Identification and Distribution of C3 and C4 Grasses in Open and Shaded Habitats in São Paulo State, Brazil[1]

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ABSTRACT

The photosynthetic pathway of grasses collected in several vegetation formations in São Paulo State, Brazil, was identified by leaf anatomy. Of the 78 species collected, 48 sun species and seven shade species possessed the C4 pathway. Twenty-three species possessed the C3 pathway, of which three were sun species and 20 were shade species. This result indicates that the C4 species are more abundant in open habitats and C3 species in shaded habitats. The data also show the taxonomic distribution of the photosynthetic pathways. All genera of the collected species are exclusively C3 or C4, except *Panicum* which has both C3 and C4 species.

RESUMO

A via do metabolismo fotossintético de espécies de gramíneas coletadas em diversas formações vegetais do Estado de São Paulo, Brasil, foi identificada pela anatomia foliar. Das 78 espécies coletadas, 55 foram identificadas como C4, sendo 48 de sol e sete de sombra; e 23 como C3, sendo três de sol e 20 de sombra. Os dados indicam que plantas C4 ocupam principalmente os ambientes abertos enquanto que as C3, os ambientes sombreados. Os dados mostram também a distribuição taxonômica das vias fotossintéticas. Todos os gêneros das espécies coletadas são exclusivamente C3 ou C4, á exceção de *Panicum,* que apresenta tanto espécies C3 quanto C4.

Since the discovery of the different types of photosynthetic pathways in higher plants, it has been shown that C3 and C4 species can differ in anatomical, biochemical, physiological, and ecological aspects (Welkie & Caldwell 1970, Edwards & Walker 1983, Pearcy & Ehleringer 1984). Teeri and Stowe (1976) have shown the influence of climate variables on the distribution of C4 grasses in North America, and since then various authors have been studying the relationship between the distribution of C4 species and climatic patterns: Chazdon (1978) in Costa Rica, Meinzer (1978) in Central America, Rundel (1980) in Hawaii, Stowe and Teeri (1978) in North America, Vogel *et al.* (1978) in South Africa, and Hattersley (1983) in Australia. Generally, these authors have noted that C4 species usually occupy hot and arid habitats, supporting the hypothesis that C4 photosynthetic metabolism is specifically an adaptation to these environments (Laetsch 1974).

However, some differences were observed among the different groups of plants studied. For example, Teeri and Stone (1976) found that the highest minimum temperature during growth was the climatic variable most correlated with the distribution of C4 grasses in North America while water deficits of the soil were most correlated with the distribution of C4 Dycotyledoneae in the same region (Stowe & Teeri 1978). Moreover, Hattersley (1983) concluded that no relationship has been established between irradiance and geographic distribution of the species. He argued that the available irradiance data are inappropriate to this kind of analysis because they "disregard" the existence of a vegetation canopy. This observation considers the fact that beyond the action of climatic variables in a geographic level, there is the action of local variables in the distribution of C3 and C4 species. According to Teeri (1979) the macroscale climatic variables provide only gross approximations of the influence of the climate on a plant tissue during its growth, and on a microclimatic scale, other variables are probably important in determining the performance of C3 and C4 species.

Our objective was to identify by leaf anatomy the photosynthetic pathway of grasses from different vegetation formations of the State of São Paulo, Brazil, and correlate the distribution of these species with the local conditions of irradiance.

MATERIAL AND METHODS

The vegetation formations which were exposed directly to the sun all day were classified as open habitats and those which were not exposed directly to the sun (under a vegetation canopy) were classified as shaded habitats.

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TABLE 1. *Species collected with identification of the vegetational formation, type of habitat (sun and shade) and the photosynthetic pathway.*

