

A contribution to the phytogeography of Brazilian *campos*: an analysis based on Poaceae

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ABSTRACT – (A contribution to the phytogeography of Brazilian *campos*: an analysis based on Poaceae). Twenty areas from eight Brazilian states were compared according to a list of 224 species of Poaceae. In order to determinate affinity patterns between the areas, a binary matrix was submitted to cluster and ordination analysis. The patterns found were then faced to climate and geographic position. The scores corresponding to the areas obtained from the cluster analysis showed a strong correlation to temperature. The scores corresponding to the species suggest a gradient that associates distribution patterns to the photosynthetic pathway (C3 or C4). The current results suggest that the traditional classification of the Southern American grasslands might require some modification in order to be broadly applicable in the Brazilian context.

Key words - Brazilian grasslands, Gramineae, multivariate analysis, South America

RESUMO – (Contribuição à fitogeografia dos campos brasileiros: uma análise baseada em Poaceae). Vinte áreas de oito estados brasileiros foram comparadas de acordo com uma lista de 224 espécies de Poaceae. Uma matriz binária foi submetida à análise de agrupamento e ordenação para determinar padrões de afinidade entre as áreas. Os padrões obtidos foram comparados com características climáticas e posição geográfica. Os valores obtidos da análise de agrupamento, correspondentes às áreas, mostraram forte correlação com a temperatura. Os valores correspondentes às espécies sugerem um gradiente que associa padrão de distribuição ao tipo fotossintético (C3 ou C4). Os resultados obtidos sugerem que a classificação dos campos sul-americanos necessita algumas modificações para ser melhor aplicada ao contexto brasileiro.

Palavras-chave - América do Sul, análises multivariadas, campos, Gramineae

Introduction

The use of geographic distribution patterns for species of Poaceae has already been done by Burkart (1975) to classify the grassland vegetation of South America. The author recognised: a) megathermic species, predominant in tropical and subtropical grasslands; b) mesothermic species, predominant in temperate grasslands; c) microthermic species, predominant in cold grasslands. In a later work with Poaceae, this same classification of species for phytogeographic inference was used (Boechat & Longhi-Wagner 2000). Otherwise Clark (1992) recognised for Brazil three types of grasslands associated with high altitudes, starting from

the taxonomic study of a section of the genus *Chusquea* (Poaceae – Bambusoideae).

The so-called *campos de altitude* (montane grasslands) are to be found at the highest points of the coastal region of South and Southeast Brazil such as the Aparados da Serra (Rio Grande do Sul and Santa Catarina States), Serra Geral (Paraná and Santa Catarina States) Serra do Mar (São Paulo and Rio de Janeiro States), Serra da Bocaina (São Paulo and Rio de Janeiro States), Serra dos Órgãos (Rio de Janeiro State), Serra da Mantiqueira (São Paulo, Minas Gerais and Rio de Janeiro States), and Serra do Caparaó (Minas Gerais and Espírito Santo States) occupying in general restricted areas, surrounded by the Atlantic Rain Forest.

Although this vegetation is usually located on protected places by environmental legislation, there are several factors that make it endangered such as burning, collect of ornamental and medicinal plants, extensive grazing and tourism, which can affect especially endemic species and the conservation of these areas.

This island-like field pattern at an ample latitudinal gradient makes them very interesting from the biogeographic point of view. The presence of grassland vegetation in places where the climatic climax would be the forest, is generally related to environmental factors such as shallow and poor soil and differentiated local

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climatic conditions, associated to hill-top conditions, with greater exposure to solar radiation and with a larger long-term variation of temperature and humidity, and further still, the constant presence of mist. Nevertheless, in certain cases the possibility of anthropic factors has been suggested by some authors. A revision of pertinent literature is provided by Garcia & Pirani (2003).

With the aim of verifying the phytogeographic placing of montane grasslands located in the Atlantic Rain Forest domain in the State of São Paulo, the present work was undertaken, especially focusing grasslands of the Núcleo Curucutu of the Parque Estadual da Serra do Mar, whose flora was recently studied (Garcia & Pirani

2005). These grasslands present altitudes considered low for classification as montane grasslands, even though they present floristic, physiographic and environmental characteristics very similar to this type of vegetation (Garcia & Pirani 2005).

Material and methods

The analysis was based on a presence/absence matrix without exotic and invasive species extracted from the original complete matrix from 20 sites (table 1, figure 1). We also excluded those species with incomplete or imprecise identification at a specific level. The original list passed

