

Brazilian Páramos. III. Patterns and Rates of Postfire Regeneration in the Campos de Altitude¹

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ABSTRACT

Postfire vegetation development was studied at two recent mountaintop burns in the Serra do Caparaó, Espírito Santo/Minas Gerais, and the Serra dos Órgãos, Rio de Janeiro, Brazil. Both fires occurred within the páramo-like “campos de altitude”, a system of orographic grass- and scrublands restricted to the highest peaks of southeast Brazil. Data collected included pre- and postfire heights and densities of shrubs and trees, and cover of all taxa. Slopes of different aspect and altitude were sampled at each site to evaluate the effects of varying physical environment on regeneration. Rapid vegetative regeneration was common among shrubs and bamboo, with most taxa surviving fire. Regeneration and postfire colonization rates varied among species, and appeared to depend both on physical variables associated with different slopes, aspects and altitudes, and biotic variables. Most plant species in the campos de altitude show some form of evolutionary adaptation to fire. The distribution of species and plant populations across the landscapes of the campos de altitude appears to be largely the result of fire and its interactions with the biota, local topography, and climate. Results suggest that fire is an integral part of the ecology in these humid, seasonally dry ecosystems. Successful management of these unique and highly threatened systems requires a detailed understanding of the fire regime and its role in structuring biotic communities.

RESUMO

A regeneração da vegetação pós-incêndio foi estudada em dois locais recentemente queimados nos campos de altitude da Serra do Caparaó, Espírito Santo/Minas Gerais e da Serra dos Órgãos, Rio de Janeiro, Brasil. Foram amostradas as alturas e a densidade de plantas lenhosas pré- e pós-incêndio, tal como a cobertura vegetal do estrato herbáceo. Em cada local foram amostradas encostas com orientações diferentes e também diferentes altitudes para avaliar os efeitos de variações do ambiente físico na regeneração. A regeneração da vegetação, especialmente de arbustos e bambu, se mostrou rápida, com a maioria das espécies sobrevivendo ao incêndio. As taxas de regeneração e colonização pós-incêndio variaram entre espécies e entre locais e aparentemente dependem tanto de variáveis físicas ligadas a rumos, declividades e altitudes diferentes, como também de variáveis bióticas. A maioria das espécies de plantas nos campos de altitude parecem adaptar-se ao fogo. A distribuição das espécies e populações de plantas na paisagem dos campos de altitude parece ser o resultado da ação do fogo e de sua interação com a biota, a topografia local e o clima. Os resultados sugerem que fogo é um fator fundamental da ecologia desses ecossistemas úmidos porém sazonalmente secos. É impossível estabelecer um manejo adequado desses ecossistemas únicos e ameaçados sem uma compreensão detalhada do regime de fogo e do papel que incêndios desempenham na estruturação de comunidades bióticas.

Key words: Atlantic Forest; campos de altitude; *Chusquea* spp.; fire; páramo; southeast Brazil; tropical alpine; vegetation.

EARLY RESEARCHERS NOTED THE APPARENT IMPORTANCE OF FIRE in Neotropical highland vegetation (Goebel 1891, Fosberg 1944, Troll 1952, Ellenberg 1979), but only recently have real attempts been made to quantify the impacts of natural and anthropogenic burning on Central and South American mountain ecosystems (Williamson *et al.* 1986; Horn 1989, 1990, 1997; Balslev & Lutelly 1992; Hofstede 1995; Ramsay & Oxley 1996). Taken as a whole, this recent work suggests that fire in the

Andean and Central American Cordillera is far from an aberration (syntheses in Ellenberg 1979, Balslev & Lutelly 1992, Miehe & Miehe 1994), being rather an integral, if largely exogenous, factor in the generation and maintenance of the high mountain landscape as we know it. Data from other tropical alpine systems (*e.g.*, east Africa and New Guinea) support similar conclusions (Gillison 1970, Beck *et al.* 1986, Miehe & Miehe 1994).

In this contribution, I seek to extend our understanding of fire in the Neotropical highlands to the “campos de altitude” (high-altitude grasslands), a series of grass- and shrub-dominated formations restricted to isolated high peaks and plateaus of the

¹ Received 17 November 1998; revision accepted 6 June 2000.

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southeastern Brazilian Highlands (Fig. 1). Although found at lower altitudes, the campos de altitude show strong environmental, physiognomic, and floristic similarities to páramo and páramo-like vegetation of the Andes and other tropical alpine systems (Brade 1956, Troll 1959, Schnell 1971, Safford 1999a). The strength of these congruities would appear to require a similar association with fire, but until now no study has directly addressed the importance of fire to the existence and ecology of the Brazilian "pseudopáramos" (*sensu* Brown 1987).

During the winter months, wildfire constitutes the single greatest preoccupation of conservation unit managers in the Brazilian Highlands. Although natural ignition certainly occurs (Soares 1990), fire in southeast Brazil is primarily anthropogenic; indeed, none of the four national parks harboring campos de altitude have recorded a definite lightning-caused burn in the past several decades (J. M. de Andrade, M. B. Rondon, M. Pitombeira, and J. O. Vargas, pers. comm.). Conflagrations in the campos de altitude and neighboring montane forests result primarily from agricultural practices and land clearing (often illegal), but fireworks, increased backcountry use, and arson also contribute to what is perceived by both park staff and the public in general as an unnatural—and almost exclusively destructive—fire regime. Considering that management priorities and practices within the campos de altitude revolve to an enormous extent simply around fire and its impacts, it is imperative that we develop a solid scientific understanding of the phenomenon of fire in these diminutive systems and a scientifically based rationale for dealing with its consequences.

The present contribution offers the first quantitative analysis of the ecology of fire in the campos de altitude. As previous data are entirely lacking, the principal objective of this paper is to present preliminary data on postfire succession and diversity patterns, species responses to fire, rates of postfire recovery, and adaptations to fire in the flora of the campos de altitude. Effects of landscape heterogeneity on these fire-response variables are assessed by comparing results from slopes of different aspect and steepness. Finally, results are used to make comparisons between the campos de altitude and physiognomically similar vegetation in pyrophytic ecosystems of tropical South America and regions of Mediterranean climate, as well as to hypothesize the role fire has played, and continues to play, in the generation and maintenance of these "Brazilian páramos."

MATERIALS AND METHODS

STUDY SITES.—Sampling was carried out in two recently burned sites within the campos de altitude of the Serra dos Órgãos, Rio de Janeiro (a subrange of the Serra do Mar; 22°28'S, 43°03'W) and the Serra do Caparaó, Espírito Santo and Minas Gerais, Brazil (20°25'S, 41°48'W) (Figs. 1 and 2); both sites are located in national parks. The study sites were chosen due to their relative accessibility and because of the existence of reliable information regarding the dates and circumstances of fire ignition and the areal extent of vegetation burned.

Isolated occurrences of campos de altitude are found scattered among the highest eminences of three major mountain chains—the Serra do Mar, the Serra da Mantiqueira, and the Serra do Caparaó—stretching from treeline (2000–2200 m) to the tops of the highest peaks (2250–2890 m). Vegetation in the campos de altitude is physiognomically dominated by graminoids, especially tall-stemmed bunchgrasses and bamboos, and sclerophyllous shrubs. The most speciose families are (in approximate order) Asteraceae, Polypodiaceae s.l., Melastomataceae, Orchidaceae, Poaceae, Lamiaceae, Ericaceae, Cyperaceae, Lycopodiaceae, and Rubiaceae (Rizzini 1954, Brade 1956, Safford 1999a). Species endemism is pronounced (Martelli & Bandeira 1989; Safford 1999a, c) but biogeographic connections with both the equatorial and southern maritime Andes are strong at the generic level (Brade 1956, Safford 1999a).

The geologic substrate in the Serra dos Órgãos is Upper Proterozoic granite, while the Serra do Caparaó is underlaid by metamorphic rocks of Archean age (Machado Filho *et al.* 1983). Soils in both sites are often rocky, but deep organic profiles are more common throughout the more humid Serra dos Órgãos. Shallower, moderately lateritic Lithosols characterize much of the Serra do Caparaó, with deeper organic soils found mostly on south-facing slopes and at elevations above 2400 m. Long-term climatic data are unavailable for either site, but shorter-term measurements (Rizzini 1954) and interpolation from regional isohyetal maps suggest that annual rainfall in the campos de altitude of the Serra dos Órgãos typically exceeds 3000 mm, while amounts in the Serra do Caparaó probably fall between 1600 and 2000 mm. Average annual temperatures, estimated from measurements at soil depths greater than 0.75 m are *ca* 10.2°C at 2263 m in the Serra dos Órgãos, while in the Serra do Caparaó annual means are *ca* 10.5°C at 2400 m and 8.5°C at 2800 m.

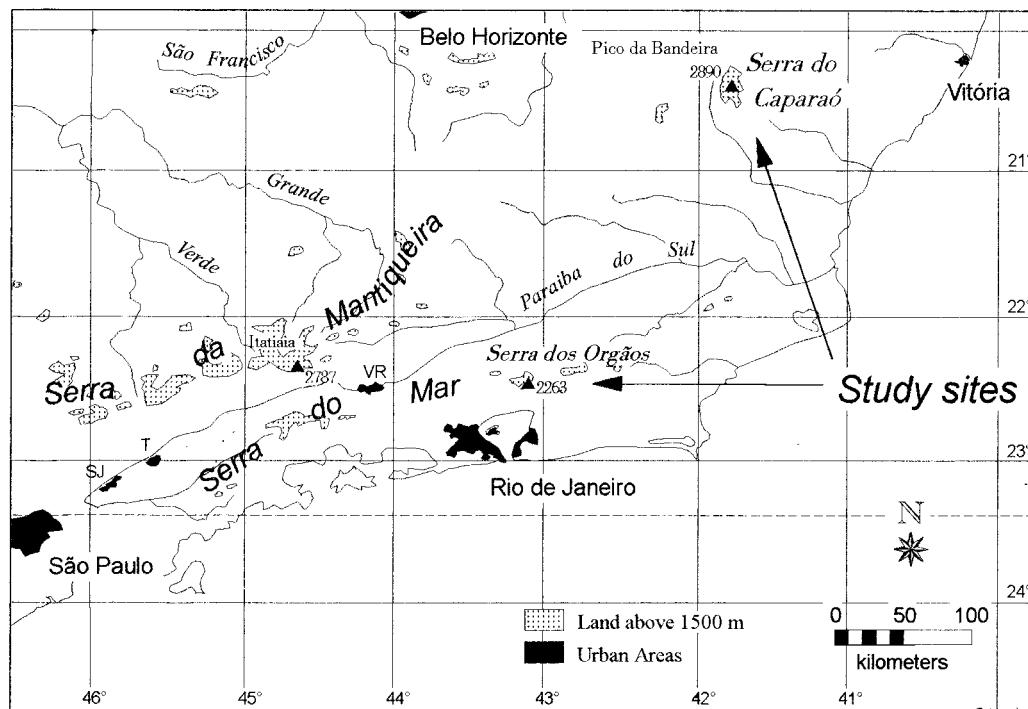


FIGURE 1. Major physiographic and hydrographic features of southeast Brazil with study sites indicated.

