

Life-form spectra of Brazilian cerrado sites

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Summary

The cerrado, the second largest vegetation type in Brazil, presents a wide physiognomic range, from grasslands to tall woodlands, but with most of its physiognomies fitting the definition of tropical savanna. We compiled Raunkiaer's life-form spectra from cerrado sites and from other vegetation types, comparing them among themselves with ordination analyses. In all cerrado life-form spectra, the main life-form classes were the hemicryptophytes and the phanerophytes, the former prevailing in sites with open physiognomies and the latter prevailing in sites with closed physiognomies. When compared with life-form spectra from other vegetation types, the cerrado sites formed a distinct group, with scores closer to those of the hemicryptophytes and phanerophytes. The cerrado sites distinguished themselves from the savanna sites by their under-representation of therophytes. The ordination plot indicated the likeliness of two gradients in the determination of biological spectra in the world, one from wet to dry, the other from hot to cold, thus stressing the role of precipitation and temperature on plant forms. Even if sometimes criticized in its application on tropical communities, Raunkiaer's system was useful to characterize the cerrado floras and to separate them from other vegetation types.

Key words: cerrado, savanna, life-form, biological spectrum, Raunkiaer, detrended correspondence analysis

Introduction

A plant life-form is usually understood as a growth form that displays an obvious relationship to key environmental factors (MUELLER-DOMBOIS & ELLENBERG 1974), being characterized by the adaptations of plants to certain ecological conditions, as, for example, mean annual temperature or precipitation (MERA et al. 1999). According to BOX (1981), the study of plant life-forms is important for the following reasons: plant life-forms provide the basic structural components of vegetation stands, being the most obvious level of subdivision for describing and explaining vegetation structure; primary physiological processes of plants are controlled by aspects of plant form; and plant form provides an useful means of getting at general principles of plant-environment relations without becoming mired in taxonomic detail.

Attempts to group plant species in life-forms began with HUMBOLDT (1806), who proposed 17 main forms (*Hauptformen*), representing families or groups more or less analogous among themselves. Since then, several

systems to group plants according to their growth habits were published (see DUCKWORTH et al. 2000 for references). In 1904, Raunkiaer proposed a classification system based on the position and degree of protection of the renewing buds, which are responsible for the renewal of the plant aerial body after the unfavorable season. In this system, which was later translated into English (RAUNKIAER 1934), holds the principle, the more pronounced the unfavorable season, the more protected the renewing buds.

There are, in Raunkiaer's classification, five major classes, arranged according to increased protection of the buds: phanerophytes, chamaephytes, hemicryptophytes, cryptophytes, and therophytes. The proportion of each life-form represented in the flora of a particular type of vegetation is called biological spectrum (RAUNKIAER 1934). Raunkiaer's system was modified, among others, by BRAUN-BLANQUET (1928) and MUELLER-DOMBOIS & ELLENBERG (1974), to include plant traits in the favorable season, which were originally neglected by RAUNKIAER (1934).

Although sometimes strongly criticized (e.g., SARMIENTO & MONASTERIO 1983), Raunkiaer's system is still the simplest and, in many ways, the most satisfying classification of plant life-forms (BEGON et al. 1996). This system has been widely applied in many vegetation types to classify plant species in life-forms, as, for example, deserts (QADIR & SHEVITY 1986; EL-DEMERDASH et al. 1994; EL-GHANI 1998), meadows (BEAMAN & ANDRESEN 1966), Mediterranean vegetation (DIMOPOULUS & GEORGIADIS 1992; CHRISTODOULAKIS 1996), prairies (STALTER et al. 1991), savannas (COLE & BROWN 1976; SARMIENTO & MONASTERIO 1983), temperate forests (BUELL & WILBUR 1948; GAO & CHEN 1998), tundra (RAUNKIAER 1934), tropical grasslands (SHANKAR et al. 1991), and tropical rain forests (CAIN et al. 1956).