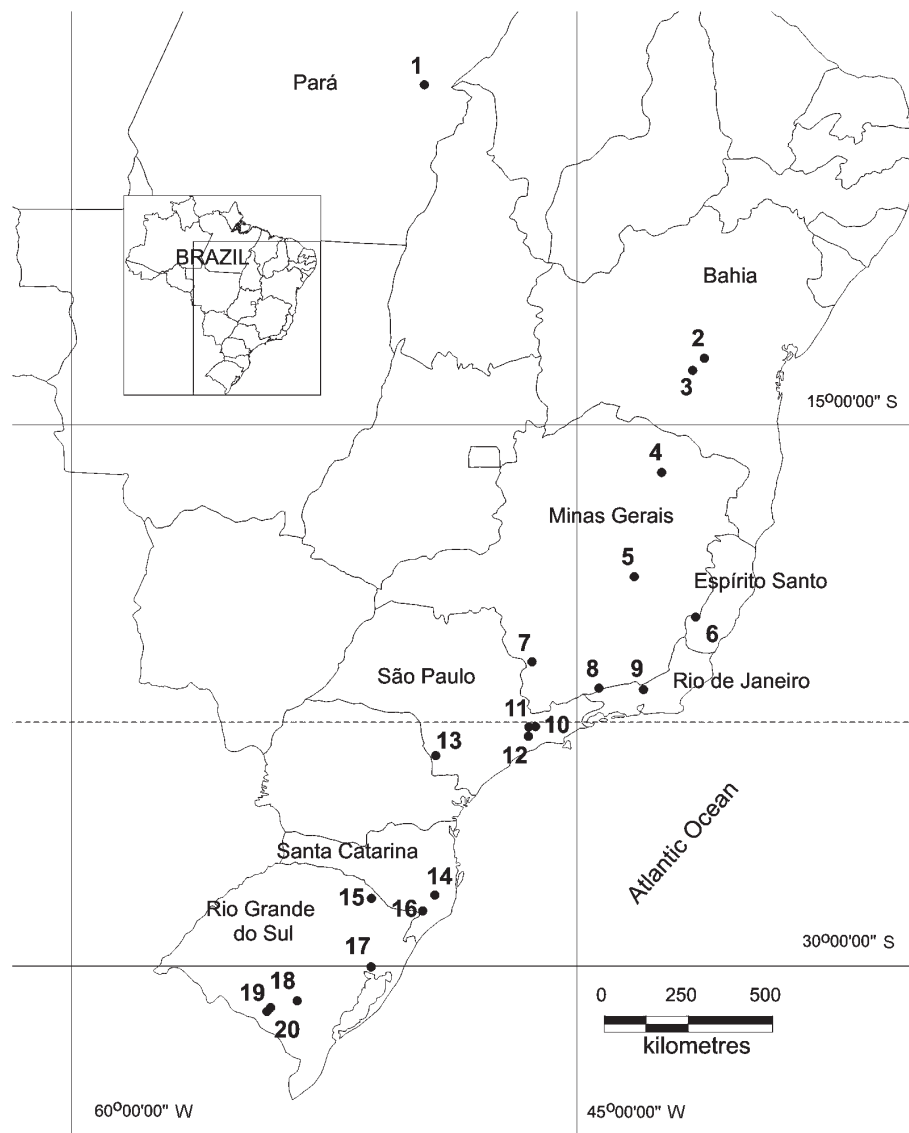


Figure 1. Location of areas compared. 1. Serra de Carajás. 2. Mucugê. 3. Pico das Almas. 4. Grão-Mogol. 5. Serra do Cipó. 6. Espírito Santo. 7. Poços de Caldas. 8. Itatiaia. 9. Serra dos Órgãos. 10. City of São Paulo. 11. Butantã. 12. Núcleo Curucutu. 13. Itararé. 14. Urubici. 15. Aracuri. 16. Serra da Rocinha – Aparados da Serra. 17. Morro da Polícia. 18. Bagé 1. 19. Bagé 2. 20. Bagé 3.

Table 1. Environmental factors of compared areas in Brazil. Local numbers as in figure 1.

Local	Reference or source of data	Vegetation	Altitude (m)	Mean annual temperature (°C)	Thermal amplitude (°C)	Mean annual rainfall (mm)	Pluviometric amplitude (mm)
1. Serra de Carajás range, PA.	Silva <i>et al.</i> (1996).	grasslands on ferrallitic deposits (<i>canga</i>)	600-800	27.5	0.0	2,200	245.0
2. Mucugê, BA.	Harley & Simons (1986).	<i>campos rupestres</i>	984	22.5	2.5	1,100	107.5
3. Pico das Almas, Chapada Diamantina, BA.	Renvoize (1995).	<i>campos rupestres</i>	1,958	22.5	5.0	900	107.5
4. Grão-Mogol, MG.	Longhi-Wagner & Todeschini (2004).	<i>campos rupestres</i>	650-1,299	22.5	6.25	1,300	170.0
5. Serra do Cipó, MG.	Burman <i>et al.</i> (1987).	<i>campos rupestres</i>	> 1,200	22.5	7.5	1,800	232.5
6. Caparaó region, ES/MG.	Ruschi (1950), Leoni (1997).	montane grasslands	1,000-2,600	17.5	1.25	1,300	107.5
7. Planalto de Poços de Caldas, MG.	S.C. Pereira (unpublished data), and data from the R herbarium collection.	grasslands	1,300	18.75	10.0	1,500	232.5
8. Itatiaia range, RJ.	Brade (1956).	montane grasslands	> 2,000	18.75	3.75	1,500	232.5
9. Serra dos Órgãos, RJ.	Rizzini (1954).	montane grasslands	2,000-2,263	17.5	11.25	1,500	187.5
10. In the outskirts of city of São Paulo, SP.	Usteri (1911).	grasslands	700-1,000	18.75	10.0	1,500	212.5
11. Butantã, at that time still a rural area of the city of São Paulo, SP.	Joly (1950), Hell (1969).	grasslands	740	18.75	10.0	1,500	187.5
12. Núcleo Curucutu do Parque Estadual da Serra do Mar, SP.	Garcia & Pirani (2005).	grasslands at the peak of the Serra do Mar	750-850	18.75	7.5	1,500	187.5
13. Itararé, SP.	Collection of the ESA herbarium, starting with the compilation and collections of Vinicius C. Souza and Carlos A.M. Scaramuzza.	grasslands	> 1,000	16.25	10.0	1,500	187.5