The sampled site in the Serra dos Órgãos (1.6 km west-southwest of Pedra do Sino) was burned in August 1996, apparently as the result of a backpacker's unintended fire; total area consumed by the blaze was *ca* 10 ha. The site sampled in the Serra do Caparaó, a collection of slopes defining the headwaters of the Rio José Pedro, constitutes part of a much larger burn, which consumed more than 7000 ha of upper montane forest and campos de altitude in October 1994.

Locale-specific fire frequencies at the two sites are difficult to ascertain. National park staff at both locations note that rarely a year passes without at least one fire in the campos de altitude (some years have multiple fires) but no formal records of fire occurrence are kept in either park: it is thus impossible to rigorously map the spatiotemporal fire mosaic. Examination of annual growth rings in burned specimens of *Vanillosmopsis erythropappa*, *Myrceugenia alpigena*, and *Escallonia* spp. yielded most-recent-fire ages of *ca* 15 years at the Serra dos Órgãos site and between 10 and 40 years at the more extensive Serra do Caparaó site. Before the creation of Caparaó National Park in 1961, fires were seasonally set in the campos de altitude by local ranchers and "carvoeiros" (coal merchants),

and grassy formations were heavily grazed by cattle (Pádua & Coimbra Filho 1979); today, large portions of campos and upper montane forests are considered "in recuperation" by park staff. Founded in 1939, the National Park of the Serra dos Órgãos is much older and active fire suppression has a much longer history there. Fire in the campos de altitude is not exclusively a post-Columbian phenomenon (Behling 1997a, b). Deep soil cores from both mountain ranges contain carbonized particles throughout the profile (Serra do Caparaó cores ^{14}C -dated to \leq 11,000 years B.P. and Serra dos Órgãos to \leq 12,000 years B.P.).

FIELD SAMPLING.—Sampling methodology was based on similar studies carried out in the physiognomically and climatically similar páramos of Costa Rica (Janzen 1973, Williamson *et al.* 1986, Horn 1989). In cool, high-altitude tropical environments, rates of organic decay are extremely slow; most woody stems killed by fire remain intact and identifiable for many years. By studying these postfire remains, it is possible to measure the composition, stature, and density of shrubs and trees in the prefire vegetation.

Belt transects and quadrat sampling were used

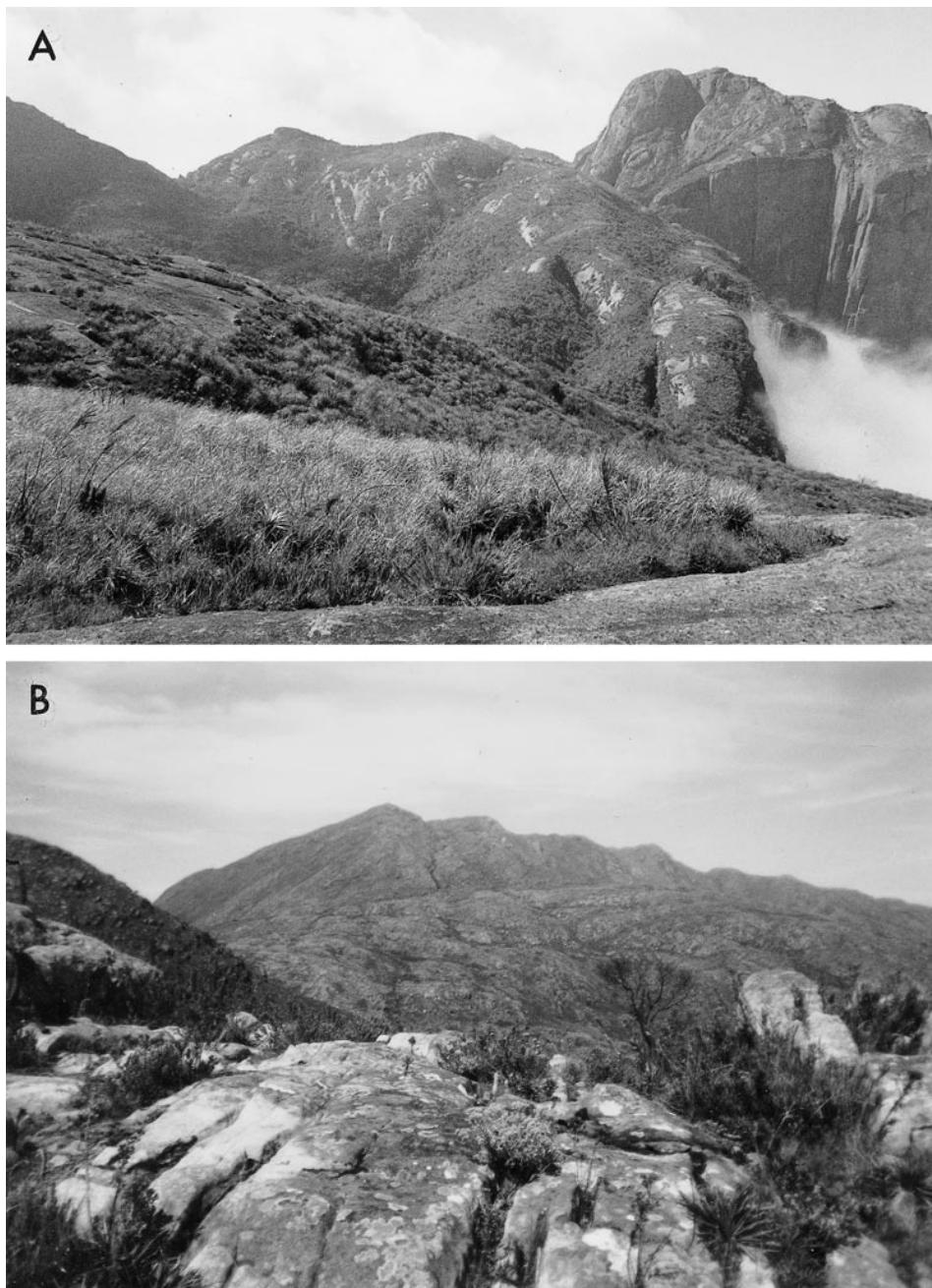


FIGURE 2. (A) Study site Serra dos Órgãos (2120 m elev.) Transect 3SDO courses the slope in the middle ground; fire-killed trees are dispersed throughout. Vegetation in the foreground is dominated by *Cortaderia modesta* and *Chusquea pinifolia*. The peak in the background is Pedra do Sino (2263 m). (B) Study site Serra do Caparaó (2550 m elev.). Photo was taken at the head of the slope sampled on transect 7CAP. Vegetation in the foreground dominated by *Chusquea pinifolia*, *Eryngium* sp., and *Lycnophora* sp. (center); the dead shrub is *Roupala rhombifolia*. Pico da Bandeira (at 2890 m, the highest point in eastern South America) is in the background.

to evaluate postfire vegetation recovery in both sites during September (Serra dos Órgãos) and October (Serra do Caparaó) of 1997. Effects of landscape heterogeneity on recovery were evaluated within each site by dispersing transects and associated quadrats among slopes of different steepness and aspect. In the Serra dos Órgãos (hereafter SDO), four transects were sampled on adjacent slopes of north, east, south, and west aspect, from slope base to ridgeline (2120 m elev.) along lines set perpendicularly to the strike of the slope; transect length averaged $57.4 \text{ m} \pm 19.1 \text{ SD}$. All transects coursed tall, grass-dominated vegetation with varying admixtures of shrubs; some small trees were present on the south-facing slope (transect 3SDO). In the Serra do Caparaó (CAP), seven transects were sampled, five between 2120 and 2280 m and two above 2500 m; again, all transects were set perpendicular to the strike of the slope and coursed from slope base to ridgeline. Transect length averaged $60.3 \text{ m} \pm 12.2 \text{ SD}$. At the lower altitudes, one transect was sampled at each major compass aspect, with one replication on an additional west-facing slope; the higher transects were located on north- and south-facing slopes. Sampled areas in CAP were more heterogeneous with respect to physical and biotic environment than in SDO, and unlike SDO, none of the transects were contiguous, all being at least 500 m distant from their nearest neighbor.

Along each transect, the following environmental variables were measured at 5 m intervals: altitude, slope aspect, slope steepness, and soil depth (the last estimated by hammering a 1.3 m length of iron rebar into the soil until further progress was impeded). All measurements were summed and averaged to give a mean value for each transect (Tables 1 and 2). A soil subsample was also taken every 5 m from a depth of 10 cm; all subsamples were combined to produce a bulk sample of the soil conditions along each transect. Potential annual solar radiation for each sampled transect was computed as a percentage of the maximum possible using tables of daily values of direct solar radiation by slope, aspect, and day given in Buffo *et al.* (1972), with the tables inverted to represent approximate southern hemisphere values.

Postfire shrub and tree cover (as well as the cover of any other taxa $>0.5 \text{ m}$ in height) was estimated using the line intercept method (Bauer 1943); plant cover within the "herb" layer ($\leq 0.5 \text{ m}$) was visually estimated using ten 1 m^2 quadrats placed at 5 m intervals on alternating sides of the transect line.