The Cerrado Domain is the second largest Brazilian phytogeographic province, occupying originally 23% of Brazil's land area (RATTER et al. 1997). As its name implies, in the Cerrado Domain, the cerrado vegetation prevails. The cerrado core area covers the Brazilian Central Plateau, and disjunct areas occur, for example, in the southeastern São Paulo State (RATTER et al. 1997). The cerrado vegetation presents a wide physiognomic range, from grasslands to tall woodlands, but most of its physiognomies fit the definition of tropical savanna (SARMIENTO 1983). Nevertheless, according to COUTINHO (1978), considering the cerrado as a savanna will always be unsatisfactory due to its wide physiognomic variation.

Even if not RAUNKIAER's (1934) main goal, the life-form spectrum of a given site should reflect the vegetation physiognomy. RAUNKIAER (1934) himself stated: "Although not part of the original design, this system of life-forms, while based on purely biological considerations, the adaptations of plants passing the unfavorable season, is in fact clearly a physiognomic system". If the cerrado physiognomic range is wide and the biological spectrum is a good descriptor of physiognomy, then we expect the life-form spectra to vary across the cerrado physiognomic gradient.

In the cerrado, some studies used Raunkiaer's system to classify the sampled species in life-forms. For instance, MANTOVANI (1983) classified the vascular plant species of an outlying cerrado site in life-forms, constructed its biological spectrum, and compared it with life-form spectra from core cerrado sites (WARMING 1892; RATTER 1980). BATALHA et al. (1997), BATALHA & MANTOVANI (2001), and BATALHA & MARTINS (2002) carried out floristic surveys in three cerrado sites and also classified the species in life-form classes. The climatic situation of these cerrado sites is characterized by climate diagrams (WALTER 1976) of Pirassununga (BATALHA et al. 1997), Santa Rita do Passa Quatro (BATALHA & MANTOVANI 2001), and Mineiros (RAMOS-NETO & PIVELLO 2000).

We constructed biological spectra, according to RAUNKIAER's (1934) system, for these cerrado sites, comparing them among themselves and with spectra from other vegetation types. Thus, our aim is to answer the following questions: What are the prevailing life-forms in cerrado sites? Are life-form spectra from open cerrado sites different than those from closed cerrado sites? In spite of the cerrado physiognomic variation, when compared with life-form spectra from other vegetation types, do the cerrado sites appear as a distinct group, especially apart from the savanna sites?

Material and methods

First, we compiled life-form spectra available from cerrado sites. We found three life-form spectra from core cerrado sites, Brasília (RATTER 1980), Emas National Park (ENP) (BATALHA & MARTINS 2002), and Lagoa Santa (WARMING 1892 as compiled by MANTOVANI 1983); and three spectra from outlying cerrado sites, Santa Rita do Passa Quatro (BATALHA & MANTOVANI 2001), Pirassununga (BATALHA et al. 1997), and Mojiguaçu (MANTOVANI 1983). On the one hand, in ENP, Lagoa Santa, and Mojiguaçu, open cerrado physiognomies prevail: *campo limpo* (a grassland), *campo sujo* (a shrub savanna), or *campo cerrado* (a savanna woodland). On the other hand, in Brasília, Pirassununga, and Santa Rita do

Table 1. Life-form spectra of different vegetation types used in the detrended correspondence analysis. Ph = phanerophyte, Ch = chamaephyte, H = hemicryptophyte, Cr = cryptophyte, Th = therophyte.

prevailing vegetation type site	life-form class (%)					reference
	Ph	Ch	H	Cr	Th	
<i>cerrado</i>						
Brasília, Brazil	39.1	13.5	44.9	1.8	0.7	RATTER et al. (1980)
Emas National Park, Brazil	31.6	12.8	49.9	2.0	3.7	BATALHA & MARTINS (2002)
Lagoa Santa, Brazil	28.8	6.1	55.1	5.4	4.6	WARMING (1892)
Mojiguaçu, Brazil	30.9	12.2	47.0	2.1	7.8	MANTOVANI (1983)
Pirassununga, Brazil	40.1	17.1	36.1	1.1	5.6	BATALHA et al. (1997)
Santa Rita do Passa Quatro, Brazil	45.3	17.2	30.0	0.8	6.7	BATALHA & MANTOVANI (2001)

Table 1. (continued)