continue

continuation

Local	Reference or source of data	Vegetation	Altitude (m)	Mean annual temperature (°C)	Thermal amplitude (°C)	Mean annual rainfall (mm)	Pluviometric amplitude (mm)
14. Parque Nacional de São Joaquim, Urubici, SC.	Collection of the ICN herbarium, including a collection undertaken in January, 2001, besides collections done by Daniel Falkenberg, in the collection of the FLOR herbarium	grasslands	1,500-1,822	11.25	5.0	1,800	0.0
15. Estação Ecológica de Aracuri, Esmeralda, RS.	Longhi-Wagner & Boldrini (1988).	grasslands	870-930	16.25	12.5	1,800	50.0
16. Serra da Rocinha, RS.	Collection of the ICN herbarium, including a collection performed in January, 2001, besides collections done by Daniel Falkenberg, in the collection of the FLOR herbarium, added classes <i>campo</i> and <i>turfeira</i> (peat) of Rambo (1956).	Campos de Cima da Serra	1,398	11.25	5.0	1,800	0.0
17. Morro da Polícia, Porto Alegre, RS.	Boldrini <i>et al.</i> (1998).	grasslands	280	18.75	10.0	1,300	0.0
18. Bagé '1', in the northern part of this county, RS.	Girardi-Deiro <i>et al.</i> (1992).	grasslands on Guaritas Association of soil with rock outcrops, on litholic (rocky) soils, with outcropping of the rock	200-500	18.75	12.5	1,500	0.0
19. Bagé '2', between samples 1 and 3 of this county, RS.	Girardi-Deiro <i>et al.</i> (1992).	grasslands on Bexigoso class of soil, on brunizem soil, in an intermediary geographic position in relation to the following group.	180-200	18.75	12.5	1,500	0.0
20. Bagé '3' on the southern part of the county, RS.	Girardi-Deiro <i>et al.</i> (1992).	grasslands on Bagé class of soil, on vertic planisols.	60-180	18.75	12.5	1,500	0.0

through a check on synonyms and exclusion of species with doubtful record, possibly due to identification errors. The initial matrix thus produced contained 384 species (Garcia 2003). During elaboration of the matrix, no species was encountered as occurring in all the areas compared not even those of pantropical or cosmopolitan distribution, or even sub-spontaneous species. After this, the exclusion of species occurring in only one of the compared areas was done. Thus, a final matrix of 224 species was obtained.

The similarity matrix was calculated using Jaccard's index. The clustering algorithm was the complete linkage procedure. For an interpretation of the clusters obtained, information from the physical environment was used, according to regional information obtained in Ministério da Agricultura (1969), Projeto Radam (1974), OMM (1975), Projeto Radambrasil (1981, 1983), IBGE (1986), Giulietti *et al.* (1987), Ross & Moroz (1997), Oliveira *et al.* (1999) and Pirani *et al.* (2003).

The ordination procedure was based on a Detrended Correspondence Analysis (DCA) using the occurrence matrix based on the floristic lists. Analysis was made using the Hill's algorithm (Digby & Kempton 1987). For providing guesses about the causes of the overall ordination arrangement, site scores obtained from species composition data were correlated with climate in each location. The Spearman rank correlation index was used to test the relationships between the site scores obtained from DCA and the following climatic data: mean annual temperature; thermal amplitude (difference between the average temperature of the hottest month and the coldest one); average annual rainfall; pluviometric amplitude (difference between the average rainfall of the rainiest month and the driest one).

Species scores were also associated with their classification in subfamilies and tribes, besides geographical distribution patterns and photosynthetic type. These attributes were compared with the species scores arrangement on the two first axis obtained from DCA. This procedure allowed for testing whether the overall ordination arrangement agrees with discernible groups of species with phytogeographical and ecological affinities.

Classification of the family Poaceae into subfamilies was according to the proposal of the Grass Phylogeny Working Group (GPWG 2001). The species are in accordance with the Sorong *et al.* (2003) and Zuloaga *et al.* (2003) catalogues. The patterns of geographic distribution were based on bibliographic research, on field experience and on herbarium material, according to proposal of Boechat & Longhi-Wagner (2000) although with certain alterations.

Characterisation of species as to photosynthetic metabolism was according to Clayton & Renvoize (1986), Renvoize (1987), Zuloaga (1987), Zuloaga & Morrone (1996), Zuloaga & Sendulsky (1988), Zuloaga *et al.* (1993) and Medina *et al.* (1999), besides Longhi-Wagner (personal communication).

During correspondence analysis, the two following species were excluded from the matrix due to their rarity

on the examined sites: *Hordeum euclaston* Steud., since it is the only example belonging in tribe Triticeae, and *Leersia hexandra* Sw., because this is the sole example belonging in tribe Oryzaceae and in subfamily Ehrhartoideae.

Results

The obtained dendrograma is to be found in figure 2. On comparing information from the physical environment with the obtained clusters, it was noted that latitude, geomorphology, soil types, climatic classification of Köppen and total rainfall, proved not to be adequate for analysis.

Data on annual average temperature proved to be reasonably coherent with the clusters (figure 2). The important exception occurs in the group [Carajás and Espírito Santo].

On using thermal amplitude, obtained values generally proved to be coherent with the clusters. The important exception occurs in the group formed by [Itatiaia, Serra dos Órgãos and Curucutu]. These variations could arise from the lack of adequate meteorological records for the elaboration of the climate map at high altitudes, as well as due to the probable differences between local and regional climates.

Pluviometric amplitude in general did not present values coherent with the clusters. The important exception occurs in the groups of the south – [Bagé 1, 2 and 3, Morro da Polícia and Aracuri] and [Urubici and Aparados da Serra], with null values except for Aracuri, presenting 50 mm, but far below the remaining sites, with values over 100 mm. In other words, there is practically no pluviometric variation in this group throughout the year.

As to altitude, it is to be noted that there is agreement with some groups, such as [Bagé 1, 2 and 3], [Urubici and Aparados da Serra] and Espinhaço Range, that include [Mucugê, Pico das Almas, Grão-Mogol and Serra do Cipó]. Nevertheless, in the remaining groups and in general clustering, altitude did not present itself as harmonious.