Shrub and tree density, pre- versus postfire height, and fire response category were assayed by identifying, examining, and measuring every live or dead woody plant 0.5 m or more in height within a 4 m wide belt centered on the line intercept transect. True prefire heights were somewhat underestimated, as fine stem termini are easily carbonized by fire or lost to wind afterward. Species identifications of fire-killed individuals were based on stem architecture, bark and wood characteristics, and other corroborative evidence (e.g., the presence of stem galls in *Rapanea ferruginea*). Plants were considered genets if more than 1 m separated them from their nearest conspecific. Each individual plant was assigned to a fire response category (1, fire killed; 2, basally resprouting after death of aboveground parts; 3, fire survivor [i.e., scorched, but alive]; or 4, postfire colonist [i.e., saplings with no sign of carbonization]), and when appropriate, the tallest (or in the case of the bamboos, the longest) live and fire-killed stems were both measured.

Areas sampled within belt transects ranged from 132.5 m^2 along transect 2SDO to 315 m^2 along transect 4CAP (Tables 1 and 2), with totals equaling ca 920 m^2 in SDO and 1680 m^2 in CAP.

Soil analyses were carried out in laboratories of the Herbário Guido Pabst, Carangola, Minas Gerais, Brazil, and the Department of Land, Air and Water Resources (LAWR), University of California, Davis, California. Soil moisture (percent by weight) was determined by gravimetric methods; pH was measured in a soil-solution ratio of 1 g soil:2 mL H₂O. Total C and total N were assayed with LAWR's Carlo-Erba combustion gas analyzer; values reported are percent by weight.

Statistics were carried out in STATA 4.0 (StataCorp 1995). Before analysis, data were tested for normality by the Shapiro-Wilks test; transformations were employed when appropriate. All percentage data were arcsine transformed.

Plots of species diversity patterns were generated using Hill's diversity function (Hill 1973, Ludwig & Reynolds 1988), which unifies some of the most commonly used diversity indices. Hill's function measures the "effective number of species" in a sample, with successively higher diversity numbers (A) increasing the function's weighting of abundant species; plots of Hill's function thus measure the degree to which proportional abundances are parceled among species. At $A = 0$, the function measures richness, the total number of species in the sample; at $A = 1$, the function measures e^{H'} (where H' is the Shannon-Wiener index), the number of "abundant" species in the sample; and

TABLE 1. Physical data, diversity measures, and postfire vegetation cover, Serra dos Orgãos.

| | Trans. 1 | Trans. 2 | Trans. 3 | Trans. 4 |
|--|---------------------|---------------------|---------------------|---------------------|
| Physical data | | | | |
| Aspect (°) | N 12 | W 248 | S 175 | E 83 |
| Slope (°) | 4 | 10 | 20 | 25 |
| Soil depth (m; \pm SE) | 0.17 (\pm 0.029) | 0.24 (\pm 0.034) | 0.72 (\pm 0.117) | 0.30 (\pm 0.027) |
| Soil moisture (% wt.) | 24.0 | 33.1 | 47.0 | 33.4 |
| C (% wt.) | 10.07 | 11.55 | 15.98 | 13.31 |
| N (% wt.) | 0.68 | 0.70 | 0.96 | 0.86 |
| pH (H ₂ O; 1:2) | 3.48 | 3.57 | 3.62 | 3.37 |
| % Max. radiation | 0.982 | 0.943 | 0.782 | 0.856 |
| Vegetation data | | | | |
| Area sampled (m ²) | 304.5 | 132.5 | 273.8 | 207.8 |
| Total species | 14 | 17 | 21 | 22 |
| λ (Simpson's index) | 0.639 | 0.562 | 0.687 | 0.568 |
| H' (Shannon-Wiener index) | 1.255 | 1.420 | 1.256 | 1.623 |
| H'/H' Max (evenness) | 0.330 | 0.347 | 0.286 | 0.359 |
| “Shrub” layer (height >0.5 m; % cover) | | | | |
| <i>Abatia americana</i> (Gardn.) Eichl. | | | | 0.3 |
| <i>Baccharis reticularia</i> DC. | + | + | 1.8 | 0.4 |
| <i>Blechnum imperiale</i> (Fée & Glaz.) Christ. | | + | 1.6 | 0.9 |
| <i>Chusquea pinifolia</i> Nees | 2.7 | 8.0 | 1.9 | 5.2 |
| <i>Cortaderia modesta</i> (Döll.) Hack. | 29.4 | 47.1 | 70.9 | 51.9 |
| <i>Escallonia organensis</i> Gardn. | 0.9 | 0.9 | + | 1.9 |
| <i>Maytenus cf. subalata</i> Reiss | | | + | + |
| <i>Myrsinopsis alpigena</i> (DC.) Landrum | + | + | | + |
| <i>Rapanea gardneriana</i> (DC.) Mez | | | + | 2.8 |
| <i>Symplocos densiflora</i> Brand | + | | + | + |
| <i>S. itatiae</i> Wawra | | + | | |
| <i>Tibouchina</i> sp. | | | + | |
| <i>Vanillosmopsis erythropappa</i> (DC.) S. Bip. | | | 0.9 | 0.5 |
| Total cover (%) | 33.1 | 55.9 | 77.1 | 63.8 |
| “Herb” layer (height ≤0.5 m; % cover)* | | | | |
| Bryophytes | 2.2 | 2.1 | x | |
| <i>Bulbostylis</i> sp. | 0.5 | x | | x |
| <i>Carex cf. brasiliensis</i> St. Hil. | | | 2.5 | 0.5 |
| <i>Chusquea pinifolia</i> Nees | 2.1 | 2.7 | | x |
| <i>Cortaderia modesta</i> (Döll.) Hack. | 8.8 | 7.7 | 2.6 | 2.4 |
| <i>Erigeron</i> sp. | 0.8 | x | | x |
| <i>Eryngium fluminense</i> Urban | 1.8 | 4.0 | 2.0 | 3.3 |
| <i>Galium</i> spp. | x | x | 0.7 | 0.8 |
| <i>Sisyrinchium</i> spp. | 0.5 | x | x | x |
| Other species <0.5% cover (no. spp.) | 0.5 (6) | 1.4 (7) | 1.6 (13) | 0.6 (6) |
| Total cover (%) | 13.8 | 12.4 | 7.6 | 5.7 |

Key: * for herb layer, only spp. with ≥0.5 percent cover on at least one transect are listed. + = not encountered on line transect but sampled within belt transect. x = cover <0.5 percent.

at $A = 2$, the function measures $1/\lambda$ (where λ is the Simpson index), the number of “very abundant” species in the sample. At $A = \infty$, only the single most abundant species would be taken into account.

Stepwise regressions on environmental parameters were carried out for a variety of dependent variables related to postfire recovery. Only results

of regressions for percent of woody plants killed are reported.

RESULTS

PHYSICAL DATA AND POSTFIRE VEGETATION.—Physical data, diversity measures, and postfire vegetation composition and cover from each of the 11 tran-

TABLE 2. Physical data, diversity measures, and postfire vegetation cover, Serra do Caparaó.

| | Trans. 1 | Trans. 2 | Trans. 3 | Trans. 4 | Trans. 5 | Trans. 6 | Trans. 7 |
|---|---------------|---------------|---------------|---------------|---------------|---------------|---------------|
| Physical data | | | | | | | |
| Aspect (°) | N 358 | W 276 | S 181 | S 171 | W 276 | N 358 | E 73 |
| Slope (°) | 20 | 25 | 19 | 30 | 24 | 27 | 27 |
| Altitude (m) | 2145 | 2240 | 2615 | 2170 | 2250 | 2530 | 2175 |
| Soil depth (m; ± SE) | 0.05 (±0.015) | 0.05 (±0.003) | 0.47 (±0.067) | 0.20 (±0.022) | 0.03 (±0.008) | 0.08 (±0.010) | 0.04 (±0.006) |
| Soil moisture (% wt.) | 3 | 19 | 60 | 38 | 6 | 30 | 6 |
| C (% wt.) | 7.77 | 7.65 | 15.15 | 14.54 | 10.20 | 13.72 | 3.20 |
| N (% wt.) | 0.44 | 0.43 | 1.00 | 0.90 | 0.61 | 0.80 | 0.20 |
| pH (H ₂ O; 1:2) | 5.64 | 5.33 | 5.62 | 5.03 | 5.95 | 5.23 | 5.40 |
| % Max. radiation | 0.978 | 0.856 | 0.791 | 0.697 | 0.862 | 0.957 | 0.900 |
| Vegetation data | | | | | | | |
| Area sampled (m ²) | 276.4 | 253.5 | 255.4 | 315.0 | 221.4 | 187.0 | 178.6 |
| Total species | 32 | 29 | 44 | 49 | 26 | 38 | 41 |
| λ (Simpson's index) | 0.149 | 0.212 | 0.103 | 0.088 | 0.199 | 0.093 | 0.090 |
| H' (Shannon-Wiener index) | 3.548 | 2.852 | 4.008 | 4.209 | 2.935 | 4.077 | 4.097 |
| H'/H' Max (evenness) | 0.716 | 0.587 | 0.734 | 0.750 | 0.624 | 0.783 | 0.770 |
| “Shrub” layer (height >0.5 m; % cover)* | | | | | | | |
| <i>Abatia americana</i> (Gardn.) Eichl. | 0.5 | 0.6 | | | | + | 1.3 |
| <i>Agarista eucalyptoides</i> (Cham. & Schl.) G. Don | 2.3 | | | | + | | 2.0 |
| <i>Axonopus</i> sp. | 2.9 | | | | | | |
| <i>Baccharis glazioui</i> Baker | | | 3.7 | 0.4 | | | |
| <i>B. platypoda</i> DC. | + | 0.6 | | 3.4 | + | 3.1 | 1.1 |
| <i>Berberis campos-portoi</i> Brade | | | + | | | | 1.3 |
| <i>Blechnum imperiale</i> (Fée & Glaz.) Christ. | | | 1.5 | 6.1 | | | |
| <i>Buddleja speciosissima</i> Taub. | | | 0.7 | | | | |
| <i>Chusquea baculifera</i> Silveira | | | 7.4 | | | + | |
| <i>C. pinifolia</i> Nees | 1.8 | 17.9 | 24.7 | | 0.3 | 4.9 | |
| <i>Croton migrans</i> Casar. | | | | 2.5 | | | |
| <i>Escallonia</i> sp. | | | 1.8 | 1.7 | | | |
| <i>Gomidesia kunthiana</i> Berg | + | | 1.2 | | + | + | |
| <i>Graphistylis</i> cf. <i>itatiaiae</i> (Dusén) B. Nord. | | | 0.9 | | | | 1.5 |
| <i>Hypsis asperrina</i> (Spreng.) Harley | 1.6 | | | 5.0 | | 1.3 | 2.2 |
| <i>Myrceugenia alpigena</i> (DC.) Landrum | 1.6 | + | | | + | 11.0 | 3.0 |
| <i>Ophryosporus</i> cf. <i>regnellii</i> Sch. Bip. ex Baker | | | | 1.1 | | | |
| <i>Pteridium aquilinum</i> (L.) Kuhn | | | | | | | 1.6 |
| <i>Rapanea ferruginea</i> (Ruiz & Pavón) Mez | 1.6 | + | | 2.4 | | + | + |
| <i>R. gardneriana</i> (DC.) Mez | | | 1.5 | | + | | |
| <i>Vanillosmopsis erythropappa</i> (DC.) S. Bip. | + | | | | | | 2.5 |