<i>prevailing vegetation type</i> site	life-form class (%)					reference
	Ph	Ch	H	Cr	Th	
<i>boreal forest</i>						
Terra Nova National Park, Canada	37.0	12.0	32.0	19.0	0.0	CHAREST et al. (2000)
<i>cold steppe</i>						
Akron, Colorado, USA	0.0	19.0	58.0	8.0	15.0	PAULSEN (1915) in CAIN (1950)
Danube, Southeastern Europe	7.0	5.0	55.0	10.0	23.0	BOJKO (1934) in CAIN (1950)
Pamir Mountain	1.0	12.0	63.0	10.0	14.0	PAULSEN (1912) in CAIN (1950)
Yekasternoslaw, Near East	5.0	3.0	55.0	13.0	24.0	PAULSEN (1912) in CAIN (1950)
<i>dry temperate forest</i>						
Sinjawi and Duki regions, Pakistan	31.1	10.7	27.7	2.5	27.9	TAREEN & QADIR (1993)
<i>hot desert</i>						
Bir Ghanam, Lybia	0.0	27.3	9.1	4.5	59.1	QADIR & SHETVY (1986)
Canary Islands	19.0	19.0	10.0	4.0	47.0	BØRGESEN (1924) in CAIN (1950)
California, USA	26.0	7.0	18.0	7.0	42.0	RAUNKIAER (1934)
Eastern Egypt	6.5	29.0	22.0	4.2	38.3	EL-GHANI (1998)
El Golea, central Sahara	9.0	13.0	15.0	7.0	56.0	RAUNKIAER (1934)
Gardhaia, north Africa	3.0	16.0	20.0	3.0	58.0	RAUNKIAER (1934)
Israel	8.0	16.0	16.0	7.0	52.0	DANIN & ORSHAN (1990)
Jazan, Saudi Arabia	10.1	31.5	5.6	4.5	48.3	EL-DEMERDASH et al. (1994)
Lybia	12.0	21.0	20.0	5.0	42.0	RAUNKIAER (1934)
Ooldea, Australia	46.0	14.0	4.0	1.0	35.0	ADAMSON & OSBORN (1922) in CAIN (1950)
Oudja, Morocco	0.0	4.0	17.0	6.0	73.0	BRAUN-BLANQUET & MAIRE (1924) in CAIN (1950)
Transcaspian lowlands	11.0	7.0	27.0	14.0	41.0	PAULSEN (1912) in CAIN (1950)
Zeltin, Lybia	0.0	14.3	9.5	0.0	76.2	QADIR & SHETVY (1986)
<i>hot steppe</i>						
Tucson, USA	18.0	11.0	24.0	0.0	47.0	PAULSEN (1915) in CAIN (1950)
Cyrenaica, north Africa	8.0	14.0	19.0	8.0	50.0	RAUNKIAER (1934)
Madeira Islands	15.0	7.0	24.0	3.0	51.0	RAUNKIAER (1934)
Timbuctu, Africa	24.0	36.0	9.0	6.0	25.0	HAGERUP (1930) in CAIN (1950)
Turhoona, Lybia	5.3	25.7	13.2	15.8	42.1	QADIR & SHETVY (1986)
Zwara, Lybia	6.3	46.9	9.4	3.1	34.4	QADIR & SHETVY (1986)
<i>mediterranean vegetation</i>						
Crete	9.0	13.0	27.0	12.0	38.0	TURRILL (1929) in CAIN (1950)
Icaria, Greece	7.0	7.0	23.0	14.0	49.0	CHRISTODOULAKIS (1996)
Israel	8.0	9.0	23.0	10.0	49.0	DANIN & ORSHAN (1990)
Mount Killini, Greece	10.2	11.0	41.9	13.1	23.9	DIMOPOULUS & GEORGIADIS (1992)
Samos, Greece	9.0	13.0	32.0	13.0	33.0	RAUNKIAER (1934)
Southern France	7.0	13.0	29.0	8.0	43.0	BRAUN-BLANQUET (1925) in CAIN (1950)
<i>prairie</i>						
Konza, USA	11.1	0.9	33.1	24.9	29.9	STALTER et al. (1991)
<i>rain forest</i>						
Alto do Palmital, Brazil	80.0	6.0	11.0	3.0	0.0	CAIN et al. (1956)
Caiobá, Brazil	87.0	7.0	3.0	3.0	0.0	CAIN et al. (1956)
Mucambo, Brazil	95.0	1.0	3.0	1.0	0.0	CAIN et al. (1956)
Queensland, USA	96.0	2.0	0.0	2.0	0.0	CROMER & PRYOR (1942) in CAIN (1950)

