GRASSLAND-FOREST BOUNDARIES IN SOUTHERN BRAZIL

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Abstract. We discuss the apparent inconsistency between climate and vegetation in southern Brazil, especially in Rio Grande do Sul, a transitional zone with elements of the broadleaf subtropical forest, mixed Araucaria-broadleaf forest and coastal rain forest vegetation types dominating to the north, and the campos grassland and shrublands dominating to the south and southwest. We show that on the large spatial scale, seasonal and annual climate fluctuations cause water deficits that may prevent the dominance of forest in some regions. This contradicts large scale vegetation models based on climate averages predicting that forest should prevail. On the small spatial scale water budget is affected by local heterogeneity related to geomorphic and soil features (slope, aspect, drainage). We review evidence and conjecture that interactions of water budget with vegetation type and fire and grazing regimes may explain the resilience of a relict vegetation pattern.

Introduction

Since long ago vegetation scientists have been puzzled by the fact that grassland dominates in a region of South America under a macroclimate that apparently would be adequate to support forests (e.g., Klein 1975, Box 1986). The same has been said for the vegetation of Rio Grande do Sul (Lindman 1900, Rambo 1956), the southernmost state in Brazil, between latitudes 27° to 33° S. The annual precipitation record in the state shows an ascending south-north gradient from 1235 mm to 2162 mm (on the northeastern plateau) and at all sites it is greater than the annual potential evapotranspiration (Mota et al. 1970). These records apparently indicate absence of zonal water deficits.

Large scale vegetation models of Holdridge (1947) and Box (1981) predict forest vegetation under these conditions. However, on large and small scales grassland, shrubland and forest mingle in a mosaic as the potential vegetation (Teixeira et al. 1986). This is consistent with the fact that the region is at a transitional zone between the subtropical forest and coastal rain forest vegetation types, which are more dominant north of the state, and the campos and pampa grassland formations, which are more dominant to the south and southwest (Cabrera 1971, Schultz 1957).

The grassland-forest transitional region is interesting for studying vegetation dynamics under local and global scale environmental change, notwithstanding the fact that, in the limit, transitions could be found anywhere at any scale, but some transitions may be more obvious than others.

We elaborate on hypotheses in this paper and attempt to explain grassland-forest vegetation patterns on large and small spatial scales in southern Brazil. We review evidence, discuss past and present day patterns, and consider their connections to climate, fire and grazing regimes.

Forests and campos

The vegetation of Rio Grande do Sul has been classified in phytogeographic regions by Reitz et al. (1983). Vegetation types are also described in Klein (1975) and Waechter et al. (1984). Based on these and existing maps (Hueck & Seibert 1972, Teixeira et al. 1986) we can define the following general types (Figure 1):

(1) Atlantic coastal rain forest, which shows its southernmost occurrence on the northern quaternary coastal plain and the eastern steep slopes and valleys of the northern plateau of the state, with several species of Lauraceae (*Ocotea catharinensis.*, *Nectandra* spp.), Myrtaceae (*Myrcia* spp.), *Ficus organensis*, *Alchornea triplinervia* and *Euterpe edulis* (palm) as characteristic tree species.

(2) Broadleaf subtropical forest of the Paraná and Uruguai river basins, up to elevations of 500-800 m, occurring in the north and northwest portions of the state, with elements penetrating along the Ibicu' and medium and lower Jacu' river basins, characterized by winter deciduous emergent trees such as *Apuleia leiocarpa*, *Parapiptadenia rigida*, *Peltophorum dubium*, *Enterolobium contortisiliquum*, *Cordia trichotoma*, *Cabralea cangerana*, by non-deciduous non-emergent trees such as *Nectandra* spp., *Ocotea* spp. and *Patagonula americana* and small trees as *Actinostemon concolor*, *Sorocea bonplandii* and *Trichilia claussenii*.