The first two axis resulting from DCA presented proportions of 15 and 11% of the overall variance. The results of correlation of site scores in the first two axis with selected variables serve as an empirical evidence of the temperature and rainfall effect in the distribution of Poaceae. Amongst the four environmental factors tested in this analysis, three showed a significant correlation with the gradients defined by the site scores: thermal amplitude ($\rho = -0.630$ on axis 1), average annual temperature ($\rho = -0.518$ on axis 1

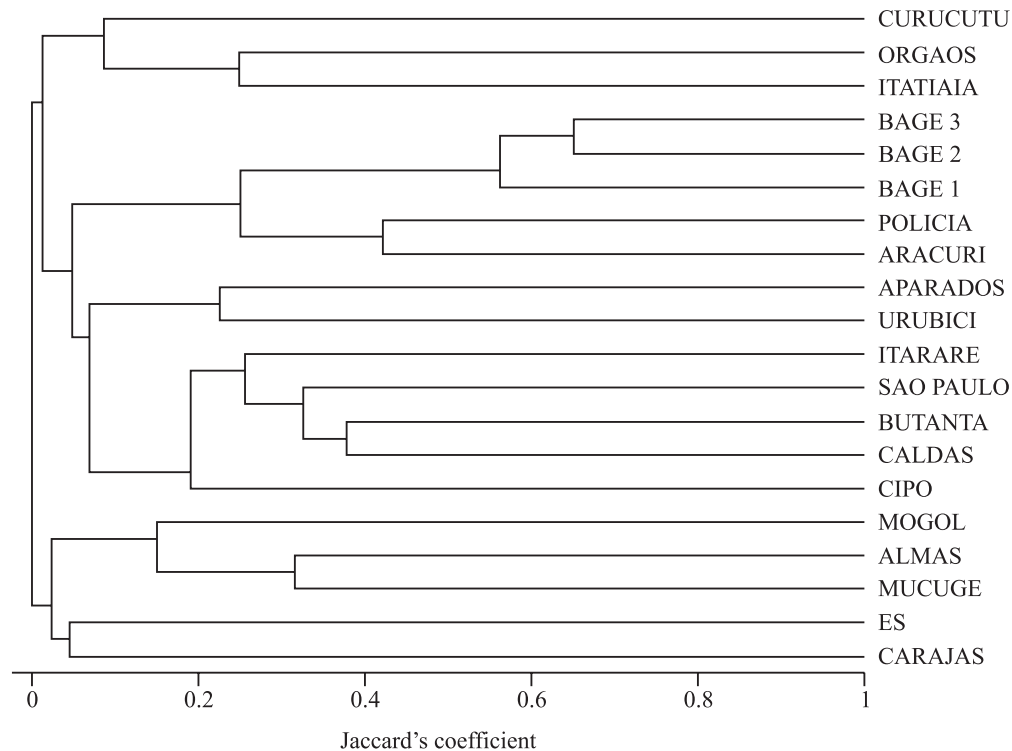


Figure 2. Similarity dendrogram obtained through a complete linkage cluster algorithm applied to a Jaccard's similarity matrix of Brazilian grasslands based on species lists of Poaceae. Site names are as follows: Serra de Carajás (CARAJAS); Mucugê (MUCUGE); Pico das Almas (ALMAS); Grão-Mogol (MOGOL); Serra do Cipó (CIPO); Poços de Caldas (CALDAS); Espírito Santo (ES); Serra dos Órgãos (ORGAOS); Itatiaia (ITATIAIA); City of São Paulo (SAO PAULO); Butantã (BUTANTA); Núcleo Curucutu (CURUCUTU); Itararé (ITARARE); Urubici (URUBICI); Aparados da Serra (APARADOS); Aracuri (ARACURI); Morro da Polícia (POLICIA); Bagé 1 (BAGE 1); Bagé 2 (BAGE 2); Bagé 3 (BAGE 3).

and $\rho = -0.645$ on axis 2) and pluviometric amplitude ($\rho = 0.566$ on axis 1).

Axis 1 and 2 allowed for setting apart four groups corresponding to the site scores, coherent with the result of cluster analysis, three of them being separated by axis 1, and one by axis 2 (figure 3). The resulting groups presented more clearly the affinities associated to site distribution on regional scale. In axis 1 the three separated groups follow a latitudinal gradient, corresponding to the following groupings (number refers to figure 3 delimited groups): 1) the states of Rio Grande do Sul and Santa Catarina; 2) São Paulo State and Poços de Caldas; 3) *campos rupestres* of the states of Minas Gerais and Bahia, and grasslands on ferrallitic crusts of Carajás. On Axis 2 the corresponding distinct group was (4) Itatiaia, Serra dos Órgãos and Espírito Santo, sites usually classified as *campos de altitude*. One-way analysis of variance (ANOVA) performed on the species scores attained on axis 1 and 2, grouped together according to attributes such as photosynthetic type, geographic distribution, tribes and subfamilies,

showed significant results. Significant effects of geographic distribution ($P < 0.01$) were found on axis 1, whilst tribes and subfamily ($P < 0.01$) were found the arrangement of species scores on axis 1 and 2. The groups corresponding to photosynthetic type appeared as significantly segregated considering scores on axis 2 ($P < 0.01$) wherein we can find the correspondent sites of Serra dos Órgãos, Itatiaia and Espírito Santo, with type C3, and the sites of Espinhaço Range with type C4.

Comparing the richness of each grass subfamily in Brazil (Burman 1985), in São Paulo (Longhi-Wagner 2001), and in our final matrix (224 species), it is observed that, proportionally:

- the Panicoideae are equally represented, with 61.26% in Brazil, 58.73% in São Paulo and 56.69% in the present study.
- the Chloridoideae and Aristidoideae treated altogether are also equally represented, with 11.48% in Brazil, 18.09% in São Paulo, and 18.74% in the present study.