Table 1. (continued)

<i>prevailing vegetation type</i> site	life-form class (%)					reference
	Ph	Ch	H	Cr	Th	
<i>savanna</i>						
Barinas, Venezuela	11.0	3.0	18.0	40.0	28.0	SARMIENTO & MONASTERIO (1983)
Calabozo, Venezuela	28.0	7.0	31.0	5.0	29.0	ARISTEGUIETA (1966) in SARMIENTO & MONASTERIO (1983)
Ghanzi, Botswana	19.9	16.4	28.2	7.6	27.9	COLE & BROWN (1976)
Lake Edward, Zaire	5.0	38.0	22.0	5.0	29.0	LEBRUN (1947) in SARMIENTO & MONASTERIO (1983)
Lamto, Ivory Coast	9.0	1.0	62.0	9.0	19.0	CÉSAR (1971) in SARMIENTO & MONASTERIO (1983)
Northern Surinam	8.0	3.0	38.0	28.0	23.0	VAN DONSELAAR-TENBOKKEL HUININK (1966) in SARMIENTO & MONASTERIO (1983)
Ookemeji, Nigeria	30.0	0.0	23.0	21.0	25.0	HOPKINS (1962) in SARMIENTO & MONASTERIO (1983)
Southern Kalahari, Africa	13.3	12.2	34.5	7.4	32.7	COLE & BROWN (1976)
Southwestern Madagascar	21.0	18.0	26.0	3.0	32.0	MORAT (1973) in SARMIENTO & MONASTERIO (1983)
<i>subtropical forest</i>						
Matheran, India	66.0	17.0	2.0	5.0	10.0	BHARUCHA & FERREIRA (1941) in CAIN (1950)
<i>temperate forest</i>						
Alabama, USA	17.6	3.1	47.8	17.1	14.4	ENNIS (1928) in CAIN (1950)
Alberta, USA	25.8	1.8	48.2	17.1	7.1	MOSS (1932) in CAIN (1950)
Cape Breton, USA	14.6	1.8	51.3	25.6	6.7	ENNIS (1928) in CAIN (1950)
North Carolina, USA	59.6	0.0	36.0	4.5	0.0	BUELL & WILBUR (1948)
North Carolina, USA	35.9	2.8	44.1	17.2	0.0	BUELL & WILBUR (1948)
China	31.5	2.3	33.9	19.7	12.7	GAO & CHEN (1998)
Cincinnati, USA	33.6	3.9	34.4	23.4	3.9	WITHROW (1932) in CAIN (1950)
Cincinnati, USA	49.9	4.2	23.5	15.9	6.5	WITHROW (1932) in CAIN (1950)
Connecticut, USA	14.8	2.0	49.4	20.3	13.5	ENNIS (1928) in CAIN (1950)
Scotland	13.5	18.0	53.0	13.0	2.0	WATT (1931) in CAIN (1950)
Georgia, USA	23.0	4.0	55.0	10.0	8.0	RAUNKIAER (1934)
Hondo, Japan	28.9	2.0	47.4	11.7	10.0	HORIKAWA & SATO (1938) in CAIN (1950)
Horto Botânico, Brazil	70.0	4.0	16.0	5.0	5.0	CAIN et al. (1956)
Illinois, USA	16.3	1.3	49.7	18.6	14.1	EWER (1932) in CAIN (1950)
Indiana, USA	14.4	1.9	49.0	18.0	16.7	MCDONALD (1937) in CAIN (1950)
Iowa, USA	15.3	1.0	48.6	20.9	14.2	ENNIS (1928) in CAIN (1950)
Long Island, USA	34.8	10.9	32.6	20.6	1.1	CAIN (1936) in CAIN (1950)
Michigan, USA	22.8	3.9	47.0	16.1	10.2	GATES (1930) in CAIN (1950)
Minnesota, USA	38.5	4.4	41.8	15.4	0.0	BUELL & WILBUR (1948)
Minnesota, USA	35.2	3.2	45.6	16.0	0.0	BUELL & WILBUR (1948)
Mississippi, USA	19.5	3.1	49.4	15.2	12.8	ENNIS (1928) in CAIN (1950)
New York, USA	16.5	5.3	33.3	31.9	13.0	TAYLOR (1918) in CAIN (1950)
Paris, France	8.0	6.5	51.5	25.0	9.0	ALLORGE (1922) in CAIN (1950)
North Carolina, USA	30.0	2.1	45.0	11.1	11.9	STALTER et al. (1991)
Serbia	28.7	11.3	46.2	9.1	4.7	TURRILL (1929) in CAIN (1950)
Stuttgart, Germany	9.0	3.0	54.0	17.0	17.0	RAUNKIAER (1934)
Tennessee, USA	19.6	1.7	52.1	15.1	11.5	CAIN (1945) in CAIN (1950)
Virginia, USA	18.6	1.4	51.7	11.3	17.0	ALLARD (1944) in CAIN (1950)
<i>tundra</i>						
Spitzbergen	1.0	22.0	60.0	15.0	2.0	RAUNKIAER (1934)