(3) Mixed Araucaria–broadleaf forest, with *Araucaria angustifolia* as the emergent tree and at a lower stratum species of Lauraceae (*Ocotea pulchella*, *O. puberula*, *Cryp-*
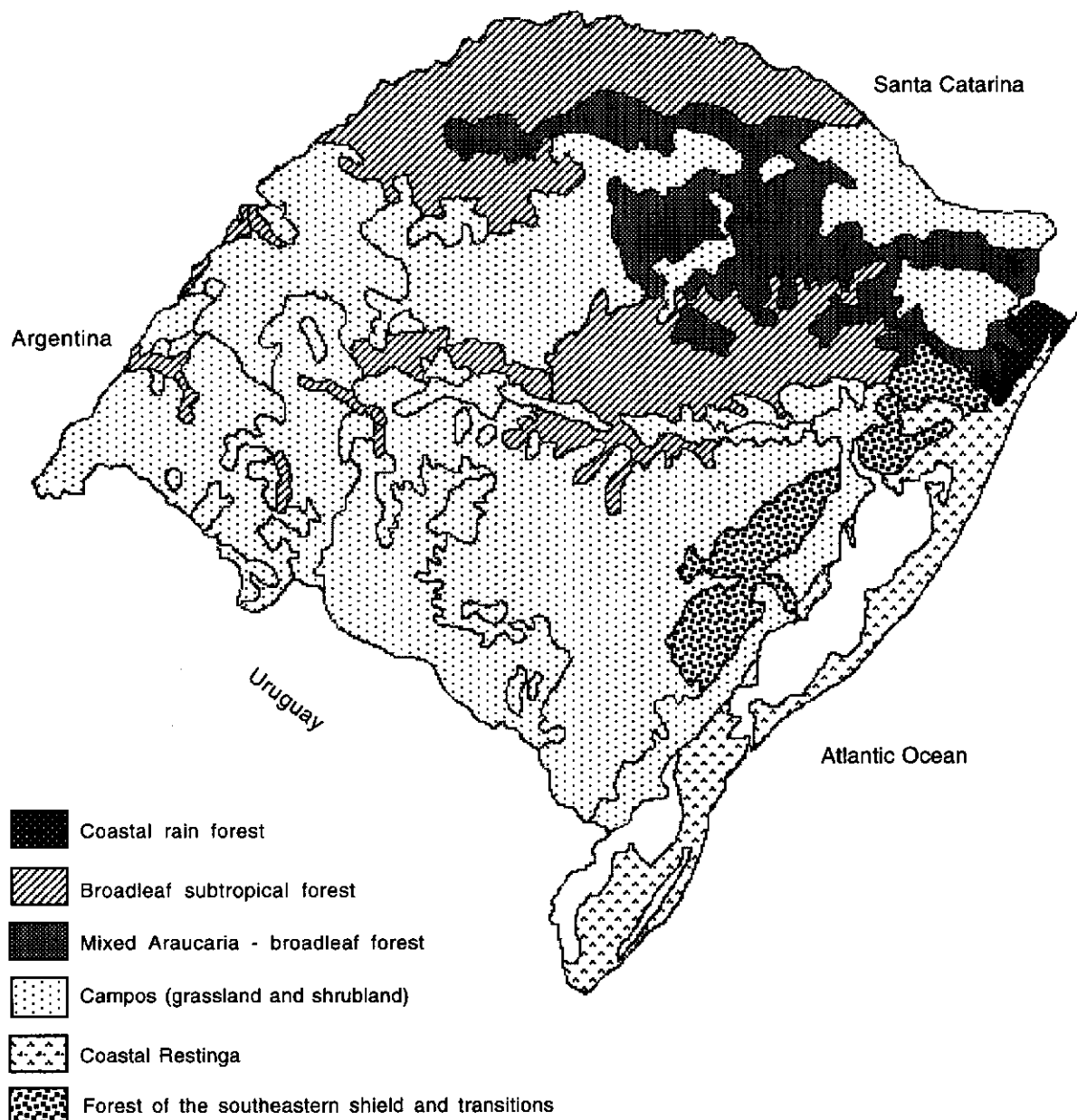
Figure 1. Map of the potential vegetation in the state of Rio Grande do Sul, Brazil. Adapted from Hueck & Seibert (1972), Klein (1975) and Teixeira et al. (1986). Subdivisions within types reflect physiognomic variation.

tocarya aschersoniana, Nectandra lanceolata, N. grandiflora, N. megapotamica), Myrtaceae (*Myrcia bombycina, Myrceugenia euosma, Gomidesia sellowiana, Psidium cattleyanum, Myrcianthes gigantea*), Aquifoliaceae (*Ilex paraguariensis, Ilex* spp.), Sapindaceae (*Matayba elaeagnoides, Cupania vernalis*), Winteraceae (*Drimys brasiliensis*), Podocarpaceae (*Podocarpus lambertii*) and Leguminosae (*Mimosa scabrella*).