TABLE 2. *Continued.*

| | Trans. 1 | Trans. 2 | Trans. 3 | Trans. 4 | Trans. 5 | Trans. 6 | Trans. 7 |
|---|----------|----------|-----------|-----------|----------|-----------|-----------|
| <i>Vernonia</i> sp. | 1.4 | | | 1.1 | | | |
| Other spp. <0.5% cover (no. spp.) | 0.2 (1) | 0.4 (3) | 1.4 (8) | 2.3 (12) | 0.0 (0) | 2.4 (6) | 0.5 (9) |
| Total cover (%) | 13.9 | 19.4 | 46.1 | 28.8 | 0.3 | 26.2 | 13.7 |
| “Herb” layer (height <0.5 m; % cover)* | | | | | | | |
| <i>Abatia americana</i> (Gardn.) Eichler. | 0.5 | 3.1 | | | | | |
| <i>Andropogon</i> sp. | 3.3 | 18.6 | | 1.8 | 13.8 | 2.1 | 1.8 |
| <i>Axonopus</i> sp. | 13.2 | | | | 11.4 | | 12.7 |
| <i>Baccharis platypoda</i> DC. | | 1.2 | | x | x | x | x |
| <i>Briza</i> sp. | | x | 7.9 | 4.5 | | 3.1 | |
| Bryophytes | x | | 9.6 | 5.6 | 0.7 | 3.6 | x |
| <i>Bulbostylis</i> sp. | 2.8 | 6.0 | | 3.6 | 3.0 | x | 5.0 |
| <i>Carex</i> cf. <i>brasiliensis</i> St. Hil. | | | 2.5 | 1.4 | | | |
| <i>Chusquea baculifera</i> Silveira | | | 7.4 | | | x | |
| <i>C. pinifolia</i> Nees | 2.5 | 4.7 | 1.1 | x | | 3.6 | |
| <i>Croton chloroleucus</i> Müll. Arg. | | | x | | x | 1.2 | |
| <i>C. migrans</i> Casar. | x | 1.0 | x | 3.5 | x | x | |
| <i>Cunila</i> cf. <i>galiooides</i> Benth. | | | 2.3 | | | | |
| <i>Eryngium</i> sp. | 4.9 | 7.2 | 6.2 | 0.8 | 1.3 | 2.4 | |
| <i>Galium</i> spp. | x | | 2.3 | 2.5 | | | |
| <i>Graphistylis</i> cf. <i>itatiaiae</i> (Dusén) B. Nord. | | | 1.5 | | | 1.1 | |
| <i>Lucilia lycopodioides</i> (Less.) S. E. Freire | 1.4 | | | | 7.0 | 0.6 | 3.3 |
| <i>Panicum</i> spp. | | x | | 6.3 | | 4.3 | 4.0 |
| <i>Paspalum</i> spp. | 1.6 | 0.6 | | | x | | 3.2 |
| <i>Phyllanthus pinifolius</i> Baill | | | 3.3 | | | | |
| <i>Plantago australis</i> L. | | | 2.7 | | | | |
| <i>Sisyrinchium</i> spp. | 0.1 | | 1.1 | | | | |
| <i>Stenophalium chionaeum</i> (DC.) A. Anderb. | | x | | | 1.2 | x | |
| <i>Xyris</i> cf. <i>augusto-coburgi</i> Szysl. | | | | | | | 1.3 |
| Other species <1.0% cover (no. spp.) | 3.7 (16) | 8.2 (15) | 11.2 (21) | 27.3 (26) | 3.0 (12) | 13.6 (19) | 18.4 (16) |
| Total cover (%) | 30.9 | 50.0 | 51.1 | 53.5 | 33.7 | 27.4 | 42.1 |

Key: * for “shrub” layer, only spp. with ≥ 0.5 percent cover on at least one transect are listed; for “herb” layer, only spp. with ≥ 1.0 percent cover are listed. + = not encountered on line transect but sampled within belt transect. x = cover <1.0 percent.

sects are given in Tables 1 and 2. For any given aspect, soil depth and soil total C and total N are usually higher in SDO. Soil moisture is also higher in SDO (time to last rain 6 d in SDO, 10 d in CAP); pH values are also lower in SDO (Tables 1 and 2). Cover is differently distributed in the two systems, with the "average" transect in SDO showing *ca* 60 percent cover in the shrub layer (due principally to *Cortaderia modesta*) and only *ca* 10 percent in the lower stratum; while in CAP, the values are 20 and 40 percent, respectively (Tables 1 and 2).

Although 19 species are common to SDO and CAP, the proportion in common is higher at SDO (19/27 = 70.4%) than at CAP (19/92 = 20.7%), and species richness and evenness are very different. Using Hill's (1973) diversity numbers, three coherent groups of transects can be identified (Fig. 3). The four SDO transects make up the basal group, characterized by relatively low species richness and a high degree of dominance by only a few species (two "abundant" species [at $A = 1$]: *Chusquea pinifolia* and *Cortaderia modesta*, and one "very abundant" species [at $A = 2$]: *C. modesta*). The intermediate group comprises transects 1, 2, and 5 in CAP (*i.e.*, lower altitude north and west-facing slopes (Table 2). South- and east-facing slopes in CAP, as well as the high-altitude north slope, make up the upper group, which is characterized by high species richness as well as an exaggerated number of abundant and very abundant species (*i.e.*, relatively high evenness). Differences between SDO and CAP in Figure 3 are due primarily to the presence of *C. modesta* in the former and its absence in the latter. This huge tussock grass, typically 2.0–2.5 m tall in undisturbed stands, dominates every transect in SDO (Table 1).

FIRE RESPONSE.—Table 3 shows the fire responses of all shrubs and trees with at least eight occurrences in either of the two sites. At both sites, burning was nearly complete, with very few aboveground stems surviving the fires. The only taxa to deviate significantly from this pattern were two species shared with areas of montane cerrado in the Minas Gerais interior: *Agarista eucalyptoides* (Eriaceae) and *V. erythropappa* (Asteraceae), both of which showed *ca* 40 percent aboveground survival in CAP. *Agarista eucalyptoides* is a tortuously stemmed 1–3 m tall shrub, while *V. erythropappa* is a medium-sized tree (usually 5–10 m tall); both plants have thick, corky bark, particularly *A. eucalyptoides*, with a habit typical of many woody plants of the cerrado.

At SDO, relatively few of the examined plants (5.3%) were killed outright in the 1995 fire (Table 3). By far, the most common fire response was basal resprouting (93.5% of examined plants), with only 1.1 percent surviving outright. No postfire colonists (woody species) were observed on any of the four transects. At CAP, fire responses were more heterogeneous among species, as evidenced by the χ^2 test for independence (carried out on the fire response distributions of those taxa with $N \geq 20$; "survived" category excluded) reported in Table 3. The overall proportion of plants killed by fire was higher in CAP than in SDO (0.22 ± 0.14 SD vs. 0.06 ± 0.03 ; $t_9 = 2.81$, $P \leq 0.05$). The coefficient of variation (CV) for survival across transects was also higher in CAP than in SDO ($CV_{CAP} = 0.17$ vs. $CV_{SDO} = 0.03$), with transects 4 and 5CAP showing elevated rates of fire mortality (45 and 35%, respectively, vs. $11.4\% \pm 2.4$ SD for the other five transects). Although more plants survived the fire intact in CAP than in SDO (3.2 vs. 1.1%), this difference was not significant. Only two taxa made up the bulk of either killed (*Croton migrans* and *R. ferruginea*) or surviving (*A. eucalyptoides* and *V. erythropappa*) plants in CAP.

Stepwise multiple regression was used to determine which of the measured environmental variables best predicted the percent of woody plants killed on the 11 sampled transects. With both sites pooled, the combination of percent of maximum solar radiation ("radiation") and soil depth best predicted percent killed, with soil depth directly explaining 22.3 percent of the variation in y , and radiation, 14.3 percent (Table 4). Within CAP, the best predictors were radiation (directly explaining 37.6% of the variation in y), soil C and N (4.8%), and soil moisture (0.8%; Table 4).

Relationships between plant height and fire response were investigated by grouping woody plants at each site by size class (0–1 m tall, >1 m to 2 m, and >2 m) and fire response category (results not shown). The overall ratio of killed vs survived did not differ significantly among size classes in either site (for all comparisons, $P(t_{adj}) \geq 0.10$); however, there was significant heterogeneity in size class response across transects (χ^2 tests: all $P \leq 0.01$), with slightly higher survival of small plants on moister slopes in both sites.

