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Distribution of homobaric and heterobaric leafed species in the Brazilian Cerrado and seasonal semideciduous forests

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ABSTRACT

Plant species can be classified into heterobaric and homobaric, depending on whether their leaves present bundle sheath extensions (BSEs) (heterobaric) or not (homobaric). Incidences of the two leaf types seem to be related to growth environment and the light stratification. The Brazilian Cerrado and seasonal semideciduous forests are contrasting environments mainly with regard to irradiance and air humidity. However, studies comparing the distributions of homobaric and heterobaric species in these vegetation types are lacking. We investigate the presence/absence of leaf BSEs across diverse habits (herbs, shrubs and trees) in a seasonal semideciduous forest, cerrado *sensu stricto* (open physiognomy) and cerradão (forest physiognomy) to evaluate the influence of plant habit and growth environment on the distribution of homobaric and heterobaric species. Leaves from 131 species in 54 angiosperm families were analysed using standard methods of light microscopy. The distribution of the different leaf types in each environment was analysed using the χ^2 test and Fisher's exact test ($P < 0.05$). Homobaric and heterobaric leafed species occur in all environments and do not correlate with plant habit. Of the total number of species examined, 103 (78.6%) exhibited homobaric leaves and 28 (21.4%) presented heterobaric leaves. Of the total of heterobaric species, 8.8% occurred in the seasonal semideciduous forest, 50% in the cerradão and 41.2% in the cerrado *sensu stricto*. This model of distribution may be related to the higher irradiances in Cerrado. Homobaric leaves of shrubs and trees were thicker in all environments, while heterobaric leaves of herbs were thicker in the Cerrado. This study finds a tendency for the distribution pattern of homobaric or heterobaric leaves to reflect both the growth environment and the taxonomic grouping. Since leaf type is a constitutive characteristic, interspecific differences in leaf type may reflect particular physiological behaviours, linking them to success in colonising particular environments.

1. Introduction

Based on the presence or absence of bundle-sheath extensions (BSEs) in their leaves, plant species are generally classified into two groups – those having heterobaric leaves and those having homobaric leaves. In a heterobaric leaf, the parenchyma or sclerenchyma cells of the BSE extend to the epidermises on each side of the leaf (Kenzo et al., 2007), effectively isolating the leaf airspaces into numerous compartments (Terashima, 1992). In contrast, the BSEs are lacking in homobaric leaves, so the internal airspaces are essentially continuous (Kenzo et al., 2007).

The presence/absence of BSEs affects both the mechanical and the physiological properties of the two leaf types (Kenzo et al., 2007; Liakoura et al., 2009; Inoue et al., 2015). In homobaric leaves, the structural continuity of the leaf allows more efficient gas diffusion (Rhizopoulou and Psaras, 2003). On the other hand, the BSEs of heterobaric leaves may act as water (Wylie, 1943) and light conduits (Karabourniotis et al., 2000) to the inner layers of the mesophyll and may also give additional mechanical support to the leaf blade (Esau, 1977). In addition, higher rates of photosynthesis and transpiration have been recorded in heterobaric species (Inoue et al., 2015). Therefore, the architectural arrangement of a leaf's tissues may influence its physiological performance (Reich et al., 2003). This adaptation has been considered important in terms of specific growth environments and/or life-form types (Kenzo et al., 2007; Rossato et al., 2015). In addition, studies indicate that homobaric leaves are thicker than heterobaric leaves (Boeger et al., 2016) and present a higher proportion of photosynthetic areas in the mesophyll which is advantageous for capturing diffuse light (Terashima, 1992).

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Table 1
Data on the environmental features of the studied sites (CER: cerradão; CSS: cerrado *sensu stricto*; SSF: seasonal semideciduous forest. PPFD: Photosynthetic photon flux density).

Environmental characteristics	Studied sites		
	CER	CSS	SSF
Average daily PPFD (μmol m^{-2} s^{-1})	437	804	337
Maximum – average – minimum daily relative humidity of air (%)	52–41–30	49–39–28	72–69–65
Average annual precipitation (mm)	1454	1454	1428
Length of dry season (months)	5	5	5
Average altitude (m)	720	720	786
Minimun – average – maximun temperature (°C)	12.5–20.8–29	13.4–21.7–30	12–20.3–28.5
Soil type	latosols and argisols	latosols and argisols	podzolics and litholics

Recent studies have sought to correlate leaf type with environment, with life-form type and with plant habit (Kenzo et al., 2016). Thus, some researchers have shown that heterobaric species are more common in dry and/or cold deciduous forests (Terashima, 1992), while homobaric species predominate in the evergreen forests of humid and warm climates (Boeger et al., 2004; Kenzo et al., 2007). However, the distribution of light intensity, temperature and humidity is variable even inside a tropical evergreen forest (Whitmore, 1988). In this sense, Kenzo et al. (2007) proposed that the leaf type seems also to be correlated to the life form type of the species in a tropical forest, *i.e.* emergent, canopy, understorey, or canopy-gap species. Species in the upper canopy and in canopy gaps are exposed to higher irradiance and lower humidity than species in the understorey (Whitmore, 1988) favouring the abundance of heterobaric leafed species in these higher canopy layers and in gaps (Kenzo et al., 2007). Moreover, heterobaric leaves seem to be more common among tree and shrub species than among herbs in xeric environments (Liakoura et al., 2009).