(4) Acacia-Prosopis parkland, a very small area on the westernmost portion of the state, containing typical floristic elements of the Chaco and Espinal formations (Cabrera 1971), such as *Prosopis nigra, P. algarobilla, Acacia caven, Parkinsonia aculeata* (Leguminosae), *Acanthosyris spinescens* (Santalaceae), *Sapium glandulatum* (Euphorbiaceae).

(5) The southeastern shield presents a complex pattern of forest, shrubland and campo patches, which have not been well studied; on the eastern slopes and valleys forest cover is denser, while in the interior of the region open forests, shrubland and campo dominate, containing elements that are also found in the other forest types, such as *Dodonaea vis-*

cosa, Schinus molle, Lithraea brasiliensis, Scutia buxifolia, Calyptranthes concinna, Gomidesia sellowiana, Ocotea pulchella, Matayba elaeagnoides, Podocarpus lambertii, Ilex paraguariensis, Araucaria angustifolia.

(6) "Restinga" on the 600 km long coast, with vegetation typical of the different successional stages on dunes and on lake shores.

(7) Grassland and shrubland (campos) dominate mostly on the southwest, central areas between the Jacu' river and the southeastern shield, associated with the mixed Araucaria - broadleaf forest on the north and northeast, and along the coastal plain, composed of many species of Poaceae (about 800 species, mainly *Paspalum, Axonopus, Andropogon, Aristida, Schizachyrium, Eragrostis, Piptochaetium*), Compositae (*Baccharis, Vernonia, Eupatorium, Gamochaeta, Chaptalia, Senecio*), Cyperaceae (*Eleocharis, Rhynchospora*), Leguminosae (*Desmodium, Vicia, Trifolium, Galactia, Stylosanthes*), Rubiaceae (*Borreria, Relbunium*), Umbelliferae (*Eryngium, Centella*), among others. The term "campo" is used to refer to physiognomies that vary from true grassland to shrubland and frequently is used in the plural as "campos".

Authors have distinguished general types of campos on the basis of forage quality and geographical distribution (Gonçalves 1990, Barreto & Boldrini 1990). The campos in the southwestern region tend to present better forage quality ("fine campos"), in general dominated by prostrate or low tussock grasses, especially of *Paspalum* and *Axonopus* among C4, summer flowering species and of *Briza, Bromus, Piptochaetium* and *Stipa* among C3, spring flowering species, and by legumes of *Desmodium, Trifolium* and *Adesmia*. The campos in the other regions are the so-called "gross campos", characterized by a lower stratum with the previously referred species and an upper stratum where predominate tall tussock grasses of *Andropogon, Aristida, Erianthus, Hypoginium, Schyzachirium* and *Trachypogon*, all C4 species, which during the growing season accumulate biomass that remain attached to the plants, increasing flammability when they are dry. However, most of the differences seem to be determined by the grazing regime, since grazing exclusions or low intensity grazed areas in both the fine and gross campo are dominated by tall tussock grasses that were mentioned and, with some variation depending on the region, *Eryngium horridum* and shrubs of *Baccharis, Campomanesia, Eupatorium, Pteridium, Senecio* and *Vernonia*. Some of the variation may be related to soil conditions. In this respect, *Aristida, Piptochaetium* and *Eryngium horridum* are found mostly on drier, upper slopes, while *Andropogon lateralis, Baccharis trimera, Schizachyrium microstachium* are found mostly on moister sites (Pillar et al. 1992). There are clear geographically determined patterns in the dominance of some conspicuous species, e.g., *Eupatorium buniifolium* is a typical shrub of the campos on the southwest and *Aristida jubata* is typical of some campos on dry sites on the northern plateau and on patches of sandy ill-developed soils in the southwest.

