaf sheaths, these are most often under the surface of white sand deposits, and emit roots along their entire length, emulating rhizomes. Hence *Vellozia crinita* is probable best classified as a subterranean shrub. *Koellensteinia tricolor*, *Galeandra montana*, *Oncidium blanchetii* and *Zygopetalum graminifolium* (Orchidaceae) are atypical geophytes which have pseudobulbs under the soil surface, and hereby withstand fires. These species still have velaminous roots, suggesting their epiphytic ancestry.

Some adaptations against fire only become evident after the fire has passed, as in *Paepalanthus planifolius* (Fig. 4d). The basal leaves of the rosette are killed by the fire, but new leaves soon sprout from the central part. This species also has a thickened corm, half of which is below the soil surface.

Though woody species constitute a major part of the floristic life-form spectrum in the studied campos rupestres, less than one third of these are actually trees and tall shrubs. The vast majority are specialized life forms, usually nanophanerophytes (subshrubs) which often combine ericoid habit, suqarrose or cruciate leaf-set, and the presence of lignotubers (Fig. 5).

The impact of wind is especially notorious in mountains, where the vegetation of exposed slopes can be determined by this factor. Entire stands of trees and shrubs are
commonly found with wind-form crowns or, in campo rupestre more often tilted in the same direction, indicating the direction of prevailing winds (Fig. 6a). In unstable white-sand vegetation of campo rupestre, the maximum height of the tree layer is ultimately controlled by wind. This is especially notorious in *Eremanthus erythropappus*: which often exceeds 12 m when rooted among outcrops, but rarely reaches 4 m in height on deep sandy soils. The taller the trees become on deep sandy soils, the more easily they are uprooted by wind or gravity (Fig. 6b). The irregular but not infrequent occurrence of strong winds is a factor typical for campo rupestre vegetation, in which it bears notorious influence on succession. As a consequence, mainly woody stands remain in a stage of blocked succession (Moravec 1969). This blocking effect can also be maintained due to the permanent process of deflation in the arid season (removal of soil by wind) and by runoff during the summers. The mechanical instability of sandy soil facilitates destructive processes of the tree and shrub layers during strong wind events.

Disturbances were found to have mutual effects: intense winds intensify the spread of fire and control its direction. Conversely the open herbaceous vegetation adapted to a fire

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**Fig. 5:** Life form spectrum of the 1134 vascular plant species of the Serra de São José:

- **T** – therophytes,
- **G** – geophytes,
- **H** – hemicryptophytes,
- **C** – chamaephytes,
- **F** – phanerophytes,
- **ph** – large phanerophytes (trees, shrubs, tall woody climbers),
- **na** – nanophanerophytes (subshrubs),
- **x** – nanophanerophytes with xylopodia (lignotubers),
- **E** – epiphytes (**ep** – hemiepiphytes and holoepiphytes),
- **li** – lithophytes,
- **Hy** – hydrophytes (the latter were not exhaustively surveyed).

The presence of lithophytes distinguishes campo rupestre from surrounding zonal vegetation.

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<table>
<thead>
<tr>
<th>Life Form</th>
<th>Percentage</th>
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<tbody>
<tr>
<td>T</td>
<td>3%</td>
</tr>
<tr>
<td>G</td>
<td>6.2%</td>
</tr>
<tr>
<td>H</td>
<td>9.7%</td>
</tr>
<tr>
<td>C</td>
<td>11.1%</td>
</tr>
<tr>
<td>F</td>
<td>55.9%</td>
</tr>
<tr>
<td>E</td>
<td>13.7%</td>
</tr>
<tr>
<td>Hy</td>
<td>0.4%</td>
</tr>
</tbody>
</table>