The Brazilian savanna (local name Cerrado) and seasonal semideciduous forests present contrasting environmental features, mainly regarding irradiance (Hoffman and Franco, 2003; Tresmondi et al., 2015). The Cerrado is a vegetation mosaic composed of different physiognomies varying from open vegetation with continuous herbaceous and sparse woody plants (cerrado *sensu stricto*) to a true forest formation (cerradão). This ecosystem is characterised by a strongly seasonal climate with distinctive rainy summers and dry winters. The soils are deep and well drained, acidic, extremely low in available nutrients and with high aluminium contents (Oliveira and Marquis, 2002). The seasonal semideciduous forest is characterised by dense vegetation with a closed canopy and a layered structure, with trees up to 30 m high. The species are conditioned to eutrophic soils (Scariot and Sevilha, 2005) and seasonal climates that determine the semideciduous nature of the forest canopy. In this sense, we hypothesise that the environmental conditions of the Cerrado could favour the higher abundance of heterobaric leafed species. However, studies comparing the distribution of homobaric and heterobaric leaves in the Cerrado and forest are lacking.

Here, we investigate the presence/absence of leaf BSEs across diverse habits (herbs, shrubs and trees) and different vegetation types (seasonal semideciduous forest, cerrado *sensu stricto* and cerradão) in order to evaluate the influence of plant habit and growth environment on the distribution of homobaric and heterobaric leafed species. In addition, we measured the blade thickness looking for a relation of this anatomical trait with the leaf type.

2. Material and methods

2.1. Areas of study and plant material

This study was conducted during 2014 and 2015 in two contiguous Cerrado physiognomies (cerradão and cerrado *sensu stricto*) located in Palmeira da Serra farm, Pratânia municipality (22° 48′ 20″ S, 48° 44′ 36″ W) and in a remnant area of seasonal semideciduous forest located in Edgardia farm, in Botucatu municipality (22° 52′ S, 48° 26′ W), both in central-west region of São Paulo State, in southeastern Brazil. Pratânia and Botucatu municipalities are 37 km distant from each other. The south marginal areas of the Cerrado and the seasonal semideciduous forest are both characterised by marked climatic seasonality (Tresmondi et al., 2015). The climate in these areas is Cfa according to Köppen classification, that is, temperate (mesothermic) climate, typical of constantly humid region (Setzer, 1966), with rains in the summer and drought in the winter, and with small hydric deficiency from April to August (Cunha and Martins, 2009).

The environmental characterization of each area is summarized in Table 1.

The cerradão (Fig. 1a) and cerrado *sensu stricto* (Fig. 1b) are contiguous areas and encompass a total of 180 ha. In the Cerrado area, 120 species of angiosperms belonging to 52 families were investigated in the cerradão and 168 species belonging to 51 families in cerrado *sensu stricto* (Ishara, 2010). The studied forest fragment (Fig. 1c) was 56 ha in size, where 61 tree species belonging to 31 angiosperm families were inventoried (Fonseca and Rodrigues, 2000).

Based on previous phytosociological surveys (Fonseca and Rodrigues, 2000; Ishara et al., 2008; Carvalho et al., 2010; Jorge et al., 2015) a square of 400 m^2 was selected inside cerradão, cerrado *sensu stricto* and forest that encompassed a representative portion of the vegetation with heterogeneity of species and habits. Ten fully-expanded and non-senescent leaves were collected from each of the plants enclosed, in the rainy season (December 2014 to February 2015). In all, 51 species were collected in the cerradão (27 trees, 17 shrubs and 7 herbs), 55 species in the cerrado *sensu stricto* (16 trees, 24 shrubs and 15 herbs) and 49 species in the seasonal semideciduous forest (22 trees, 17 shrubs and 10 herbs). A total of 131 species belonging to 54 angiosperm families were examined. Since some species occurred in two or more environments, the total number of plants studied was 155 (Table 2).

Vouchers were incorporated in the collection of Herbarium Irina Delanova de Gemtchujnicov (BOTU), IBB UNESP, Botucatu/SP.

2.2. Light microscopy

For anatomical analysis, samples excised from the median region of the leaf blade were fixed in FAA 50 (Johansen, 1940) and processed according to two protocols. Most samples were cross-sectioned (12 μm thickness) using a Ranvier microtome, stained with safranine and astra blue (Bukatsch, 1972) and mounted in glycerine jelly. Others were dehydrated in an alcohol series and embedded in methacrylate resin, cross sectioned (5 μm in thickness) using a rotatory microtome and stained with toluidine blue O 0.05% pH 4.7 (O'Brien et al., 1964). Permanent slides were mounted using synthetic resin.

The slides were examined under a light microscope (Olympus BX 41) equipped with a digital camera. The leaf thickness was cal-