The forest vegetation of the state of Rio Grande do Sul has been under strong human interference mainly after the 19th century intense colonization by Europeans. Historical records and present day mature or recovering, secondary forest fragments are indicative of the potential vegetation in some areas (see map in Figure 1). Forest dominates as potential vegetation in large areas in the northern half of the state, mainly on the slopes and valleys along the east and south edges of the northern basaltic plateau and on the slopes and valleys of the Uruguai river basin. Forest also dominates on some parts of the southeast granite shield, mainly on the eastern slopes. Though less dominant, riparian forests and smaller patches on moist sites on slopes are observed throughout typical campo areas in other parts of the state, containing floristic elements of the aforementioned forest types.

The campos vegetation presently covers about 120 000 km^2 in the state of Rio Grande do Sul, which corresponds to about half of the state's land mass. In the 17th century, during the establishment of the Jesuit missions on the eastern side of the Uruguai river, cattle and horses were introduced (Kern et al. 1991) and large ranches ("vacarias") were run by natives, including campos in the Araucaria forest region. A century later, immigrants from Azores and other parts of Brazil colonized campo areas, mainly along the medium and lower Jacu' river valley and on the southeastern shield, with a relatively slight effect on forests comparing to the colonization of the northern half of the state a century later. Since then the campo vegetation has been the major support for a cattle ranching economy. Fire is regularly used in late winter when ranch management is such that excessive biomass accumulates during the growing season, being senescent by the next spring. In the last three decades a large proportion of areas with campo vegetation has been allocated to cropland. Sometimes crops are cultivated on a rotational basis in which the natural grassland recovers during the few years the land is left fallow but grazed.

Factors affecting the patterns

Climate

The climate in southern Brazil is mainly a Cfa type in Köppen's classification, with a small portion with a Cfb type on the higher elevation plateau. In the state of Rio Grande do Sul the mean annual temperatures range from 15 to 20°C, with mean temperatures in the coldest month ranging from 11 to 14°C, when frost is frequent, but snow rarely observed and only in the high elevation areas. Seasonal and annual fluctuations in precipitation cause notable water deficit in the summer in some areas (Buriol et al. 1979, see map in Figure 2). The water budget figures shown in the map are based on series of meteorological observations (30 years). Instead of using the normal (average) values of precipitation and estimated evapotranspiration, the method computes the water budget at each time step and, on the basis of the series of water budget figures, generates probabilities for different levels of water excess and deficit at the different sites and
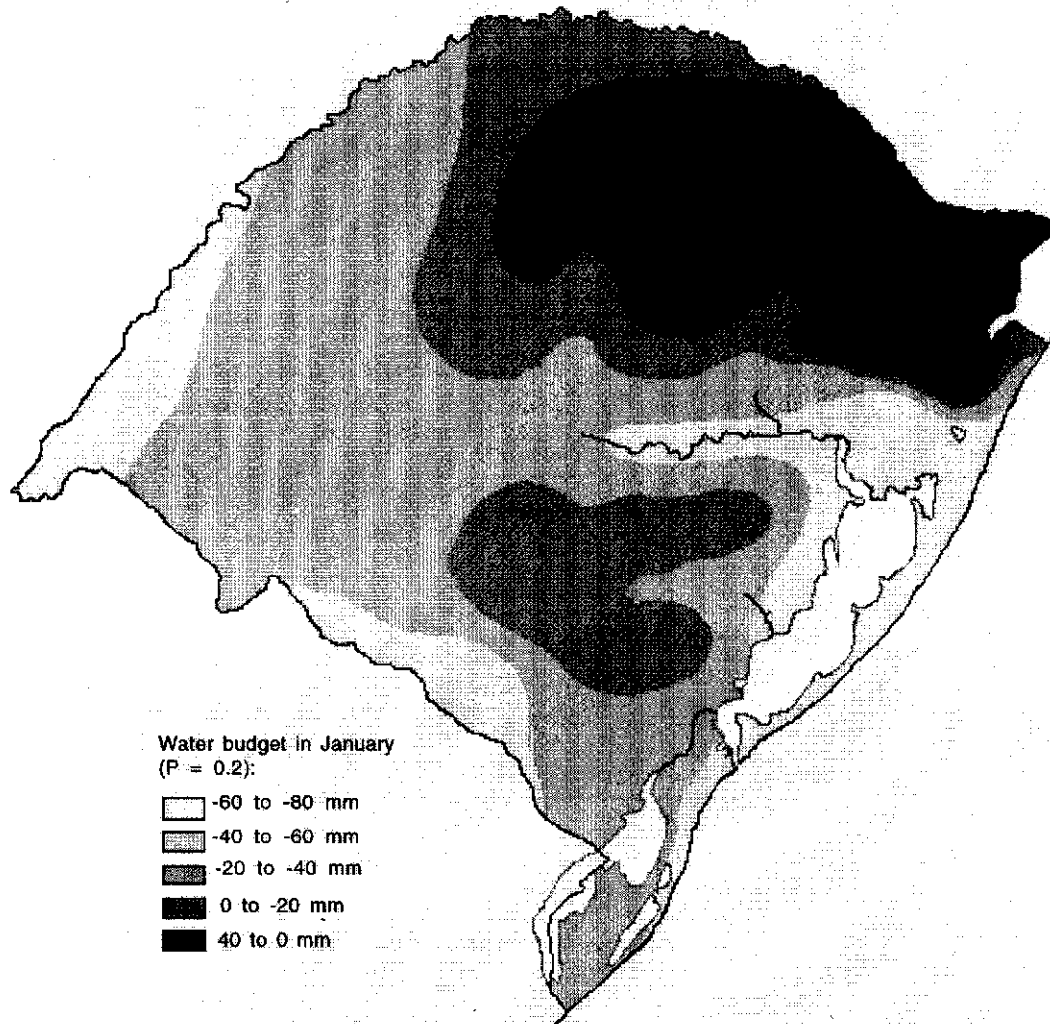
Figure 2. Water budget in January, in the state of Rio Grande do Sul, Brazil. There is a probability of 0.2 that in a given year the indicated water budget will occur. Negative values imply water deficit, positive values imply water excess, considering a soil water storage capacity of 100 mm (from Buriol et al. 1979).