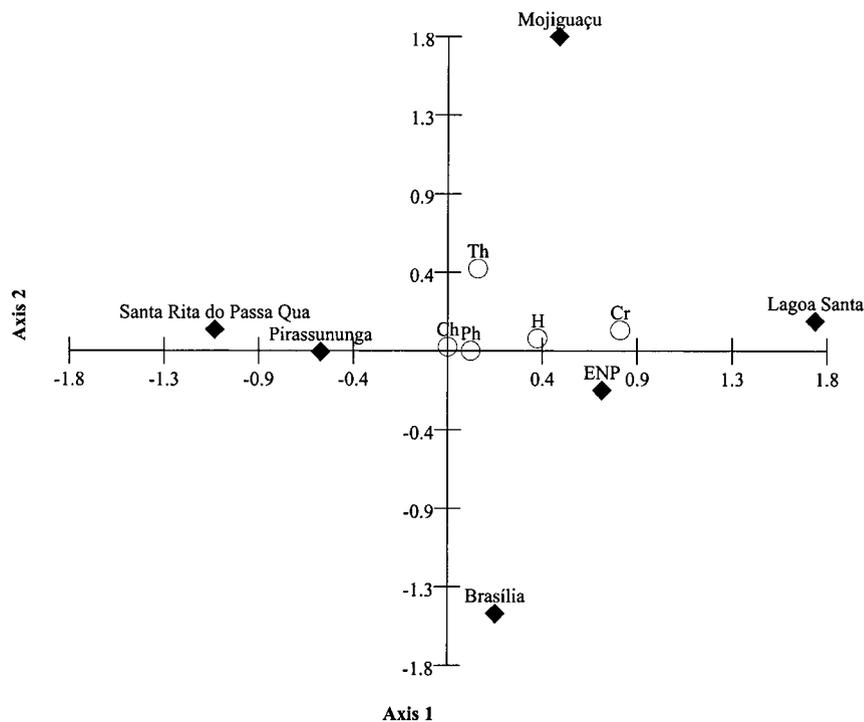


Fig. 1. Detrended correspondence analysis biplot of cerrado sites and life-form classes. Santa Rita do Passa Quatro = 21°36–44'S, 47°34–41'W; Pirassununga = 22°02'S, 47°30'W; Brasília = 15°57'S, 46°53'W; Mojiguaçu = 22°15–16'S, 47°08–12'W; ENP (Emas National Park) = 17°49'–18°28'S, 52°39'–53°10'W; Lagoa Santa = 19°40'S, 43°51'W; Ph = phanerophyte, Ch = chamaephyte, H = hemicryptophyte, Cr = cryptophyte, Th = therophyte.

Passa Quatro, closed cerrado physiognomies prevail: *cerrado sensu stricto* (a woodland) or *cerradão* (a tall woodland).