CHANGES IN SPECIES COMPOSITION.—Due to varying rates of mortality and seedling establishment (Table 3), postfire densities of bamboos and woody dicots were often different than prefire densities, with the magnitude of such differences dependent on the

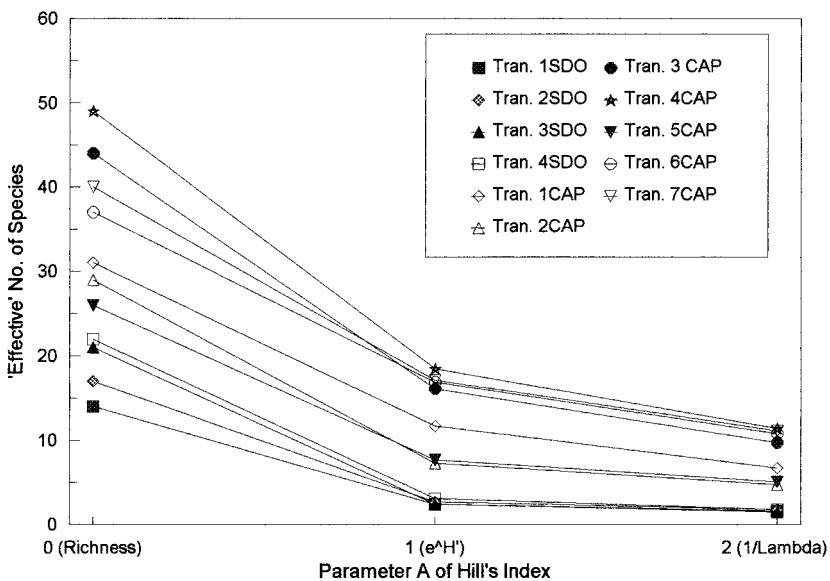


FIGURE 3. Plot of Hill's "effective" number of species for the 11 sampled transects versus the parameter A . At $A = 0$, the y-axis measures species richness; at $A = 1$, the y-axis measures the number of "abundant" species; at $A = 2$, the y-axis measures the number of "very abundant" species. SDO = Serra dos Órgãos; CAP = Caparaó.

species, site, and transect in question (Fig. 4). Slight declines in density were common among most shrubby species in SDO, but, overall, losses were negligible. Shifts in density were most pronounced in CAP, where fire response distributions were more heterogeneous among species (Table 3). Two species of shrubs (*C. migrans* and *R. ferruginea*) suffered high mortality during the 1994 fire (96 and 32%, respectively), with a third (*Baccharis platyptoda*) losing ca 12 percent of its prefire population. The latter species has been particularly successful in regaining and even exceeding prefire densities, especially on the upper parts of moist slopes like the south-facing slope sampled on transect 4CAP. This same transect is one of only two locations where *R. ferruginea* has been able to recoup fire losses, as well as the only site where *C. migrans* densities have rebounded at all (Fig. 4). The bamboo *Chusquea pinifolia*, the most common woody species at both sites, suffered practically no losses due to either fire.

In Figure 5, fire-mediated changes in diversity patterns of woody species are plotted by transect as a function of Hill's diversity numbers, with the plotted values representing the difference between the post- and prefire values (computed using species densities, *not* cover) for each transect. Differences in A_0 represent species losses due to fire; dif-

ferences in A_1 (e^H) and A_2 ($1/\lambda$) represent fire-caused changes in relative species abundances, with A_2 stressing changes in the more abundant species. The woody plants along transects 1, 3, and 4 in SDO showed very similar response patterns to fire: no species were lost and distributions of relative abundance remained remarkably stable; transect 2SDO lost one species (*M. alpigena*) and hence had relative abundances less evenly distributed among taxa; but the slope of the line between A_1 and A_2 is analogous to those of the other transects, hinting at otherwise similar fire responses among the surviving woody plants.

The situation in CAP is very different, with divergent values characterizing the various transects (Fig. 5). Transect 2 lost one species (*C. migrans*) while transect 7 gained one (*Galactia speciosa*); yet both ultimately converge on zero with respect to differences in relative abundances of common species (A_2). The transects that show the greatest changes in abundances of dominant species are numbers 5 and, especially, 4. Three years after fire, the woody vegetation along transect 5 is much less "even" with respect to species abundances: even though the most common species (*B. platyptoda*) lost ca 10 percent of its original population to fire, the second most common plant (*C. migrans*) was nearly wiped out (losing 97% of prefire individu-

TABLE 3. Fire responses of shrubs and trees, Serra dos Orgãos (A) and Serra do Caparaó (B).

| Species | Response category (%) | | | |
|--|-----------------------|------------|----------|-------------------|
| | Killed | Resprouted | Survived | Postfire colonist |
| A. Serra dos Orgãos | | | | |
| <i>Baccharis reticularia</i> | 12.5 (6) | 87.5 (42) | 0 | 0 |
| <i>Chusquea pinifolia</i> | 4.8 (4) | 95.2 (79) | 0 | 0 |
| <i>Escallonia organensis</i> | 3.8 (1) | 88.5 (23) | 7.7 (2) | 0 |
| <i>Myrceugenia alpigena</i> | 7.7 (1) | 92.3 (12) | 0 | 0 |
| <i>Rapanea gardneriana</i> | 8 (2) | 88 (22) | 4 (1) | 0 |
| <i>Symplocos densiflora</i> | 0 | 100 (8) | 0 | 0 |
| <i>Vanillosmopsis erythropappa</i> | 0 | 100 (15) | 0 | 0 |
| χ^2 invalid | | | | |
| % Totals (incl. other taxa) | 5.3 (14) | 93.5 (245) | 1.1 (3) | 0 |
| B. Serra do Caparaó | | | | |
| <i>Agarista eucalyptoides</i> | 4.3 (1) | 56.5 (13) | 39.1 (9) | 0 |
| <i>Baccharis platypoda</i> | 9.0 (8) | 76.4 (68) | 0 | 14.6 (13) |
| <i>Chusquea pinifolia</i> | 0 | 100 (101) | 0 | 0 |
| <i>Croton migrans</i> | 74.2 (89) | 2.5 (3) | 0 | 23.3 (28) |
| <i>Myrceugenia alpigena</i> | 6.6 (4) | 91.8 (56) | 1.6 (1) | 0 |
| <i>Rapanea ferruginea</i> | 28.2 (20) | 59.2 (42) | 0 | 12.7 (9) |
| χ^2 (categories 1, 2, 4) = 276.89, $P < 0.000001$, df = 10 | | | | |
| <i>Abatia americana</i> | 0 | 85.7 (12) | 7.1 (1) | 7.1 (1) |
| <i>Baccharis glazioui</i> | 0 | 100 (10) | 0 | 0 |
| <i>Chusquea baculifera</i> | 0 | 100 (11) | 0 | 0 |
| <i>Escallonia</i> sp. | 0 | 100 (11) | 0 | 0 |
| <i>Gomidesia kunthiana</i> | 0 | 100 (14) | 0 | 0 |
| <i>Hyptis asperrima</i> | 0 | 100 (15) | 0 | 0 |
| cf. <i>Koanaphyllum baccharifolium</i> | 18.2 (2) | 63.6 (7) | 0 | 18.2 (2) |
| <i>Rapanea gardneriana</i> | 30 (3) | 70 (7) | 0 | 0 |
| <i>Roupala rhombifolia</i> | 12.5 (2) | 81.3 (13) | 6.3 (1) | 0 |
| <i>Symplocos densiflora</i> | 42.9 (3) | 57.1 (4) | 0 | 0 |
| <i>Vanillosmopsis erythropappa</i> | 0 | 54.6 (6) | 45.4 (5) | 0 |
| % Totals (incl. other taxa) | 20.0 (136) | 67.7 (461) | 3.2 (22) | 9.1 (62) |

als). Transect 4 coursed the shrubby edges of a previously forested, south-facing slope, where postfire recruitment of shrubby species has been especially rapid. In this environment, the number of "abundant" species has increased (*i.e.*, the density of

woody vegetation is more evenly distributed among species), due principally to 40 percent losses in the *C. migrans* population and accelerated recruitment of heliophilic pioneers like *R. ferruginea*, *B. platypoda*, and *Vernonia* sp., all of which have already

TABLE 4. Summary statistics for multiple regressions of percent (square-root transformed) of woody plants killed vs. environmental variables. Soil depth was also square-root transformed.

| N | F | P | R ² (adj.) | Variable | Coeff. | t | P |
|-----------------------|-------|------|-----------------------|---------------|--------|------|-------|
| (A) Both sites | | | | | | | |
| 11 | 8.68 | 0.01 | 0.827 (0.684) | intercept | 1.74 | | |
| | | | | soil depth | -0.58 | 3.70 | 0.006 |
| | | | | radiation | -1.32 | 3.45 | 0.009 |
| (B) CAP only | | | | | | | |
| 7 | 30.16 | 0.01 | 0.984 (0.968) | intercept | 1.78 | | |
| | | | | radiation | -1.65 | 8.08 | 0.004 |
| | | | | soil moisture | -1.04 | 7.38 | 0.005 |
| | | | | %C + %N | 0.03 | 4.88 | 0.016 |

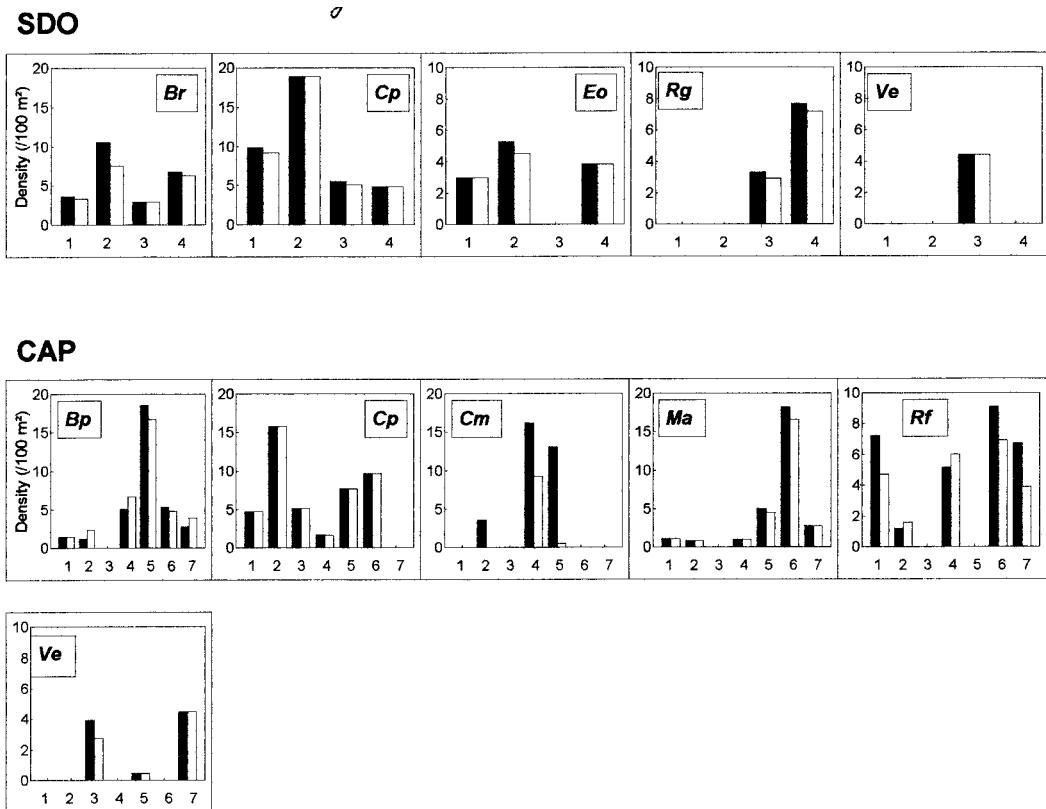


FIGURE 4. Pre- (black) and postfire (white) densities of important woody species (including bamboo) in the two study sites. Numbers along the horizontal axes represent transect numbers. Br = *Baccharis reticularia*, Bp = *B. platypoda*, Cm = *Croton migrans*, Cp = *Chusquea pinifolia*, Eo = *Escallonia organensis*, Ma = *Myrceugenia alpigena*, Rf = *Rapanea ferruginea*, Rg = *Rapanea gardneriana*, and Ve = *Vanillosmopsis erythropappa*.

exceeded prefire population densities (by between 19 and 31%).