months of the year, giving a more realistic picture of the soil moisture conditions faced by vegetation. The map in Figure 2 indicates the water deficit levels that may occur, at a 0.2 probability, on the different regions of the state of Rio Grande do Sul. The northeastern part of the state is the least affected by water deficits, while areas in the southwest and east are the most affected.

The computation of water budget in Buriol et al. (1979) does not take into account surface and subsurface runoff, percolation and outflows of water, which are impossible to es-

timate in such a large scale study and are associated with geomorphic and soil related features (slope, soil texture, depth of impermeable layer), aspect, vegetation cover (Miller 1977). Therefore, we can consider that water deficits can be aggravated or moderated by these factors at the smaller spatial scales. Under a given regional climate regime, the local heterogeneity determines water budgets that may prevent the development of forest on some portions of the landscape (mostly ridges and upper slopes), while facilitating forest development on other portions (valleys). It

is assumed that plants of the campos are more tolerant to water deficit than plants of the forests (Pillar & Boldrini 1997). Information is yet scanty regarding the degree to which these water deficits would be directly detrimental to the development of forest tree saplings. However, there is a reasonable coincidence between the zones with more water deficit (Figure 2) and potential vegetation cover with campos (Figure 1), except in the area of campos associated with

mixed Araucaria - broadleaf forest, which we will discuss later. The coincidence is an evidence that water deficits may have prevented directly or indirectly (by influencing fire regimes) the dominance of forest in some regions of the state. Local heterogeneity also may explain the occurrence of forest in regions where the regional climate would indicate campo.