When comparing these spectra, we used only RAUNKIAER's (1934) five main classes. For example, epiphytes, lianas, vascular semiparasites, and vascular parasites were included in the "phanerophyte" class, as in RAUNKIAER's (1934) original system. As long as RAUNKIAER's (1934) system was modified by other authors (e.g., BRAUN-BLANQUET 1928 and MUELLER-DOMBOIS & ELLENBERG 1974), some distinctions exist among these authors, as, for example, between phanerophytes and chamaephytes, between chamaephytes and hemicryptophytes, and between hemicryptophytes and geophytes. We used RAUNKIAER's (1934) delimitations and, when a given author used another one, we reclassified its list according to RAUNKIAER's (1934) criteria. We did a detrended correspondence analysis (JONGMAN et al. 1995) with these six cerrado sites, plotting then both site and life-form scores.

Second, we compiled life-form spectra from other vegetation types (RAUNKIAER 1934; BUELL & WILBUR 1948; CAIN 1950; CAIN et al. 1956; COLE & BROWN 1976; SARMIENTO & MONASTERIO 1983; QADIR & SHEVTY 1986; DANIN & ORSHAN 1990; STALTER et al. 1991; DIMOPOULOS & GEORGIADIS 1992; TAREEN & QADIR 1993; EL-DEMERDASH 1994; CHRISTODOULAKIS 1996; EL-GHANI 1998; GAO & CHEN 1998; CHAREST et al. 2000). We found 103 spectra, of which we selected 83, including those from the cerrado sites and RAUNKIAER's (1934) normal spectrum. We excluded some spectra in which the prevailing vegetation type was not mentioned and some spectra whose total percentages were different than 100%. Several spectra related by RAUNKIAER (1934) and CAIN (1950), for instance, summed up 99, 102, or 103% and were thus excluded from our analysis. As in the previous case, we used only RAUNKIAER's (1934) five main

classes. Then, we also did a detrended correspondence analysis (JONGMAN et al. 1995), plotting both site and life-form scores. We did the ordination analyses with the MVSP 3.1 software (KOVACH 1999).

Results

In all biological spectra from cerrado sites, hemicryptophytes and phanerophytes were the life-form classes with highest proportions (Table 1). The highest percentage of cryptophytes was found in Lagoa Santa, where they accounted for 5.42% of the total number of species. The highest percentage of therophytes was 7.10%, in Mojiguaçu. In the detrended correspondence analysis (Fig. 1), the first axis explained 75.10% of the variation, and the second axis, an additional 12.35%. On the first axis, Pirassununga and Santa Rita do Passa Quatro presented negative scores, while Brasília, ENP, Lagoa Santa, and Mojiguaçu presented positive scores. On the second axis, Brasília and ENP presented negative scores, while the remaining sites presented positive scores. Regarding the life-form classes, we found higher positive scores for cryptophytes and hemicryptophytes on the first axis, and for therophytes on the second axis.

In the detrended correspondence analysis in which biological spectra from other vegetation types (Table 1) were also included, the first two axes explained 69.97% and 13.81% of the variation, respectively. The ordination biplot of this analysis showed that the cerrado sites