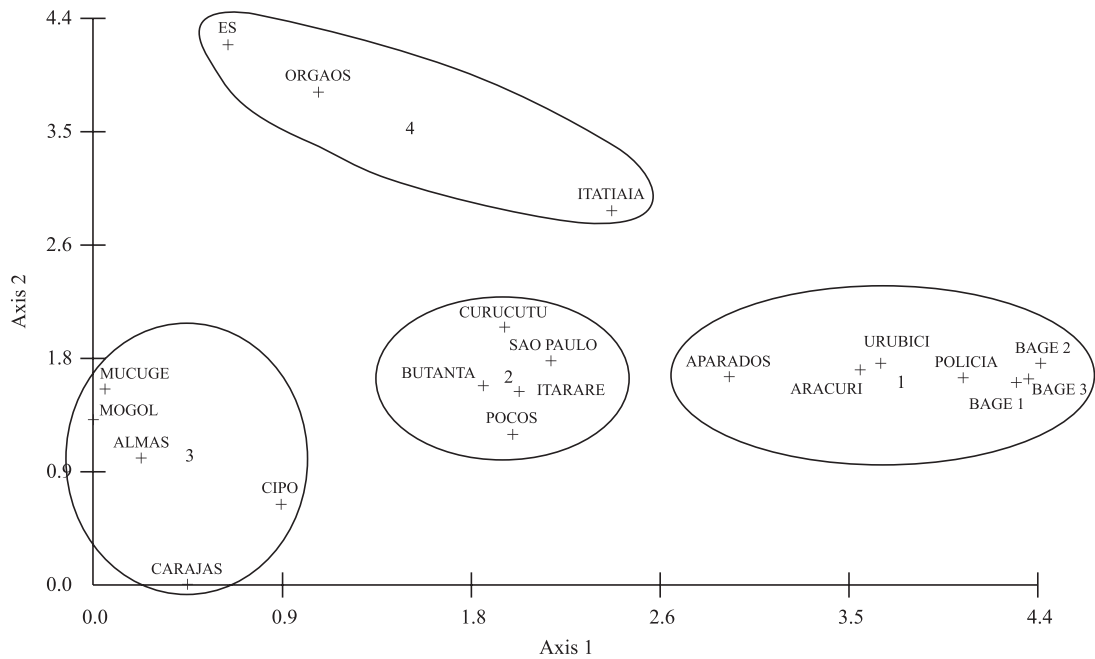


Figure 3. Interpolation of the site scores on the two first axis resulting from the DCA applied on a matrix of Poaceae species collected in Brazilian grasslands. Affinities among sites are delineated in ellipses corresponding to groups as follows: GROUP 1 – Urubici (URUBICI); Aracuri (ARACURI); Aparados da Serra (APARADOS); Morro da Polícia (POLICIA); Bagé 1 (BAGE 1); Bagé 2 (BAGE 2); Bagé 3 (BAGE 3). GROUP 2 – City of São Paulo (SAO PAULO); Butantã (BUTANTA); Curucutu (CURUCUTU); Itararé (ITARARE); Poços de Caldas (POCOS). GROUP 3 – Carajás (CARAJAS); Mucugê (MUCUGE); Pico das Almas (ALMAS); Grão-Mogol (MOGOL); Serra do Cipó (CIPO). GROUP 4 – Espírito Santo (ES); Itatiaia (ITATIAIA); Serra dos Órgãos (ORGAOS).

- the Pooideae showed a higher proportion in our study (19.64%), while they are similarly represented in Brazil (9.36%) and in São Paulo (7.78%).
- the Bambusoideae, treated altogether with the Anomochloideae and the Pharoideae, are equally represented in Brazil (15.50%) and in São Paulo (10.94%), with a lower proportion in our study (1.78%).

Discussion

The richness of grasses plotted in the initial matrix (384 species) represents 28% of the Brazilian grass flora, according to Burman (1985). Considering the grass flora of the São Paulo State (Longhi-Wagner 2001), it is observed that 33.8% of the species occur in open formations (*campos*). São Paulo State is placed on a transition area between the tropical and subtropical zones, encompassing a large diversity of plant formations (tropical wet forests, mixed forests with *Araucaria angustifolia* (Bertol.) Kuntze, semideciduous forests, mangroves, *restingas*, areas of *cerrado*, *campos*, swamps, and several disturbed areas). The fact that four

of the compared sites belong are situated in São Paulo makes it seem that the sampling used in the present analysis is suitable. Nevertheless, further comparison of our data to other open vegetation types in Brazil, like the *campos cerrados*, are necessary in order to obtain a broader panorama.

Data about richness of each grass subfamily are consistent with the distribution patterns of the grass subfamilies (see below), emphasizing a major importance of temperate species (Pooideae) in our data. The similar relative importance of the Panicoideae, Chloridoideae and Aristidoideae reflects a contribution of tropical pattern. The low relative proportion of the Bambusoideae in our study is a consequence of the major importance of that subfamily in forests. That is meaningful in São Paulo State, where 14.52% of the species occur exclusively in forests, and where the Bambusoideae represent 10.94% of the total grass flora in the state.

The groups found in cluster and correspondence analysis (figures 2 and 3) are generally consistent with the grassland vegetation types suggested by Clark (1992) based on a study of *Chusquea*. Specifically, the

grasslands of the Atlantic Range (*e.g.* Itatiaia, Serra dos Órgãos, and Curucutu), the *campos rupestres* of the Espinhaço Range (*e.g.* Mucugê, Pico das Almas, and Grão-Mogol), and grasslands associated with the mixed ombrophilous forest of southern Brazil (*e.g.* Urubici and Aparados da Serra). However, there are exceptions, for example, the position of Espírito Santo together with Carajás and distant from the montane grasslands. The three distinct grassland we identified are also consistent with results of Almeida *et al.* (2004) for Eupatorieae (Asteraceae), a group which is very representative of the grasslands flora, in which the following associations were distinguished: the Mantiqueira (from São Paulo and Minas Gerais), Espinhaço Range (from Minas Gerais) and Campos de Cima da Serra (from Santa Catarina and Rio Grande do Sul).