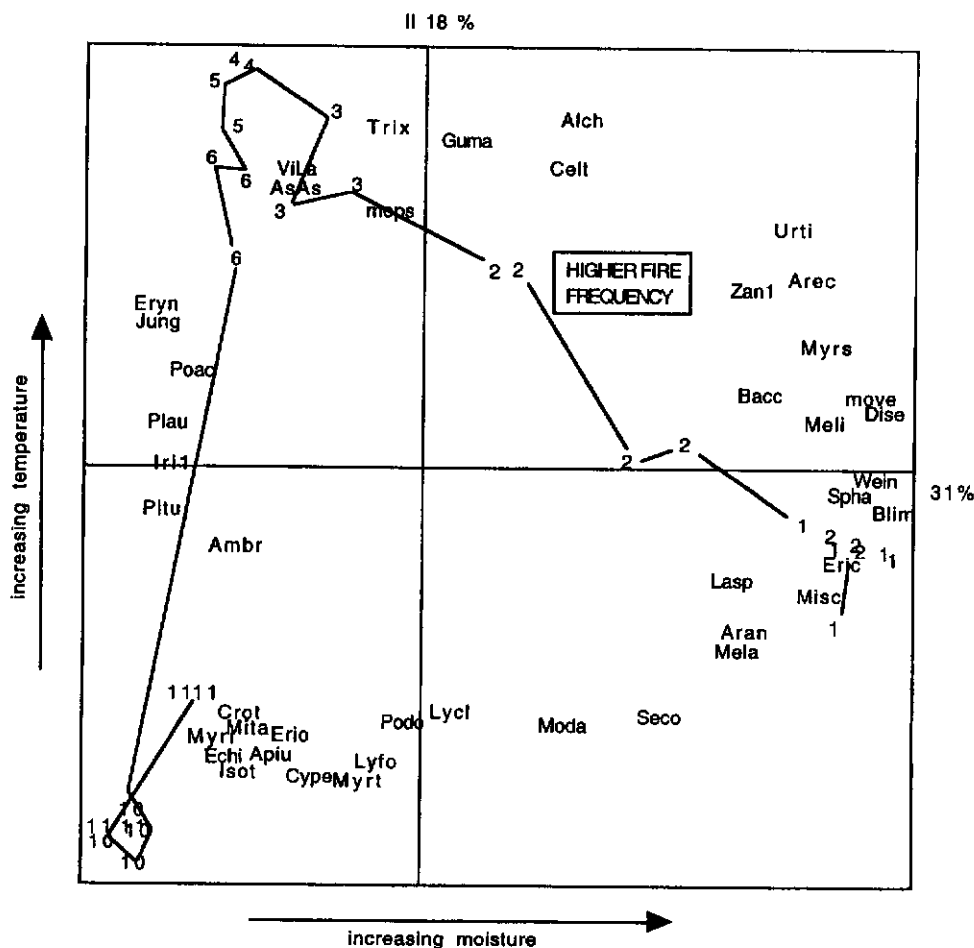

Figure 3. Ordination of the pollen record in 30 sections of a core taken at Serra do Rio do Rastro, Santa Catarina, Brazil. Data are from Behling (1993). The numbers identify radiocarbon estimated age in thousand years B.P. (from 800 to 11013 are connected in sequence). Ordination method is principal coordinates analysis, applied to Euclidean distances, with pollen counts square root transformed and standardized by the total count in each core section. Species most correlated (I r I > 0.6) to the ordination axes are plotted (correlations rescaled accordingly are the coordinates). Species labels: Alch *Alchornea*, Ambr *Ambrosia*-type, Apiu *Apium*, Aran *Araucaria angustifolia*, Arec Arecaceae, AsAs Asteraceae subf. Asteroideae undiff., Bacc *Baccharis*-type, Blim *Blechnum* cf. *B. imperiale*, Celt *Celtis*, Crot *Croton*, Cype Cyperaceae, Dise *Dicksonia sellowiana*, Echi *Echinodorus*, Eric Ericaceae, Erio *Eriocaulon/Paepalanthus*, Eryn *Eryngium*-type, Guma *Gunnera manicata*, Iri1 Iridaceae (type I), Isot *Isotes*, Jung *Jungia*-type, Lasp *Lamanonia* cf. *L. speciosa*, Lycl *Lycopodium clavatum*-type, Lyfo Lycopodiaceae (foveolate), Mela Melastomataceae, Meli *Meliosma*, Misc *Mimosa* cf. *M. scabrella*, Mita *Mimosa* cf. *M. taimbensis*, Moda *Moritzia dasiantha*, Myri *Myriophyllum*, Myrs *Myrsine*, Myrt Myrtaceae, Plau *Plantago* cf. *P. australis*, Pltu *Plantago* cf. *P. turficola*, Poac Poaceae, Podo *Podocarpus*, Seco *Sebastiana commersoniana*, Spha *Sphagnum*, Trix *Trixis*, Urti Urticales, ViLa *Vicia/Lathyrus*, Wein *Weinmannia*, Zan1 *Zanthoxylum* (type I), mops Pteridophyta (monolete psilate), move Pteridophyta (monolete verrucate). Climate interpretation is based on Behling (1995). Fire regime is inferred based on data from a similar area in Paraná (Behling 1996).