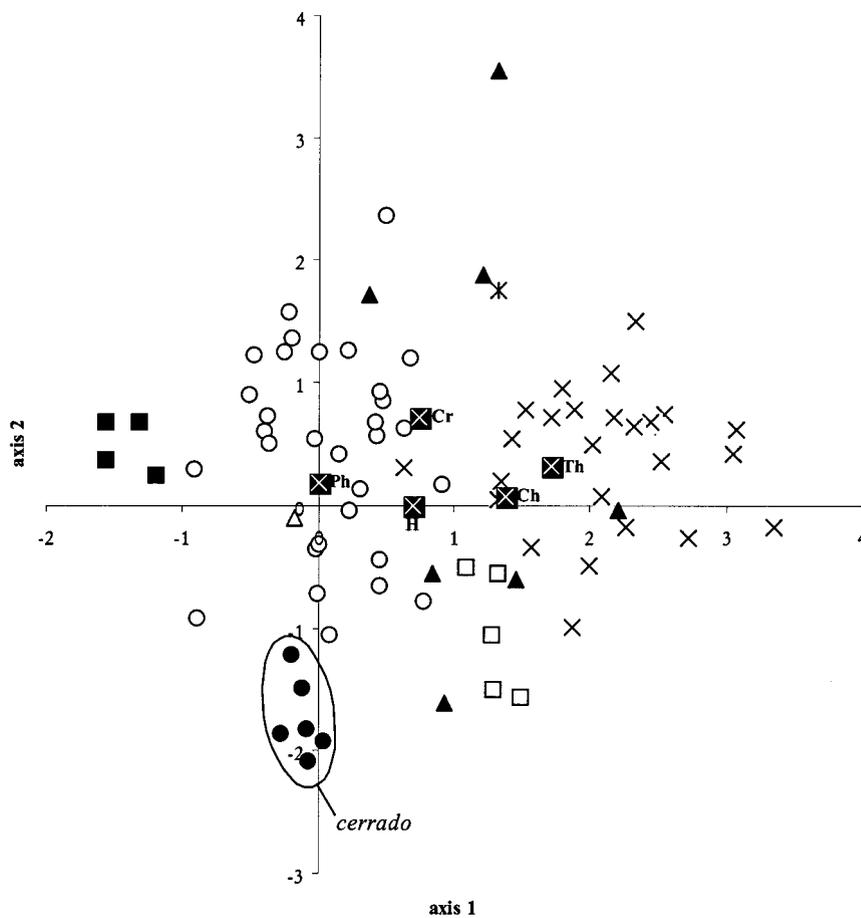


Fig. 2. Detrended correspondence analysis biplot of biological spectra and life-form classes. Ph = phanerophyte, Ch = chamaephyte, H = hemicryptophyte, Cr = cryptophyte, Th = therophyte, ■ = rain forest, ○ = temperate, subtropical, or boreal forest, ● = cerrado, ▲ = savanna, * = prairie, × = mediterranean vegetation, hot steppe, or hot desert, □ = tundra or cold steppe, △ = Raunkiaer's normal spectrum.

formed a group quite distinct from the other vegetation types, with scores closer to those of the phanerophytes and hemicryptophytes (Fig. 2). The savanna sites appeared with higher scores on both axes, although widely dispersed. Sites under dry climate appeared generally with higher scores in the first axis than sites under wet climate. Sites under cold climate presented positive scores on the first axis and negative scores on the second axis.

Discussion

The most represented classes in the cerrado life-form spectra (WARMING 1892; RATTER et al. 1980; MANTOVANI 1983; BATALHA et al. 1997; BATALHA & MANTOVANI 2001; BATALHA & MARTINS 2002) were the hemicryptophytes and the phanerophytes. RAUNKIAER (1934), in his life-form classification, used a trait that would indicate an adaptation of plants to a particular climate, namely the degree of protection of the renewing buds; therefore, the vegetation would be an expression of the climate. According to SARMIENTO & MONASTERIO (1983), although the seasonal stress imposed by

extended drought allows the plants a wide range of responses, generally, in savanna floras, the hemicryptophytes and cryptophytes are the prevailing life-forms. Considering the cerrado sites, this statement was partially corroborated, since the hemicryptophytes were one of the prevailing life-form, but the cryptophytes were under-represented.

According to RAUNKIAER (1934), a hemicryptophytic phytoclimate corresponds to a cold-humid climate, typical of high latitudes or high altitudes. SARMIENTO & MONASTERIO (1983) criticized the applicability of Raunkiaer's system to tropical communities, because it classifies life-forms on the supposition that the limiting factor for plant growth is low winter temperatures, which obviously is not an important ecological factor in such communities. Even if in RAUNKIAER's (1934) model a direct correspondence between climate and life-forms exists, other factors play a significant role in the determination of the occurrence of the cerrado and its physiognomic gradient.

LOPES & COX (1977), for instance, pointed out five theories proposed by several authors to explain the occurrence and the physiognomic gradient of the cerrado: water stress, fire, water logging, oligotrophic

scleromorphism, and aluminum toxicity. The theory of soil toxicity was enlarged to include also the excess of manganese (MALAVOLTA et al. 1977). These factors could somehow be analogous to the stress imposed by cold in high latitude or altitude regions and, in this case, they would favor species with renewing buds protected at the level of the soil surface, as the hemicryptophytes, or under the ground, as the cryptophytes. Xeromorphic features are frequently present in plants adapted to conditions of nutrient deficiency, which may have evolved independently in response to aridity and low fertility (SMALL 1973; BECKER et al. 1999).