Perhaps one of our most significant findings is the consistent link between Curucutu, Itatiaia, the transitional grasslands of São Paulo, and the *campos rupestres*. More generally this link reflects similarities between the grasslands of the Núcleo Curucutu and more typically montane grasslands. For example the only species of *Chusquea* found at the Curucutu site was *Chusquea attenuata* (Döll) L. G. Clark, a species that is otherwise recorded only from the montane grasslands of Rio de Janeiro and the *campos rupestres* of Minas Gerais. Moreover, a preliminary evaluation suggests that the Curucutu site be dominated, both in terms of cover area and biomass by C3 species such as *Chusquea attenuata* and *Danthonia montana* Döll. The dominance of C3 species is expected for high altitudes (see below). However, the altitude at the Núcleo Curucutu site (750–850 m) is considerably lower than is typical of a montane grassland (Garcia & Pirani 2003).

However, these species composition data are consistent with studies on isotopic values for present grassland vegetation, owed to the importance of the open habitat for C3 species: Pessenda *et al.* (2009) showed changes in the isotopic values of the soil organic matter of the Núcleo Curucutu, during the Holocene, indicating a higher importance of C4 species in the past, and allied with pollen data, indicating also that the flora may have been assembled progressively. Specifically, these data suggest that a more ancient floristic contribution from the grasslands of Itatiaia was supplemented by species from tropical grasslands to the flora of the Núcleo Curucutu. Certainly floristic connections between different grassland types could have been established as a result of cyclical paleoenvironmental changes that have altered both the distribution and extent of South American grasslands (Behling 2002).

Burkart (1975) proposed a general scheme for classifying the grasslands of South America. Using these criteria the southern Brazilian grasslands fall into two categories. The first contains what Burkart (1975) called tropical and subtropical grasslands (*i.e.* megathermic) including Carajás, Espírito Santo and sites in the Espinhaço Range. These vegetation types are characterized by tropical areas with 20 °C or more mean annual temperature and over 15 °C mean winter temperature and predominance of tribes Paniceae, Andropogoneae, Arundinelleae, Eragrostae, Chlorideae and Aristideae in *campos*. All the remaining locations fall into a temperate grassland category (*i.e.* mesothermic), which is characterized as intermediate in temperature requirements, and grow mainly in areas with 10–20 °C mean annual temperature and 5–15 °C mean winter temperature and large representation of tribes Bambuseae, Triticeae, Danthoniae, Melicae, Stipeae, Chlorideae, Paniceae, Eragrostiae, Andropogoneae and Aristideae in *campos*.

This distinction is broadly consistent with the distribution of the areas along axis 1 in the DCA analysis (figure 3). Specifically, the northernmost locations (*i.e.* Espinhaço Range and Carajás) are on the left and southern sites (*e.g.* Bagé 1, 2 and 3) are to the right. Consistent with their geographical position, sites in São Paulo State are in an intermediate position. This geographic pattern reflects the characteristic distributions of the lineage that occur in each of the areas. For example, at the tribal level Group 1 locations are dominated by a lineage with tropical distribution patterns, Group 2 by tribes that are tropical-subtropical, and the last group by tribes with subtropical distribution patterns. This pattern also holds at the level of subfamily. Sites on the left are dominated by Aristidoideae, Danthonioideae, and Pooideae, the first subfamily predominantly tropical, the others mainly temperate, whereas sites to the right are dominated by Bambusoideae, Chloridoideae and Panicoideae, which have predominantly tropical distribution patterns.

The current study points to temperature as the major environmental factor explaining the observed distribution patterns in Brazilian Poaceae. This is not surprising, since although the family is cosmopolitan various groups within it have highly characteristic distribution patterns or associations with distinct climatic conditions.

Grasses that differ in photosynthetic strategy are successful under quite different climatic conditions. Characteristically locations that fall into Burkart's (1975) megathermic category are dominated by species with C4 photosynthetic type. We see this pattern in the *campos rupestres* of the Espinhaço Range where C4

species represent 59.3-84.8% of the totals; for other megathermic locations (*e.g.* Carajás and Espírito Santo) the two photosynthetic types are almost equally represented.

In the mesothermic locations there is a correlation between increasing altitude and photosynthetic system C3, an observation that is consistent with studies in other mountain systems (*e.g.* Tieszen *et al.* 1979). Specifically, sites at Itatiaia, Serra dos Órgãos, and Urubici, which range in altitude from 1,500 to 2,200 m, are dominated by C3 species, whereas the lower elevation sites (60-1,300 m) at Poços de Caldas, São Paulo, Butantã, Itararé, Morro da Polícia, and Bagé have more C4 species.

The sites at Aracuri, Aparados da Serra, and Curucutu, which are somewhat intermediate in altitude (750-1,400 m), have similar numbers of C3 and C4 species. The broad overlap between the two lower elevation groups may reflect the influence of other environmental factors, such as temperature, or perhaps some are closer to the ocean which depresses the altitudinal zones. Studies on plant community structure will help provide a better understanding of the influence of altitude on the grassland species composition in Brazil (*e.g.* Boldrini *et al.* 1998).

The current results suggest that the characterization of the Southern American grasslands proposed by Burkart (1975) might require some modification in order to be broadly applicable in the Brazilian context. Here we have included several sites – specifically, Aparados da Serra, Urubici, Itatiaia and Serra dos Órgãos – not considered by Burkart (1975). However, based on his criteria these locations should be placed in the mesothermic category. Each of these locations fit well within this category – occurring on acid soils along the Atlantic coast from Rio Grande do Sul to São Paulo they are typically small, fragmented grasslands surrounded by forest. While that author have assigned these locations to the megathermic category in the type “The South Brazilian Campos”, we suggest that the areas in this class may be more appropriately described as mesothermic based on the Poaceae tribes registered there and on climatic characteristics.