Past climate and vegetation shifts

There are evidences that the climate in South America during the last glacial period were in general cooler than today, but moisture patterns showed strong regional differentiation (Markgraf 1989). More specific evidence of past climate changes is found in pollen records in Rio Grande do Sul (Lorscheitter 1992) and Santa Catarina (Behling 1993, 1995). The climate was colder and drier until 10 000 years B.P., warmer and drier from 10 000 to 2900 years B.P. and cooler and moister from 2900 to present (Behling 1995). Behling's data from the Araucaria region in Santa Catarina (Figure 3) indicates that until around 2600 years B.P. the vegetation was much more campo-like than at present, which confirms the hypothesis advanced by Klein (1975) that the campos within the Araucaria forest region are relicts of a drier climate period.

Grazing and fire regimes

By the time European settler's cattle herds and horses started to graze in the campos and pampa regions in South America, grazing animals of the native fauna were small, such as deer, rhea and small rodents. These could subject the grassland vegetation only to low and localized grazing pressure. There is, however, fossil evidence that large grazing mammals of Equidae (*Equus*), Camelidae and Cervideae existed in the region until 8000 B.P. (Kern 1994, Bombin & Klamt 1975). As conjectured by Schüle (1990), since the collision of North and South America in the Upper Pliocene, about 3 million years B.P., until the end of the Pleistocene, the South American vegetation may have been considerably damaged by these invading large Laurasian ungulates and other megafauna elements. If this is true, intensive grazing is not far away in the evolutionary history of the present day flora of the campos.

A quite interesting question is to know if fire has been always a high frequency element of the natural campos ecosystem or if it has intensified after the arrival of humans in the region around 12-13 thousand years B.P. (Kern et al. 1991). The phytopalaeofire history in southern Brazil is not well known, but recent findings in the mixed Araucaria - broadleaf forest region in Paraná (Behling 1996), which shows a similar mosaic of forest and campos as in Rio Grande do Sul, indicate that the frequency of palaeofires increased at the beginning of the Holocene, likely anthropogenic at that time. This finding further supports the idea that the pre-Colombian anthropogenic influence on the vegetation, including dissemination of naturally occurring plants, should not be overlooked (Schüle 1990, Dean 1995). Also, Behling found that the highest frequency of fires was during the late Holocene, coinciding with the migration of the mixed Araucaria - broadleaf forest from the valleys into the areas with campos. Fire could have been a driven factor in the Araucaria forest expansion (Soares 1990).

The campos, even the areas dominated by shrubs, are fire prone if sufficient senescent biomass has accumulated. The rate of senescence of older leaves in grasses increases during dry spells. Furthermore, senescent leaves of tall tussock grasses in general remain attached to the plants, increasing flammability of the whole plant (Bond & Wilgen 1996). Accumulation of biomass, and therefore flammability levels, are related to grazing regimes (Bond & Wilgen 1996). Ranchers usually adjust the stocking rate of pastures on the campos on the basis of the carrying capacity during the winter. The consequence is more accumulation of ungrazed biomass during the main growing season in the spring and summer in the campos presenting more seasonality in the biomass production, which are the ones in the colder winter areas, associated to the mixed Araucaria - broadleaf forest.