POSTFIRE RECOVERY.—For all species pooled, mean pre- and postfire heights and percent recovery of prefire height varied significantly across transects (Fig. 6). Prefire heights were tallest on south-facing slopes in both sites (3SDO and 3 and 4CAP), but the distribution of postfire heights was variable. Percent recovery tended to be low for slopes with relatively tall prefire vegetation but was not necessarily high on slopes with very low prefire vegetation; rather, the greatest amounts of recovery in each site were on “mesic” west-facing slopes (transects 2SDO and 2CAP). Whereas south-facing slopes in CAP showed no significant differences in percent recovery from other local transects (except 2CAP), percent recovery on south-facing 3SDO was least at the site. The extremely rapid recovery of *C. modesta* on this slope may herald a shift to-

ward greater domination by grass in what probably was originally forest.

Within SDO, postfire heights and recovery rates were lowest for *Baccharis reticularia*, while postfire heights were typically highest in *C. pinifolia*; the highest percent recovery was measured for *Escallonia organensis* (Fig. 7). The fact that the recovery rate of *B. reticularia* was lowest on transect 2SDO, where average recovery of other shrub and bamboo species tended to be highest (Fig. 7), suggests that over time, given sufficiently frequent fire, this species may be eliminated from this and similar habitats in SDO. *Vanillosmopsis erythropappa* and *Rapanea gardneriana*, both trees, also exhibited relatively low rates of postfire recovery (Fig. 7). In general, postfire height and percent recovery of individual species appear to be sensitive to environmental and/or biotic variations associated with different slopes and aspects.

At CAP, *C. pinifolia* always exhibited the great-

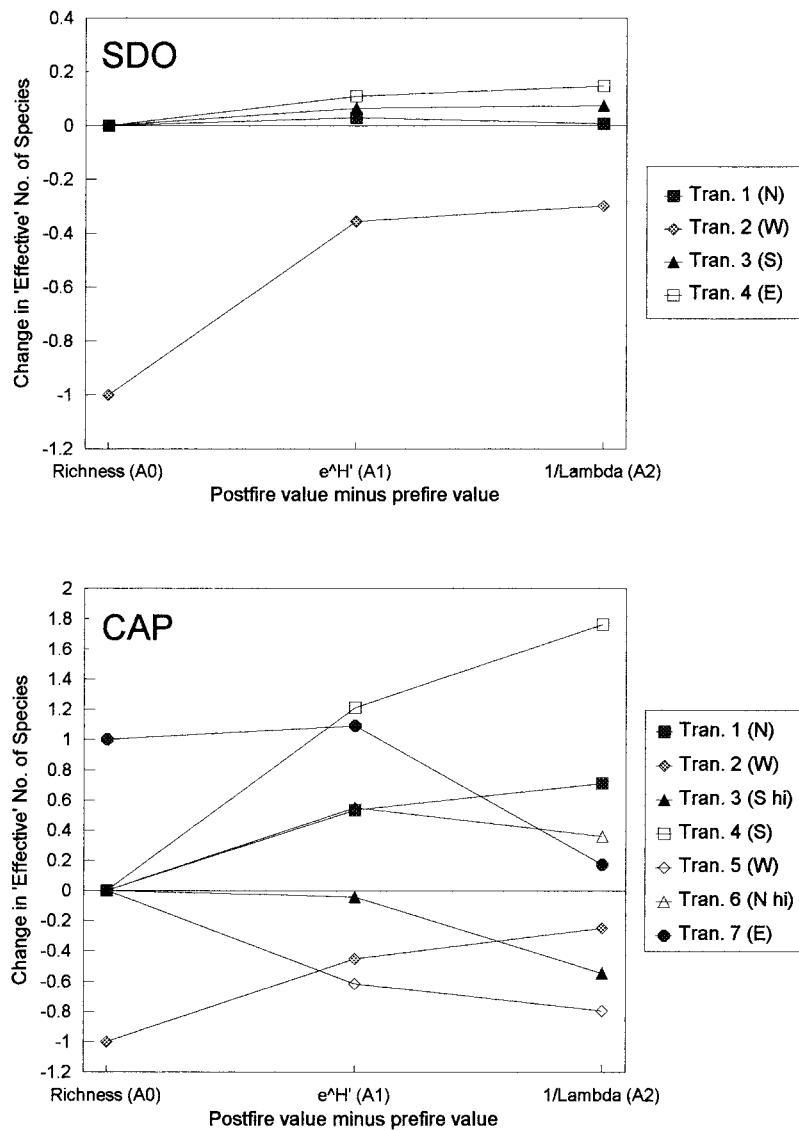


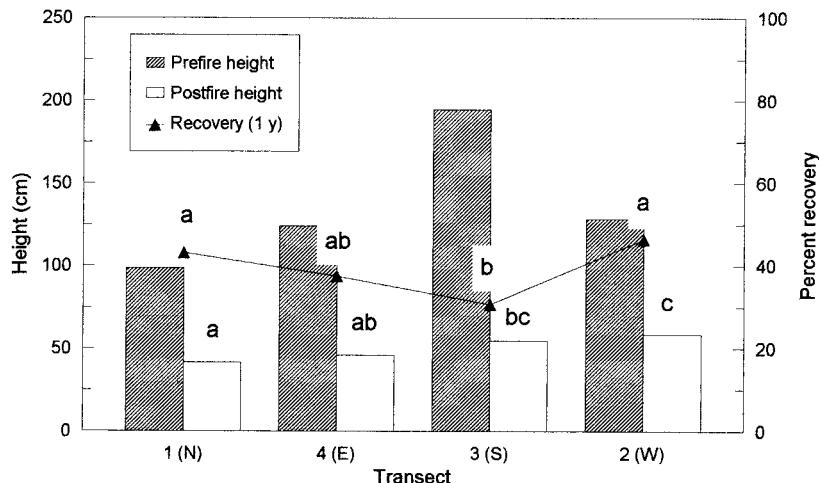
FIGURE 5. Fire-mediated changes in the "effective" number of species for Hill's diversity numbers ($A = 0-2$) for all woody dicot and bamboo species (by transect and site). Values for A are as in Figure 3.

est postfire height (not shown) as well as the most complete recovery of prefire height, reaching nearly 95 percent of its original stature on transect 2CAP in the three years since fire (Fig. 7). For both *C. pinifolia* and *B. platypoda*, rates of postfire growth were extremely sensitive to environmental differences between transects; in the former, postfire heights varied by nearly three-fold. For these species, however, environmental differences seem to have little or no effect on recovery of prefire height: variation in percent recovery across transects was

nonsignificant in *B. platypoda* and only marginally significant in *C. pinifolia* (Fig. 7). The situation for *R. ferruginea*, another heliophilic pioneer, was different: percent recovery varied by nearly 100 percent between lower, more mesic slopes (2 and 4 CAP) and higher or more xeric slopes (1 and 6CAP; Fig. 7).

Linear regressions were fitted to postfire versus prefire heights of four woody species common to both sites (not shown). For each of the analyzed species, older/larger plants exhibited more vigorous

SDO



CAP

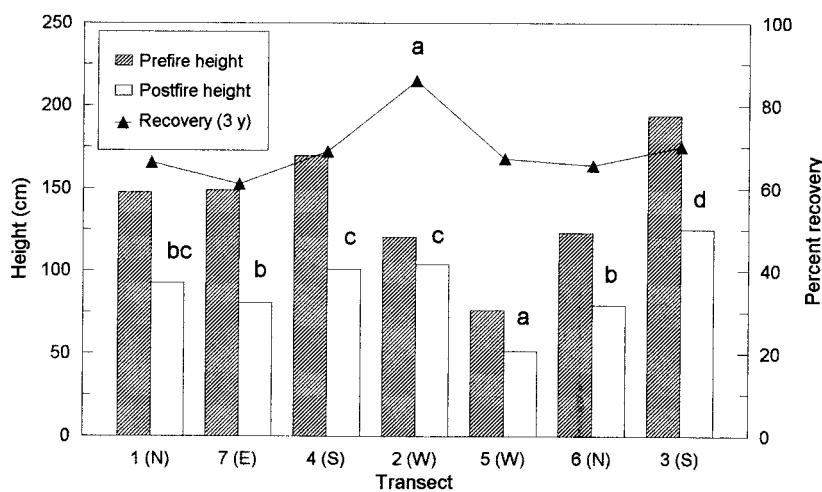


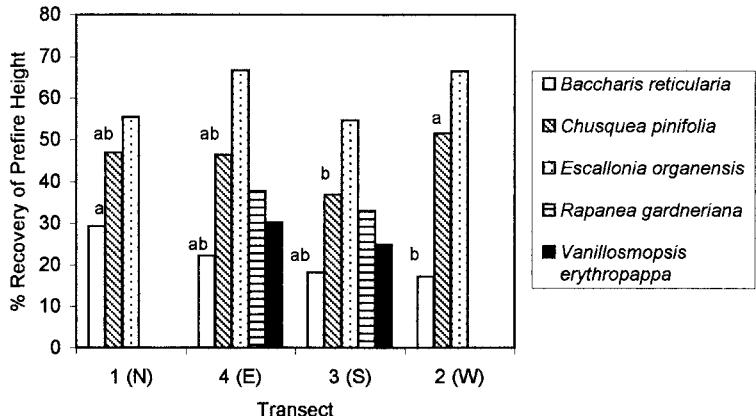
FIGURE 6. Comparisons of pre- and postfire height (by transect and site) for all woody dicot and bamboo species pooled. Within sites, transects are listed by aspect in a clockwise direction beginning with north; in Caparaó (CAP), the high altitude transects (6 and 3) are listed last. Values for postfire height and percent recovery denoted by different letters are significantly different at $P < 0.05$ (Tukey test); differences in prefire heights were not statistically tested.

postfire growth than their smaller/younger conspecifics, presumably because their larger root masses store more reserves to support such growth (Gill 1981, Whelan 1995, Bond & van Wilgen 1996). Larger individuals of *C. pinifolia* and *M. alpigena* enjoyed less of an advantage in SDO than in CAP. This may have been due to intrinsic differences in resource availability, differences in elapsed time since disturbance, or perhaps competitive effects of *C. modesta* in the former.