120

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**Serra de São José (1134 species)**
Fig. 6: Effects of wind in campo rupestre: a – population of giant *Vellozia* sp. tilted in the direction of the prevailing winds in the Ouro Branco range, 2005, b – a 3.5 m tall individual of *Eremanthus erythropappus*: one of many toppled by wind in the São José range in 2005
Fig. 7: Campo rupestre on the summit of the Carrancas range (2006): a – intensely grazed area with only grass *Melinis minutiflora* in herb layer, b – adjacent area protected from cattle by fences, with *Andropogon leucostachyus, Aspilia foliacea, Camarea ericoides, Croton antisiphyliticus, Hyptis coccinea*, and *Loudetiopsis chrysothrix* in the herb layer. The whitish subshrub in the foreground is *Macrosiphonia velame*
regime poses less resistance to wind, potentially increasing its velocity. The frequency of fire is intensified to a bi-annual cycle by cattle ranchers. Molasses grass forms a dense cover in the herb layer and intensifies the spread of fire. Though fire can temporarily eliminate the cover of invasive species such as molasses grass, it does not prevent this species from re-sprouting from the seed bank. In fact, *Melinis minutiflora* is able to establish in clearings made by fire much faster than most native species. The spread of invasive species is intensified by dung-deposition (by both seed dispersal and nutrient increments to the otherwise poor soil). Invasive species subsequently eliminate native r-strategists by competition for light and other resources.

The effect of cattle grazing in campo rupestre is well exemplified by two adjacent areas in the Carrancas range, separated by a fence: in the area with cattle, the herb layer is entirely composed by invasive grasses (Fig. 7a), while in the cattle-free area just over the fence, a rich herbaceous community dominated by the native grass *Loudetiopsis chrysothrix* occurs (Fig. 7b).

Due to the physical nature of rock outcrops and associated shallow sandy soils, successful diaspor establishment is rare in these environments. Hence, most species of vascular plants, bryophytes, lichens and other cryptogams which live on rock outcrops depend on vegetative and clonal growth following successful diaspor establishment.

**DISCUSSION**

From the ecological point of view, the presence of plants adapted to fire is very important. A large proportion of plant species in savannas and campo rupestre are adapted to or even require fire. In forest ecosystems, fires are usually believed to reduce biodiversity (Melo et al. 2007). In some cases fire can eliminate epiphytes while their phorophytes can remain relatively unharmed (Bartareau and Skull 1994). The effects of fire upon distinct forest types are not uniform: for instance they can increase species diversity in clearings (Cochrane 2003), or decrease diversity in forest edges (Melo et al. 2007). Due to these differences, the impact of fire and subsequent recovery do not depend exclusively on the burned area itself, but on the characteristics of the surrounding unburned vegetation.

In savannas and woodlands, species richness can increase with increasing fire frequency up to biennial (Tester 1989; Brockway and Lewis 1997) or annual fires (Walker and Peet 1983). On the other hand, high fire frequencies can reduce the competitive dominance of overstory trees and understory woody plants (particularly on sandy soils), which would otherwise suppress and competitively displace many of the native grasses and forbs (Peterson and Reich 2008). In a mosaic of grassland, oak savanna, oak woodland, and forest, these authors found that annual to biennial fire frequencies prevent shrubs and trees from competitively excluding grasses and prairie forbs, while spatially variable shading from overstory trees reduces grass dominance and provides a wider range of habitat conditions. These effects were also observed in the studied campo rupestre vegetation, in which the heterogeneity is further enhanced by rock outcrops.
However, in cerrado vegetation, a great proportion of plants, especially subshrub and shrub species, exhibit peculiar adaptations to fire, such as lignotubers (Gottsberger and Silberbauer-Gottsberger 2006). This also seems true for the white-sand component of campo rupestre (see results). Though both cerrado can campo rupestre have comparable proportions of trees and herbs, their soil conditions differ greatly, hence the maintenance of a stable savanna ‘condition’ of coexistence of trees with grasses in campo rupestre can hardly be explained by mechanisms proposed for the cerrado (viz. Walter 1971; Walker and Noy-Meir 1982; Gardner 2006).

Campo rupestre has several documented cases of fire-adapted plants. Shrubby species of *Vellozia* have their stems concealed by a layer of dead leaf sheaths (Menezes 1971, 1984), which insulate and protect the stem and adventive roots from fire. According to Coile and Jones (1981), the genus *Lychnophora* (Asteraceae) “is endemic to campo rupestre habitats, and is entirely composed of shrubs whose adaptations to a seasonally dry environment subject to fires have given the plants a somewhat bizarre appearance”. They consider campo rupestre fires as typically “low and cool” and that *Lychnophora* is adapted to fire by the dense tomentum on their stems. However, we have documented that fires usually kill the aerial stems in *Lychnophora*, and that populations recover by resprouting new aerial stems from underground lignotubers and by increased germination forming very dense stands of seedlings from the seed bank following fires.