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References

- ALMEIDA, A.M., PRADO, P.I. & LEWINSOHN, T.M. 2004. Geographical distribution of Eupatorieae (Asteraceae) in the South-eastern and South Brazilian Mountain Ranges. *Plant Ecology* 174:163-181.
- BEHLING, H. 2002. South and southeast Brazilian grasslands during Late Quaternary times: a synthesis. *Palaeogeography, Palaeoclimatology, Palaeoecology* 177:19-27.
- BOECHAT, S.C. & LONGHI-WAGNER, H.M. 2000. Padrões de distribuição geográfica dos táxons brasileiros de *Eragrostis* (Poaceae, Chloridoideae). *Revista Brasileira de Botânica* 23:177-194.
- BOLDRINI, I.I., LONGHI-WAGNER, H.M., PILLAR, V.D.P. & MARZALL, K. 1998. Aspectos florísticos e ecológicos da vegetação do Morro da Polícia, Porto Alegre, RS, Brasil. *Acta Botanica Brasilica* 12: 89-100.
- BRADE, A.C. 1956. A flora do Parque Nacional do Itatiaia. *Boletim do Parque Nacional do Itatiaia* 5:1-114.
- BURKART, A. 1975. Evolution of grasses and grasslands in South America. *Taxon* 24:53-66.
- BURMAN, A.G. 1985. Nature and composition of the grass flora of Brazil. *Willdenowia* 15:211-233.
- BURMAN, A.G., SENDULKY, T., LONGHI-WAGNER, H.M. & RENVOIZE, S. 1987. Gramineae. In *Flora da Serra do Cipó, Minas Gerais: caracterização e lista de espécies* (A.M. Giulietti, N.L. Menezes, J.R. Pirani, M. Meguro & M.G.L. Wanderley, eds.). *Boletim de Botânica da Universidade de São Paulo* 9:117-123.
- CLARK, L.G. 1992. *Chusquea* sect. *Swallenochloa* (Poaceae: Bambusoideae) and allies in Brazil. *Brittonia* 44: 387-422.
- CLAYTON, W.D. & RENVOIZE, S.A. 1986. *Genera Graminum – grasses of the world*. Royal Botanic Gardens, Kew.
- DIGBY, P.G.N. & KEMPTON, R.A. 1987. *Multivariate analysis of ecological communities*. Chapman and Hall, London / New York.
- GARCIA, R.J.F. 2003. *Estudo florístico dos campos altomontanos e matas nebulares do Parque Estadual da Serra do Mar – Núcleo Curucutu, São Paulo, SP, Brasil*. Tese de doutorado, Universidade de São Paulo, São Paulo.
- GARCIA, R.J.F. & PIRANI, J.R. 2003. Revisão sobre o diagnóstico e caracterização da vegetação campestre junto à crista de serras, no Parque Estadual da Serra do Mar, São Paulo, SP, Brasil. *Hoehnea* 30:217-241.
- GARCIA, R.J.F. & PIRANI, J.R. 2005. Análise florística, ecológica e fitogeográfica do Núcleo Curucutu, Parque Estadual da Serra do Mar (São Paulo, SP), com ênfase nos campos junto à crista da Serra do Mar. *Hoehnea* 32:1-48.