		C3	C4
Mangrove	Sun		*Spartina brasiliensis* Raddi
Flood prairie	Sun	*Panicum laxum* Sw.	*Arundinella* sp. *Hypoginium virgatum* (Desv.) Dandy *Setaria geniculata* (Lam.) Beauv.
Coastal tropical rain forest	Sun	*Hymenachne* sp.	*Digitaria insularis* (L.) Ruz ex. Ekman
	Shade	*Acroceras zizanioides* (H.B.K.) Dandy *Chusquea* sp. *Olyra latifolia* L. *Merostachys ternata* Nees *Olyra* sp. 1 *Oplismenus hirtellus* Roem. & Schult. *Streptochaeta spicata* Schrad ex. Nees	
Upland forest	Sun	*Panicum laxum* Sw.	*Setaria geniculata* (Lam.) Beauv. *Eragrostis* sp. 2
	Shade	*Ichnanthus pallens* (Swartz) Munro ex. Benth. *Ichnanthus* sp. 1 *Olyra latifolia* L. *Olyra humilis* Nees *Oplismenus hirtellus* Roem. & Schult. *Panicum multinodosum* Swallen *Panicum pilosum* Sw. *Pharus lappulaceus* Fusee-Aublet *Streptochaeta spicata* Schrad ex. Nees	*Paspalum mandiocanum* Trin. *Setaria poiretiana* (Schult.) Kenth. *Setaria scabrifolia* Kenth. *Setaria* sp. 1 *Setaria* sp. 2
Cultivated and ruderal fields	Sun		*Andropogon bicornis* L. *Aristida* sp. 2 *Brachiaria decumbens* Stapf *Brachiaria humidicola* (Rendle) Schweick *Brachiaria plantaginea* (Link.) Hitch. *Cenchrus echinatus* L. *Chloris* sp. *Digitaria insularis* (L.) Ruz ex. Ekman *Digitaria* sp. 1 *Hyparrhenia rufa* (Nees) Stapf *Melinis minutiflora* Beauv. *Panicum maximum* Jacq. *Paspalum notatum* Flugge *Paspalum paniculatum* L. *Pennisetum purpureum* Schum. *Rhynchelitrum repens* (Willd.) C. E. Hubb. *Setaria geniculata* (Lam.) Beauv. *Sporobolus* sp. 1
Rainy and high elevation subtropical forest	Sun		*Axonopus* sp. 3 *Digitaria* sp. 2 *Eragrostis* sp. 5 *Eragrostis* sp. 6 *Paspalum polyphillum* Nees ex. Trin. *Paspalum* sp. 1 *Paspalum* sp. 2 *Setaria* sp. 3 *Sporobolus* sp. 3 *Sporobolus* sp. 4 *Sporobolus* sp. 5
	Shade	*Chusquea capituliflora* Trin. *Ichnanthus pallens* (Swartz) Munro ex. Benth. *Lasiacis divaricata* (L.) Hitch. *Oplismenus hirtellus* Roem. & Schult. *Panicum laxum* Sw. *Panicum millegrana* Poiz *Panicum pilosum* Sw.	

TABLE 1. *Continued.*

		C3	C4
		Pharus lappulaceus Fusee-Aublet *Pseudechinolaena polystachia* (H.B.K.) Stapf	
Cerrado	Sun	*Panicum laxum* Sw. *Ichnanthus* sp. 3	*Andropogon selloanus* Hack. *Aristida riparia* Trin. *Aristida* sp. 1 *Axonopus* sp. 1 *Axonopus* sp. 2 *Digitaria insularis* (L.) Ruz ex. Ekman *Eragrostis* sp. 1 *Eragrostis* sp. 3 *Eragrostis* sp. 4 *Erianthus* sp. *Gymnopogon foliosus* Nees *Leptocoryphium lanatum* Nees *Loudetiopsis* sp. *Panicum cervicatum* Chase *Rytachne* sp. *Setaria geniculata* (Lam.) Beauv. *Sporobolus* sp. 2 *Tristachya leiostachya* Nees
	Shade	*Echinolaena inflexa* (Poiz) Chase *Ichnanthus pallens* (Swartz) Munro ex. Benth. *Lasiacis* sp.	

The plants were collected from open habitats in Cerrado (a savanna like formation) at Itirapina Experimental Station (22°15′S; 47°48′W) and at Campininha Experimental Station (22°22′S; 46°57′W) of the Forestry Institute of São Paulo State, in a flood prairie in Itirapina, in cultivated and ruderal fields in Campinas (22°53′S; 47°05′W), and in a mangrove in Ubatuba (23°27′S; 45°05′W). The shaded habitats studied were an upland forest at Santa Genebra Farm in Campinas, the rainy and high-elevation subtropical forest at Japy Range Mountain in Jundiaí (23°11′S; 45°54′W), and the coastal tropical rain forest at Juréia Ecological Station (25°00′S; 47°55′W). Specimens of each species were deposited at Campinas State University Herbarium (UEC).

Leaf anatomy was observed in leaf blade transverse sections. Segments of grass leaf blades were fixed in FAA in the field and with this material two lamina (at least) with several leaf blade transverse sections were prepared. The leaf sections were stained with Safranin and Alcian-blue and set in Canada balsam or stained with Safranin and Fast Green and set in commercial gelatin. The leaf blade transverse sections were examined under a light microscope.

The plants which presented a radial clorenchyma and bundle sheath cells with preeminent chloroplasts were classified as C4 species and those without this feature were classified as C3 species (Laetsch 1974, Baskin & Baskin 1981).