The broadleaf subtropical forest and the coastal rain forest types are not fire prone, i.e., usually do not burn. Young trees of these and other forests types cannot tolerate fire, since fire tolerance is related to the protection to the cambium that develops as the bark becomes thicker. References indicate that in general tree species are sensitive to fire when the plants are younger up to 2 m height or with a bark thickness less than 10 mm (Peterson & Ryan 1986, Uhl & Kauffman 1990). *Araucaria angustifolia* seedlings and young trees cannot tolerate fire (Veblen et al. 1995). However, there is evidence that the regeneration of *Araucaria angustifolia* is dependent on regular disturbances, mainly fire. Human induced light fires in old pine stands may in fact increase regeneration (Soares 1990). Veblen et al. (1995) give similar indications for the forest in Southern Chile and Argentina. Fires in the mixed Araucaria-broadleaf forest can be ignited by lightning , based on a long term study of forest fire occurrence in the central Paraná state, in which lightning was responsible for 20% of the fires (Soares 1990, Soares & Cordeiro 1974). If natural fires are possible in the pine forest, would they be in the campos? This question may not be relevant for campos in the pine forest region, since when a fire starts in the forest it is probable that, if fuel is accumulated, the fire will spread to adjacent campo, no matter where it started. But, outside the pine forest region, knowing whether or not natural fires were possible is critical to understand the pattern dynamics of campo and non-fire prone forest types. Although there is no formal study on this topic in the region, at present the occurrence of natural fires starting on grassland areas is very rare (see also references in Bond & Wilgen 1996:218). However, this is not an indication that natural fires in grassland were also rare at pre-Colombian times; a high frequency of palaeofires was detected since 35 000 B.P. in data from a mountain region in São Paulo, which was dominated by campos until the end of the Pleistocene (Behling 1997). It is quite obvious that grazing intensity of grassland areas increased after the introduction of domestic cattle, resulting in a reduction of the number of areas with enough fuel accumulation for extended naturally ignited fires. Furthermore, when grassland is left ungrazed for a long time fuel accumulates and any fire tends to be much more intense, being capable of burning plant types that would not burn under a low intensity fire, such as forest trees invading grassland.

Data of long term field studies evaluating the effects of (the absence of) fire and grazing on the dynamics of boundaries between campos grassland and forest are yet to be made available by ongoing research at long term ecological research sites near Porto Alegre and Santa Maria. Data from exclosures (Boldrini & Eggers 1996) and our own observations of areas in which grazing and fire were excluded, some for more than 10 years, indicate that in some of them the grassland vegetation tended to evolve to shrubland and to a forest type vegetation but not in others. Also, observations of excluded areas at grassland-forest boundaries indicated that in general forest tended to invade adjacent grassland. Although the data set is scanty and in some areas where informal observations were made the history of disturbances is unknown, we can conjecture that under suppression of fire and grazing the grassland-forest boundaries would tend to shift up (mostly in the elevation gradient) to a new equilibrium state determined by the soil water budget and by the new type of vegetation cover. The reversed effect is expected only upon imposing an intense grazing or fire regime, and may take longer. Also, there is a clear effect of cattle trampling hindering tree regeneration within forest patches.

We could conjecture that in the mixed Araucaria - broadleaf forest region natural or anthropogenic fires have determined a mosaic of forest and grassland, notwithstanding the fact that in that region periods of soil water deficit are rare in the present climate, and therefore the extent of areas that would be too limiting for forest is smaller. Green's (1989) simulation model predicts a mosaic pattern in the case when two fire prone vegetation types (which is the case here) mingle with regard to environmental requirements (moisture is adequate for both grassland and forest). That is, fire may have been the main factor explaining grassland-forest patterns in the mixed Araucaria-broadleaf forest region.

Final remarks

Whether the environmental limit for plant types is set by water budget or by fire may not change the resulting pattern in the areas with greater water deficits. If fire prone plants characterize grassland, and grassland is typical of drier sites, a forest plant may not occur on drier sites because at younger age cannot withstand droughts, or because at some stage is fire sensitive, or because of both. For one reason or another the resulting vegetation cover may be a campo. However, in the moister areas at present covered with a mosaic of fire prone Araucaria forest and campos, fire may be the major factor explaining the resilience of relict campos; the water budget - fire mechanism may be relevant only on the drier portions of the landscape which are unsuitable for Araucaria plants. Although empirical evidence is not clear, long term suppression of grazing and fire in the campos in both areas may determine local grassland-forest boundaries shifts (up in the elevation gradient) to a new equilibrium state determined by the soil water budget and by the new type of vegetation cover.

We therefore conclude that the hypothesis is tenable that on the large spatial scale seasonal and annual climate fluc-

tuations cause water deficits that prevent the dominance of forest in some regions. On the small spatial scale, water deficit is aggravated or moderated by local heterogeneity related to geomorphic and soil features. Interactions of water budget with current vegetation cover, fire and grazing disturbances explain observed vegetation patterns and grassland - forest boundaries.

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126

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