DISCUSSION

Pyrogenic mortality is rare among woody plants in the campos de altitude, with most species resprouting from underground buds after crown loss. Such “obligate sprouters” (Keeley & Zedler 1978) are species in which recruitment does not depend on fire, but instead possess strategically protected bud primordia that allow for persistence through all but the most severe fires (Bond & van Wilgen 1996).

SDO



CAP

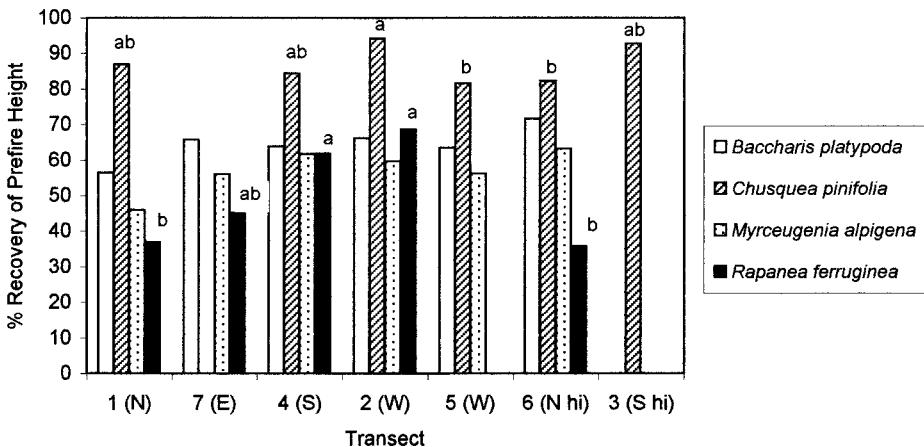


FIGURE 7. Comparisons of percent recovery of prefire height for important individual species on those transects in which each species had at least five occurrences. Significant differences across transects were shown by *Baccharis reticularia* and *Chusquea pinifolia* in SDO and by *C. pinifolia* and *Rapanea ferruginea* in CAP. Values denoted by different letters are significantly different at $P < 0.05$ (Tukey test).

Non-riparian taxa with biology that does not allow for rapid postfire sprouting were presumably driven from these environments long ago. In the campos de altitude, obligate sprouters typically produce nuts or fleshy fruits within one to three years of fire, and their dispersal tends to be zootrophic (mostly avian; Safford 1999c). For these taxa, postfire recruitment from seed appears to be an exceptionally rare event.

Few species in the campos of Caparaó appear to be “facultative sprouters” (Keeley & Zedler 1978), i.e., plants that reproduce from both sprouts and seeds in the postfire environment. *Baccharis*

platypoda and *R. ferruginea* fit loosely in this category (Table 3), although, at least for *R. ferruginea*, it is unlikely that any of the sampled seedlings actually germinated from a fire-surviving seed pool. The fleshy drupes of this species are primarily bird-dispersed, and in fact, most *R. ferruginea* seedlings were found in relatively close proximity to forest remnants. Given the anemochorous nature of dispersal in *B. platypoda*, many of the seedlings of this species probably owe their origins to nearby postfire sprouters, or even to distant populations.

Croton migrans and *C. chloroleucus* are the only woody species sampled in this study in which the

primary mode of postfire regeneration appears to be by seed. "Obligate seeders" (Keeley & Zedler 1978) tend to be killed by fire; their postfire recruitment is effected by the germination of a dormant seed pool. Within the tropics and subtropics, species of *Croton* are characteristic members of secondary vegetation (Webster 1993), but, as with *B. platyptoda*, it is difficult to know whether postfire recruitment in these particular *Croton* spp. stems at all from a long-term soil seed bank or whether it is purely a function of distance to surviving populations. Elucidation of seed bank dynamics in the campos de altitude is needed.

Members of the Poaceae seem especially well-adapted to the repeated occurrence of fire in the campos de altitude; they may owe their present dominance as much to the fire regime as to climatic or edaphic conditions. The prevalence of short-stemmed, adventive, often xeric grasses in the lower campos of Caparaó and other sites is most probably the result of frequent burning in what was originally upper montane forest. Many members of the genera *Andropogon*, *Aristida*, *Axonopus*, and *Paspalum* belong in this category.

In the higher and more humid campos de altitude, two grass taxa are typically both physiognomic and ecological dominants (Brade 1956, Segadas-Vianna 1965, Martinelli & Bandeira 1989, Safford 1999a): bamboos of the genus *Chusquea* and the giant tussock grass *C. modesta*. These two grasses probably best typify the largely beneficial relationship that the Poaceae have with fire in the campos de altitude. The clump-forming bamboo *C. pinifolia* exhibited the fastest postfire growth of all "woody" taxa in both sites. It was also much less likely to be killed by fire than all but a few of the dicotyledonous species (Table 3). Limited data from *Chusquea baculifera* in Caparaó (and other bamboo species in other campos) show similar response patterns. Postfire densities of *C. pinifolia* (and *C. baculifera*) were in most cases unchanged from prefire densities (Fig. 4), putting the species in a unique position to dominate postfire communities through both space and resource preemption.

J. Keeley and W. J. Bond (pers. comm.) have recently speculated that bamboos in general have evolved tolerance to fire. Bamboos accumulate large amounts of highly flammable dead biomass, and wildfire fueled by this litter kills competing shrubs and trees. Keeley and Bond's hypothesis is based on the well-known mast flowering phenomenon observed in many bamboo species (Janzen 1976), the subsequent occurrence of fire, and sat-

uration of the postfire environment with seedlings; however, the absolute lack of *Chusquea* seedlings in this study, observations in other campos de altitude (L. S. Sarahyba, pers. comm.), and data from the equatorial Andes and Costa Rica (Horn 1989), suggest that many high altitude populations of *Chusquea* may be, if not functionally sterile, at least largely unable to recruit from seed, even after fire. The probability of seed-set aside, spotty, nongregarious flowering occurs with regularity in both the campos de altitude and páramos and often seems to have little, if any, relationship to fire events. Furthermore, data from this study show no significant correlation between postfire growth or percent recovery of *C. pinifolia* and postfire cover or percent mortality of other woody taxa. Finally, in the campos de altitude (and páramos), biomass accumulation by bamboos, although rapid in comparison to other (non-graminoid) taxa, seems insufficiently pronounced to play any significant role in fire promotion; fires simply occur with too great a frequency for this to be the case.

The giant tussock grass *C. modesta* also seems well-adapted to the present fire regime. The dense tussocks of this species provide protection and insulation from high temperatures and internal physical damage from fire. This is due to high thermal mass of densely packed leaf bases in the tussock center and also to the ability of this grassy "sponge" to retain free water many days after the last rainfall.

It is difficult to determine whether the life-form of *C. modesta* represents an adaptation to fire or to some other selective force(s) that only serendipitously provides it with protection from fire. This seems to be the case with many "fire-adapted" taxa in the cold tropics (Lægaard 1992), and indeed, with many plants worldwide (Vogl 1974, Ferri 1980, Bond & van Wilgen 1996). *Cortaderia modesta* does well in seasonally flooded areas, where its stature may allow development of permanently oxygenated roots within the tussock center (Nishikawa 1990); it also dominates closed basins, where nighttime pooling of descending cold air leads to frequent frost during the dry season. In addition, *Cortaderia* species in general are highly invasive. They are typically found as postfire pioneers throughout the Neotropical highlands (Lægaard 1992, Verweij & Budde 1992). A few species, including *C. modesta*, have evolved postfire flowering responses (Brade 1956, Young & Kimerer 1994). Invasive taxa that possess life-forms well adapted to cold, fire, high humidity, and seasonal drought will likely thrive on any tropical mountaintop they can get to. This is certainly the

case for *C. modesta*, which is a (co)dominant species in most of the campos de altitude (Rizzini 1979). The absence of *Cortaderia* in Caparaó is puzzling and begs a sound explanation.

In the Serra dos Órgãos (and in other campos de altitude), the presence and local abundance of *C. modesta* is closely linked to a number of key community characteristics, including the life-form spectrum (*i.e.*, reduced cover and density of woody dicots), fire recovery patterns, community composition, and species diversity. Tussock size of *C. modesta* and fuel loads suggest fires within *Cortaderia* grassland are probably so intense as to preclude the local survival of many woody species. Because most woody plants in the campos de altitude rely on root reserves to regenerate after fire, frequent fires may restrict them to less flammable slopes where fire frequencies are low enough to allow reasonable levels of biomass accumulation (Bond & van Wilgen 1996). In sites less than optimal for woody plant growth (*e.g.*, deep, moist organic clays and marshes), sufficiently frequent fires may stimulate growth of *Cortaderia* and other tall, sod-forming and rhizomatous grasses and sedges to such an extent that they ultimately eliminate all but the hardest of woody competitors (Vogl 1974). Given the dense shade and heavy litter generated by mature stands of *C. modesta*, the existence and abundance of many herbaceous species in *Cortaderia* grassland may depend on fire, with the spatial and temporal scope of opportunities to germinate/sprout and subsequently mature largely dependent on the fire mosaic (Grubb 1977, Bond & van Wilgen 1996).