- GIRARDI-DEIRO, A.M., GONÇALVES, J.O.N. & GONZAGA, S.S. 1992. Campos naturais ocorrentes nos diferentes tipos de solo no município de Bagé, RS. 2: fisionomia e composição florística. *Iheringia, Série Botânica* 42:55-79.
- GIULIETTI, A.M., MENEZES, N.L., PIRANI, J.R., MEGURO, M. & WANDERLEY, M.G.L. 1987. Flora da Serra do Cipó, Minas Gerais: caracterização e lista de espécies. *Boletim de Botânica da Universidade de São Paulo* 9:1-151.
- GPWG – Grass Phylogeny Working Group. 2001. Phylogeny and subfamilial classification of the grasses (Poaceae). *Annals of Missouri Botanical Garden* 88: 373-457.
- HARLEY, R. & SIMONS, N.A. 1986. *Florula of Mucugê – Chapada Diamantina – Bahia – Brazil. A descriptive check-list of a campo rupestre area.* Royal Botanic Gardens, Kew.
- HELL, K.G. 1969. Anthropogenic changes in a grassland community. *Revista Brasileira de Biologia* 29:459-468.
- IBGE – Instituto Brasileiro de Geografia e Estatística. 1986. Folha SH 22 – Porto Alegre e parte das folhas SH 21 – Uruguaiana e SI 21 – Lagoa Mirim. Fundação IBGE, Rio de Janeiro.
- JOLY, A.B. 1950. Estudo fitogeográfico dos campos de Butantã (São Paulo). *Boletim da Faculdade de Ciências e Letras da Universidade de São Paulo, Botânica* 8: 5-67.
- LEONI, S. 1997. Catálogo preliminar das fanerógamas ocorrentes no Parque Nacional do Caparaó – MG. *Pabstia* 8:1-28.
- LONGHI-WAGNER, H.M. 2001. Poaceae. *In* Flora Fanerogâmica do Estado de São Paulo (M.G.L. Wanderley, G.J. Shepherd & A.M. Giulietti, eds.). Fapesp / Hucitec, São Paulo, v.1, p.1-291.
- LONGHI-WAGNER, H.M. & BOLDRINI, I.I. 1988. Gramíneas da Estação Ecológica de Aracuri, Esmeralda, Rio Grande do Sul, Brasil. *Iheringia, Série Botânica* 38:21-42.
- LONGHI-WAGNER, H.M. & TODESCHINI, B.H. 2004. Flora de Grão-Mogol, Minas Gerais: Gramineae (Poaceae). *Boletim de Botânica da Universidade de São Paulo* 22:143-165.
- MEDINA, E., MARTINELLI, L.A., BARBOSA, E. & VICTORIA, R.L. 1999. Natural abundance of ^{13}C in tropical grasses from the INPA, Instituto Nacional de Pesquisas da Amazônia, herbarium. *Revista Brasileira de Botânica* 22:43-51.
- MINISTÉRIO DA AGRICULTURA. 1969. Atlas climatológico do Brasil (reedição de mapas selecionados). Escritório de Meteorologia, Rio de Janeiro.
- OLIVEIRA, J.B., CAMARGO, M.N., ROSSI, M. & CALDERANO FILHO, B. 1999. Mapa Pedológico do Estado de São Paulo. Folha 4 – Sudeste. IAC / Embrapa, Campinas.
- OMM – ORGANIZAÇÃO METEOROLÓGICA MUNDIAL. 1975. Atlas climatológico da América do Sul – I – mapas de temperatura e precipitações médias. Cartographia, Budapest.
- PESSENDA, L.C.R., DE OLIVEIRA, P.E., MOFATTO, M., MEDEIROS, V.B., GARCIA, R.J.F., ARAVENA, R., BENDASSOLI, J.A., LEITE, A.Z., SAAD, A.R. & ETCHEBEHERE, M.L. 2009. The evolution of a tropical rainforest / grassland mosaic in southeastern Brazil since 28,000 ^{14}C yr BP based on carbon isotopes and pollen records. *Quaternary Research* 71: 437-452.
- PROJETO RADAM. 1974. Folha SB-22 – Araguaia e parte da folha SC-22 – Tocantins: geologia, geomorfologia, solos, vegetação e uso potencial da terra. Ministério das Minas e Energia, Rio de Janeiro.
- PROJETO RADAMBRASIL. 1981. Folhas SD.24 – Salvador: geologia, geomorfologia, pedologia, vegetação e uso potencial da terra. Ministério das Minas e Energia, Rio de Janeiro.
- PROJETO RADAMBRASIL. 1983. Folhas SF-23/24 – Rio de Janeiro/Vitória: geologia, geomorfologia, pedologia, vegetação e uso potencial da terra. Ministério das Minas e Energia, Rio de Janeiro.
- PIRANI, J.R., MELLO-SILVA, R. & GIULIETTI, A.M. 2003. Flora de Grão-Mogol, Minas Gerais, Brasil. *Boletim de Botânica da Universidade de São Paulo* 21:1-24.
- RAMBO, B. 1956. A flora fanerogâmica dos Aparados Riograndenses. *Sellowia* 7:235-298.
- RENVOIZE, C.A. 1987. A survey of leaf-blade anatomy in grasses XI. Paniceae. *Kew Bulletin* 42:739-768.
- RENVOIZE, C.A. 1995. Gramineae. *In* Flora of the Pico das Almas – Chapada Diamantina – Bahia, Brazil (B.L. Stannard, ed.). Royal Botanic Gardens, Kew, p.704-719.
- RIZZINI, C.T. 1954. Flora Organensis – Lista preliminar dos Cormophyta da Serra dos Órgãos. *Arquivos do Jardim Botânico do Rio de Janeiro* 13:115-259.
- ROSS, J.L.S. & MOROZ, I.C. 1997. Mapa Geomorfológico do Estado de São Paulo – escala 1:500.000. FFLCH-USP / IPT / Fapesp, São Paulo.
- RUSCHI, A. 1950. Fitogeografia do Estado do E. Santo – I – Considerações gerais sobre a distribuição da Flora no Est. do E. Santo. *Boletim do Museu de Biologia “Prof. Mello Leitão”*, Série Botânica 1:1-353.
- SILVA, M.F.F., SECCO, R.S. & LOBO, M.G.A. 1996. Aspectos ecológicos da vegetação rupestre da Serra dos Carajás, Estado do Pará, Brasil. *Acta Amazonica* 26:17-44.
- SORENG, R.J., PETERSON, P.M., DAVIDSE, G., JUDZIEWICZ, E.J., ZULOAGA, F.O., FILGUEIRAS, T.S. & MORRONE, O. 2003. Catalogue of New World Grasses (Poaceae): IV. Subfamily Pooideae. National Museum of Natural History, Washington.

- TIESZEN, L.L., SENYIMBA, M.M., IMBAMBA, S.K. & TROUGHTON, J.H. 1979. The distribution of C3 and C4 grasses and carbon isotope discrimination along an altitudinal and moisture gradient in Kenya. *Oecologia* 37:337-350.
- USTERI, A. 1911. Flora der Umgebung von Stadt São Paulo in Brasilien. Gustav Fischer, Jena.
- ZULOAGA, F.O. 1987. A revision of *Panicum* subgenus *Panicum* section *Rudgeana* (Poaceae: Paniceae). *Annals of Missouri Botanical Garden* 74:463-478.
- ZULOAGA, F.O. & MORRONE, O. 1996. Revisión de las especies americanas de *Panicum* subgénero *Panicum* sección *Panicum* (Poaceae: Panicoideae: Paniceae). *Annals of Missouri Botanical Garden* 83: 200-280.
- ZULOAGA, F.O. & SENDULSKY, T. 1988. A revision of *Panicum* subgenus *Phanopyrum* section *Stolonifera* (Poaceae: Paniceae). *Annals of Missouri Botanical Garden* 75:420-455.
- ZULOAGA, F.O., ELLIS, R.P. & MORRONE, O. 1993. A revision of *Panicum* subgenus *Dichantherium* (Poaceae: Panicoideae: Paniceae) in Mesoamerica, the West Indies, and South America. *Annals of Missouri Botanical Garden* 80:119-190.
- ZULOAGA, F.O., MORRONE, O., DAVIDSE, G., FILGUEIRAS, T.S., PETERSON, P.M., SORENG, R.J. & JUDZIEWICZ, E.J. 2003. Catalogue of New World Grasses (Poaceae): III. Subfamilies Panicoideae, Aristidoideae, Arundinoideae, and Danthonioideae. National Museum of Natural History, Washington.