If there are other variables, besides the climatic ones, involved in the determination of the occurrence of the cerrado, then biological spectra of cerrado sites should reflect it. For example, if two cerrado sites are under the same climate, but for other reasons present different physiognomies, then their biological spectra should be different (MANTOVANI 1983). Indeed, when we compared the cerrado sites with the correspondence analysis, those in which open physiognomies prevail (ENP, Lagoa Santa, and Mojiguaçu) appeared in the upper diagonal of the ordination biplot, while those in which closed physiognomies prevail (Brasília, Pirassununga, and Santa Rita do Passa Quatro) appeared in the lower diagonal.

In the physiognomic gradient of the cerrado, the importance of trees and shrubs increases from open to closed physiognomies (COUTINHO 1978). We expect then, from open to closed physiognomies, a decrease in the proportion of hemicryptophytes, cryptophytes, and therophytes and an increase in the proportion of phanerophytes. This pattern was found in the comparison of the cerrado sites, when those sites in which closed physiognomies prevail (Brasília, Pirassununga, and Santa Rita do Passa Quatro) presented a higher proportion of phanerophytes; and those sites in which open physiognomies prevail (ENP, Lagoa Santa, and Mojiguaçu) presented a higher proportion of hemicryptophytes and cryptophytes.

In the ordination analysis in which spectra from other vegetation types were included, the cerrado sites formed a distinct group, with scores closer to those of phanerophytes and hemicryptophytes, as expected by the prevalence of these life-form classes in their biological spectra. Although most cerrado physiognomies fit the definition of savanna (SARMIENTO 1983), the cerrado sites grouped quite apart from the savanna sites, due mainly to the higher proportion of therophytes in the latter. Thus, our study corroborates COUTINHO's (1978) idea that the cerrado cannot be considered simply as a savanna.

RAUNKIAER (1934) expected the therophytes, the best protected plants against drought, to appear under hot and dry climates, in which the favorable season is very short. Indeed, in our analysis, the scores of annual

plants were closer to those from deserts, steppes, and Mediterranean vegetation sites, all under hot and dry climates. Almost every author dealing with the cerrado vegetation noted the under-representation of annual plants (SARMIENTO & MONASTERIO 1983).

Water stress is not considered the main environmental factor determining the occurrence of the cerrado, since shrubs and trees have deep root systems and access to water during the whole year (NAVES-BARBIERO et al. 2000). However, herbaceous species, as the therophytes, suffer a period of water shortage in the dry season (SARMIENTO & MONASTERIO 1983). Comparing the values of net photosynthesis, stomatal conductance and transpiration rate in woody plants of two cerrado physiognomies (*cerradão* and *cerrado sensu stricto*) in dry and wet seasons, MORAES & PRADO (1998) observed a severe restriction of gas exchange during the dry period in the winter, together with partial leaf fall and a decrease of osmotic potential of the remaining leaves (osmotic adjustment) in response to water shortage. Hence, we could expect a higher representation of annual plants in the cerrado, but no author found that. If savanna and cerrado climates are similar (SARMIENTO & MONASTERIO 1983), then the under-representation of therophytes in the cerrado could be due to the low fertility of its soils (LOPES & COX 1977). This under-representation of therophytes in the cerrado vegetation poses an interesting question and deserves further investigation.

The ordination biplot also showed forest sites with scores closer to the phanerophytes, and tundra or cold steppe sites closer to the chamaephytes, in accordance with RAUNKIAER's (1934) hypotheses. Among the forests, the temperate and boreal forests presented a higher proportion of hemicryptophytes than the rain forests, getting closer to the hemicryptophytic climate, as proposed by RAUNKIAER (1934). The ordination plot indicated the likeliness of two gradients in the determination of biological spectra in the world, one from wet to dry (from left to right), the other from hot to cold (from top-left to bottom-right), thus stressing the role of precipitation and temperature on plant forms.

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