RESULTS

Of the 78 species collected, 55 exhibited the C4 photosynthetic pathway and 23 exhibited the C3 photosynthetic pathway. Of the C4 species, 48 were collected in open habitats and seven in shaded habitats, while of the C3 species 20 were collected in shaded habitats and only three in sun habitats (Table 1). The C4 species were predominant in the vegetational formations with open habitats, like mangrove, flood prairie, cultivated and ruderal fields, and Cerrado. On the other hand the majority of C3 species were encountered in the vegetational formations with shaded habitats like coastal tropical rain forest, upland forest, and rainy and high-elevation, subtropical forest.

Some C4 species were collected in shade, but always in a less dense vegetation like forest boundary or trails where the diffusive light was most intense. Some of the C3 species were collected in sun, two of them in a saturated soil: *Hymenachne* sp. in Itamambuca river at Ubatuba in the coastal rain forest and *Panicum laxum* in streams and flooded areas in upland forest, flood prairie, and Cerrado. This species was also encountered in a stream in the rainy and altitudinal subtropical forest, but in a shaded habitat (Table 1).

Two C4 species were collected in the closed vegetational formations, *Digitaria insularis* in coastal rain forest and *Setaria geniculata* in upland forest. These species were encountered in open and disturbed sites in these formations, such as gaps and roads. They are weed species and certainly are not native plants for these formations.

DISCUSSION

The results are consistent with previously observed patterns that C4 grasses occupy "preferentially" open habitats with high light intensity while C3 grasses occupy more frequently shaded habitats. It was verified that both C3 and C4 grasses occur in shaded and open habitats, but the proportion of C4 grasses in open sites is higher (Teeri 1979). Chazdon (1978) and Meinzer (1978) have showed similar data, indicating that this distributional pattern of C3 and C4 grasses is common to tropical America.

The occurrence of C4 species in shade shows that some C4 plants can utilize low light intensity. For example, Winter *et al.* (1982) showed that the production of dry matter by *Microstegium vimineum,* a C4 grass, was similar both at 100 percent and at 18 percent of total sunlight. They suggested that C4 species do not necessarily have growth limitations at low light intensity. According to Pearcy and Ehleringer (1984) the rarity of C4 species in shaded habitats may be due to an insufficient time for an evolutionary adaptation of this photosynthetic pathway to these environments, since the pathway has evolved only recently in hot and arid environments.

Species with the C3 pathway can also utilize high light intensities (Teeri 1979). Two of the three C3 sun species collected were encountered in sites with saturated soils, indicating that these species need high water availability in the soil. It has already been demonstrated that the proportion of C3 species in moist environments is higher than that of C4 species (Tieszen *et al.* 1979). Also, a replacement of C4 grasses by C3 grasses has been observed with an increase in moisture availability in the soil at Serra dos Carajás, Pará State, Brazil (Joly, unpublished data). These results corroborate the idea that the distribution of C3 and C4 species can depend on the action of more than one environmental variable. Archer (1984) believes that the distribution and performance of C3 and C4 plants depend not only on the action of one variable but on the integration of several variables such as temperature, water availability, soil texture, and light intensity.

The results also show the differential taxonomic distribution of C3 and C4 species collected; all the genera are exclusively C3 or C4, except the genus *Panicum* which has both photosynthetic pathways.

Our data were compared with those from Burman and Filgueiras (in press) who show the photosynthetic pathways of the genera of grasses encountered in Brazil. The identification of the photosynthetic pathways in our study is in agreement with the identification presented by them except for *Chusquea, Merostachys, Streptochaeta,* and *Pseudechinolaena,* not mentioned by these authors.

The genus *Panicum* was unique in showing species of both photosynthetic pathways, and several genera in higher plants have C3 and C4 species (Teeri 1982). Moss *et al.* (1969) suggested that the existence of C3 and C4 species in the same genus, although in different subgenera, indicate that these groups should be considered distinct taxa because they may not be genetically related.

As for the subfamilies, Bambusoideae was identified as C3. It has been shown that all the studied species of this subfamily show C3 features (as the ones studied by us), and possibly all of its species are C3 (Waller & Lewis 1979). Aristidoideae and Eragrostoideae possessed a C4 photosynthetic pathway, while Panicoideae contained both C3 and C4 species. Waller and Lewis (1979) believe that the presence of some C3 species in this subfamily indicates the necessity of a taxonomic revision. The identification of the photosynthetic pathway utilized by plants and the construction of lists of C3 and C4 species are important tools in many fields of plant biology. The list of C3 and C4 species shown in this study will complement others (Downton 1975, Waller & Lewis 1979) as well as amplify the knowledge about native Brazilian grasses.

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