Adaptations to burning in the campos de altitude are not restricted to the grass family. As in Andean grass páramo (Lægaard 1992), most plant taxa in the campos de altitude are able to survive at least occasional fire. Many woody plants regenerate from root structures, including members of the Ericaceae, Asteraceae, and Scrophulariaceae (Safford 1999c, d). Bulb- or corm-forming geophytes are common and include Orchidaceae, Iridaceae, Amaryllidaceae, Oxalidaceae, and Xyridaceae; many appear to flower in response to fire. Sedges typically survive fire with bud primordia in a variety of subterranean structures. Many taxa also regenerate from taproots or woody caudices, often with apical meristems protected within a dense rosette of basal leaves. These include the genera *Pae-*
palanthus, *Erigeron*, *Hypochoeris*, *Lucilia* and *Plan-*
tago, and species within *Graphistylis* and *Senecio*. The therophytic life-form, generally well represented in pyrophytic ecosystems, is very rarely encountered in the campos de altitude. This is due not

only to environmental constraints common to most cool-humid milieus (*i.e.*, cold, wet, nutrient-leached, and highly acidic soils), but also to the small pool of native therophytes in southeast Brazil in general (Safford & Martinelli 2000).

In terms of classic successional paradigms, vegetation recovery in both sites appears to best fit the Initial Floristic Composition (“tolerance”) model of Egler (1954) and Connell and Slatyer (1977), although the “autosuccessional” processes described by chaparral ecologists are perhaps more fitting (Hanes 1971, Barbour *et al.* 1987). In the case of the campos de altitude, the survival or rapid postfire resprouting of bunchgrasses, shrubs, and bamboo, coupled with the scarcity of annual species, results in very close floristic similarity between pre- and postfire vegetation. Colonization of burn sites by woody species not originally present in the pre-fire vegetation appears to be rare, even three years after fire.

This study is the first within the tropical highland vegetation to explicitly take into account environmental heterogeneity within the landscape in its evaluation of the ecological effects of fire. Fire behavior changes across both edaphic and topographic gradients as a function of fuel properties, fuel moisture content, and the effects of topography on wind (Cheney 1981, Miller & Findley 1994). Topographically dependent factors such as radiation, air temperature, and precipitation define local climates and drive differences in soil moisture, depth, and fertility. By regulating the type of vegetation that may exist in a given landscape unit, these factors affect fire seasonality, intensity and frequency (Whelan 1995, Bond & van Wilgen 1996), and patterns and rates of postfire recovery. Topographic features (ridges and valley bottoms) may largely determine the spatial component of the fire mosaic by acting to inhibit the spread of wildfire; they may also act to channel or impede the flow of propagules through the postfire landscape (Swanson *et al.* 1988, Glenn-Lewin & van der Maarel 1992). In this study, radiation, temperature, and a combination of soil factors—all dependent primarily on slope, aspect, and topographic position—were found to be closely related to a variety of biotic responses to fire, including plant mortality, postfire growth, and postfire patterns in species diversity.

Some researchers have drawn analogies between tropical alpine shrublands and shrublands of Mediterranean climates, based primarily on their similar physiognomies (overwhelmingly frutescent, evergreen, and sclerophyllous) and the prevalence of

postfire basal sprouting among the woody flora (Hedberg 1964; Williamson *et al.* 1986; T. P. Young, pers. comm.). As in California chaparral (Hanes 1971), those shrubs dominating the “mature” prefire vegetation also dominate postfire vegetation due to their ability to quickly resprout after crown loss. Also as in chaparral, colonization of burn sites by new woody species appears to be very limited in the campos de altitude. Humid, high altitude stands of South African fynbos (van Wilgen *et al.* 1992) are also evocative of the campos de altitude, particularly with respect to plant life-forms, regeneration strategies, and the fire-mediated coupling of landscape features to vegetation physiognomy. Unlike fire-prone vegetation in many Mediterranean regions, the campos de altitude (and páramos; Horn 1989) do not shelter a dormant seed bank from which herbaceous species germinate *en masse* in the postfire environment.

Response of vegetation to fire in the campos de altitude appears to be quite similar to responses observed in high altitude páramo of the equatorial Andes and Costa Rica, where shrublands are composed primarily of taxa able to resprout following fire and the existence of extensive non-edaphic bunchgrasslands (pajonales) is now largely thought to be the consequence of repeated burning (Janzen 1973; Ellenberg 1979; Williamson *et al.* 1986; Horn 1989, 1990, 1997; Lægaard 1992; Hofstede 1995; Ramsay & Oxley 1996). Although less well-studied in this respect than the Andean systems, tropical alpine vegetation in east Africa and New Guinea also seems to owe much of its extent and character to the effects of fire, anthropogenic or otherwise (Hedberg 1964, Gillison 1970, Beck *et al.* 1986, Miehe & Miehe 1994). Quantitative comparisons show that postfire recovery rates are faster in the campos de altitude than in Costa Rican páramo, the only place from which comparable data are available. Horn (1989) reported recovery rates for three Costa Rican species that can be compared with congeners in Brazil: *Chusquea subtesselata* (Costa Rica = CR) requires 8–10 years to regain prefire height, whereas *C. pinifolia* appears to require 4–6 years; *Escallonia poasana* (CR) requires 8–10 years and *E. organensis*, 4–6 years; *Rapanea pittieri* (CR) requires *ca* 15 years and *R. ferruginea* 7–10 years. Recuperation of total biomass takes much longer in both systems. In both Costa Rica and Brazil, species of *Escallonia* are among the few woody dicots capable of postfire growth rates rapid enough to keep pace with *Chusquea*.

As a result of their geographic proximity, their often savanna-like physiognomy, and the pyrophy-

tic nature of much of their vegetation, the campos de altitude are sometimes referred to as a high altitude variant of the Brazilian savannas, or cerrado. This comparison seems inappropriate; although the campos de altitude are savanna-like in some respects, differences between the two systems far outweigh similarities (Goodland 1971, Eiten 1982, Rizzini 1979, Martinelli & Bandeira 1989, Coutinho 1990, Safford & Martinelli 2000). For example, the cerrado climate is much warmer, drier, and more seasonal, and cerrado soils are typically older and more lateritic. With regard to floristics, very few species are shared between the two systems and even generic similarities are not especially strong. In the cerrado, plants are typically xeromorphic; subterranean perennating structures are more common and more highly developed than in the campos de altitude; therophytes are widespread; and fire-controlled flowering and seeding is commonplace. Finally, fire frequency is much higher in the cerrado than in the campos de altitude, and the fire season is much longer as well.

The campos de altitude support a classic poly-climax landscape (Whittaker 1975) characterized by a mosaic of different climax communities and successional seres. Considering the geography and climate of the campos de altitude (tropical maritime, humid, elevations <3000 m), the patchiness of these mountain landscapes is remarkable and stands in direct contrast to the uniformity of the forest vegetation just below. Grass and sedge formations cover hilltops and convex slopes, as well as poorly drained valley bottoms, where they may represent an edaphic or microclimatic climax. Forest vegetation dominates in narrower, more protected valleys, in erosion amphitheatres and in rocky gulches, with isolated pockets of forest found well above the present timberline. Shrubby communities are somewhat transitionally situated and often dominate well-drained lower slopes. Forest-grassland transitions in the campos de altitude are typically abrupt, with bamboo- and shrub-dominated ecotones restricted mostly to areas of broken ground (talus slopes and rocky clefts) or locations where fire rarely or never occurs. Abrupt forest boundaries—particularly at treeline—have long been considered characteristic of high tropical mountains, as has the occurrence of discrete “tree-islands” far above the altitudinal limit of closed canopy forest (Troll 1959). It is only recently that rather tenuous climatic and edaphic explanations for these features have given way to the realization that they are, in most cases, fire-induced (Ellenberg 1979, Lægaard 1992, Miehe & Miehe 1994). The

results of both this and other recent studies similarly suggest that the campos de altitude landscape is in great part pyrogenic.

Results of this study, coupled with paleoecological data and results of investigations in similar habitats in other tropical mountain ranges, implicate fire as a major abiotic force in both the history and ecology of the campos de altitude. Human intervention in the natural fire cycle poses a threat to the abundance and existence of a variety of plant taxa in the campos de altitude. High frequencies of anthropogenic fire threaten the survival of many endemic taxa presently restricted to mesic habitats (Safford 1999c, d). At the same time, overzealous fire-suppression policies could have negative impacts on fire-dependent species by lengthening fire-return intervals beyond their reproductive life span, as well as on non-fire-dependent heliophilic taxa that depend on a disturbance-generated mosaic to successfully reproduce. Given the current situation, the latter scenario seems improbable. It is nonetheless advisable that conservation unit managers in the Brazilian Highlands finally discard the notion of fire as an exclusively destructive agent and adopt

a more balanced view of its fundamental role in the ecology of the campos de altitude.

ACKNOWLEDGMENTS

I am grateful to Tim Moulton (Universidade do Estado do Rio de Janeiro), Lucio Leoni (Herbário Guido Pabst, Carangola), Tiago and Teresa da Silva, and Paulo Rocha for advice, lodging, and board. Thanks also to David Pooley (University of Hertfordshire, England) and Erika Vohman (Crested Butte, Colorado) for field help in the Serra dos Órgãos. Marcel Rejmánek, Art Shapiro, Hermann Behling, and two anonymous reviewers read and commented on an early version of the manuscript. Jim Richards, Cathy Millikin, and Jeff Bird (LAWR, UC-Davis) provided laboratory space and aided in soil chemical analyses. Finally, José Olímpio Vargas and Jairo de Barros (Parque Nacional do Caparaó) and Jovelino Muniz de Andrade Filho (Parque Nacional da Serra dos Órgãos) furnished logistical support and the benefit of many years of experience with fire and its consequences. Field research was carried out under license from the CNPq (Portaria No. 368/97) and IBAMA (Licença No. 62/97). Funding was partially provided by a Jastro-Shields Research Scholarship and a Graduate Research Award from the University of California-Davis. Preliminary results were reported at the 1998 conference of the Association for Tropical Biology with the financial support of an ATB Travel Award.

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