Not all plants with thickened underground organs can automatically be considered geophytes, since their renewal buds are quite often at or slightly above the soil surface. Lignotubers are shared by many campo rupestre taxa as a convergent adaptation to fire, permitting secondary growth and survival of buds under the soil surface in a thermally isolated layer, and also a protection against the unfavorable season as suggested by Gottsberger and Silberbauer-Gottsberger (2006). According to these authors, lignotubers could be developed due to high Aluminum concentrations in the soil. However, the abundance of species without lignotubers in both cerrado and campo rupestre indicates that these organs are not simply a morphological and physiological response to environmental conditions.

In the campos rupestres, lignotubers are common to species from many different genera and families. Their above-ground stems or branches can be woody or herbaceous, erect or prostrate, annual or potentially perennial (lasting at least till the next major fire), and can be present only in juvenile plants (for instance *Tibouchina heteromalla*), only in adults (for ex. *Oxalis hirsutissima*) or, usually, during the entire life of the individual. Regeneration buds are always present on plants with lignotubers, either underground, level with the soil surface but often also at considerable heights on the aerial stem; hence the term *xylohemicryptophytes* cannot correctly define a large proportion of plants with lignotubers. With so many variables at hand, rather than defining a new life-form (for instance the *xylopodites* of Veloso 1992), it seems simpler and more adequate to indicate the presence of the lignotuber, within the Raunkiaer system modified by Braun-Blanquet (1932), by means of a suffix added to the existing life-forms (for instance *geophyta geopolodiosa*) following Donselaar-Ten (1966).

Fire intensity depends on the amount of fuel buildup, and is therefore dependent upon the difference between biomass production and fire frequency (Gardner 2006). Even the
most fire-resistant species may succumb to very intense fire. One of the most aggressive invasive grass species is *Melinis minutiflora*, which poses a serious threat to biodiversity in the cerrado biome, since they may obstruct tree regeneration at forest edges, increase fire intensity by increasing fuel load, compete for light with seedlings and occupy the space left by fire leaving out native species (Hoffmann et al. 2004). In the Cerrado biome, *M. minutiflora* produces most seeds at the beginning of the rainy spring season, between August and November (Freitas and Pivello 2005), and its seeds in the seed bank are resistant to fire (Martins 2006). Attempts to control this species by one prescribed annual fire have failed (Martins et al. 2004) but were relatively successful when fire was applied twice in the same year (Martins 2006). As this grass is strictly heliophilous (Silva et al. 2003), shading by trees can eventually eliminate it (Salles et al. 2002). In Venezuela, Barger et al. (2003) found that native savanna is relatively resistant to *M. minutiflora* invasion, since seedlings persisted in intact savanna but exhibited little or no growth during the first year, while in disturbed plots they proliferated vigorously.

*Melinis minutiflora* was present in all three main habitat types in the studied campo rupestre sites. It achieved the largest cover on rock outcrops, where it is relatively well protected from fire, but it achieved greatest constancy in the white-sand savannas, in which dung-deposition by cattle facilitates its establishment (Tab. 2). Though *Melinis minutiflora* is considered African, it is worthy of note that this species was described in 1812 based on a holotype (G) collected by de Jussieu in Brazil, probably in Rio de Janeiro.

In areas with nutrient-rich soils and/or sufficient rainfall, open “grassland” vegetation has relatively high net productivity and can be adapted to large herbivores. However, this is not the case of campo rupestre, where soils are poor to extremely poor, shallow and unstable. In such areas, trampling, grazing and dung deposition are bound to have severe impact on vegetation. In the Carrancas, Ouro Branco and São José ranges, the soils are so unstable that a single event of trampling by passing cattle, and even tire-tracks from cars, often become deep erosive gullies within a few years (Fig. 8a, b). These processes may eventually lead to a total loss of soil cover and consequently of natural vegetation.

Cattle dung deposition can triplicate the Nitrogen content in soil under the dung, and thus selectively modify the patterns of plant-species distribution in the herb layer in several distinct manners, for instance:

1. by modifying the relative abundance of species in the soil seed bank under dung,
2. by influencing the deposition of seeds in the dung,
3. by stimulating the growth of some species while hindering others because of the increased nutrient content (Dai 2000).

Medina and Fernandes (2007) presumed that rock outcrops are habitats where most of the plant species depend on seed dispersal and seed banks to reproduce and maintain viable populations. In a pioneer experiment, they compared distinct components of campo rupestre vegetation (rock outcrops, sandy and peaty bogs, forests, gallery forests) and adjacent “cerrados” by germinating field-collected seeds and determining the plantlets. They found that though outcrops had the poorest seed banks in terms of density and species-richness, the harbored a considerably higher proportion of seeds of endemic and endangered species. In campo rupestre soils, spodic horizons and dark water rivers are
Fig. 8: Erosive gulleys in quartzitic white-sand soils: a – this trail from Tiradentes to Águas Santas over the São José range was level with the surrounding terrain in the early 1990s, and became an erosive gulley which reaches 3 m depths by the year 2000, b – what used to be subtle tire-tracks in the Ouro Branco range in 1992 became this gulley by 2005
typically associated with quartzite and quartzite outcrops, formed by illuviation of organic compounds and the very low nutrient content of these soils and other environmental limitations required the development of specific physiological and morphological plant adaptations (Benites et al. 2007). Hence, the outcrop seeds collected from “clay-pockets” in fissures by Medina and Fernandes (2007) represent an environment distinct from the outcrops themselves. A single variable such as salt content bears influence on seed germination, which greatly varies from species to species (viz. Larson et al. 2000). Due to the aforementioned reasons, many campo rupestre plants are unable to germinate or grow in fine-particled soils, and this could possibly influence the outcome of the experiment by Medina and Fernandes (2007), since many seedlings “were transplanted to seedling bags with standard soils to reach a size where the identification could be possible”.

Maret and Wilson (2000) studied the impact of prescribed fire on the timing and rates of seedling emergence and mortality in three prairie vegetation types in western Oregon, USA. As they sowed seeds into burned and unburned plots, their results can hardly be compared with what would be expected to occur in nature, where the seeds are already present prior to fire.

Though several people were seen collecting firewood and ornamental plants in several localities, the impacts of these activities could not be evaluated satisfactorily, because these activities could not be monitored during a long period, and because they rarely leave visible traces in the field. However, it is evident that, due to the nutrient-poor soils, campo rupestre environments take a long time to recover from the impacts of selective collection of ornamental plants (usually epiphytic orchids, bromeliads and cacti) and the extraction of firewood. On the summits of the Ouro Branco and Carrancas ranges, even today, the scanty firewood available is transformed into charcoal and taken away by truck!

CONCLUSIONS

1. In campo rupestre, due to the extremely poor soils, the presence of invasive plants is usually a direct consequence of the impacts of cattle (especially of dung-deposition).
2. The presence of cattle in the fragile campo rupestre ecosystems should be avoided at all cost. Since most fires are set by cattle ranchers, the removal of cattle from campo rupestre shall automatically reduce the frequency of fire towards the desired natural values.
3. Though wind is a natural impact factor, it intensifies the spread and dictates the direction of fire.
4. The ideal frequency for fire in campo rupestre cannot be generalized: it must be inferred from fuel load separately for each component (outcrops, crevices and white-sand vegetation).
5. The presence of roads facilitates the access of motor vehicles and aggravates the pressure on campo rupestre biota, especially the impacts of firewood collection.

The very nature of campo rupestre (with a large proportion of endemic species, high beta diversity, high concentration of r-strategists, and an extremely diversified suite of
microhabitats) is largely consistent with the intermediate disturbance hypothesis (IDH): With fewer fire and wind events, the buildup of organic debris (fuel) tend to increase fire intensity and eliminate even those native species which are variably adapted to these disturbances. However, due to the poor and unstructured soils, opportunities for immigration and establishment of new species in campo rupestre are naturally few. Successful establishment of new, non-native (frequently invasive) species is conditioned to the alteration of the original soil characteristics, mainly due to dung-deposition by cattle. Grazing occurs in various intensities in different parts of the campo rupestre mosaic, and thus various degrees of impact to the native vegetation can be observed. Unfortunately the pressure of cattle ranching has intensified in several rocky savannas during the past decade. Campo rupestre is relatively less resistant to the disturbances caused by cattle than the zonal biomes which surround it. On the other hand, this biome has many species adapted to an intermediate frequency of fire. Occasional strong winds, combined with the exceptionally unstable and nutrient-poor soils, seasonal droughts and other severe environmental factors also contribute to the savanna physiognomy of campo rupestre.

In comparison to lignotubers, which simply permit seasonal recovery of above-ground branches, underground trees apparently represent an additional strategic advantage, since they allow for continued growth of the “crown” under the surface, protected from fire.

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