Polish Journal of Environmental Studies Vol. 6, No. 4 (1997), 17–21

Potential Desiccation Tolerant Vascular Plants from Southeastern Brazil

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Received 28 October, 1996
Accepted 3 January, 1997

Abstract

A survey of the capacity to endure desiccation was obtained for several Brazilian rock outcrop plants. Seedlings, leaves and entire plants were subjected to dehydration. After dehydration, survival was observed as the ability to recover growth, chlorophyll content and/or by the absence of leakage of leaft contents. A total of 30 species growing in rock outcroppings in southeastern Brazil showed some ability to undergo extreme dehydration. The species belong to the cryptogams *Polypodiaceae, Pteridaceae, Schizaeaceae* and *Selaginellaceae* and to the angiosperms *Cyperaceae, Poaceae* and *Velloziaceae.* All cryptogams were homeochlorophyllous. Among the angiosperms *Microchloa indica* (Poaceae) was the only species with the capacity to retain chlorophyll content during dehydration. All species showed some evidence of desiccation tolerance similar to that previously reported for tolerant angiosperms in Africa. The data suggest that rock outcroppings from the southeastern and central regions of Brazil give support to typical vegetation in which a great number of species exhibit a desiccation-tolerant comportment.

Keywords: desiccation tolerance, rock outcroppings, southeastearn Brazil, water stress

Introduction

The majority of the vascular plants survive water stress by reducing transpiration between living tissues and the environment [14]. However, a small group of species of vascular plants are characterized by their capacity to survive the equilibrium of internal water content with the atmosphere during extreme water depletion [4].These plants can endure intense water stress periods by a state of anabiosis, when physiological activity is suppressed. As a rule, the recovery of normal physiological activity is achieved during favorable conditions. Plants that endure extreme drought at equilibrium with air of low humidity are named "poikilohydric" [12, 21] or "desiccation tolerant" [14]. Some desiccation tolerant vascular plants can survive losses of more then 90% of their normal water content [8]. This figure is remarkable, considering the structural complexity of a typical vascular plant. Other peculiarities are uniquely found in desiccation-tolerant plants, such as the loss of their chlorophyll contents during dehydration. This phenomenon is termed "poikilochlorophylly" [12], as opposed to chlorophyll conservation or homeochlorophylly. In general, all desiccation tolerant plants seem to be found in habitats with a very shallow soil layer, mainly over rock outcroppings [1, 8]. Due to soil scarcity, this habitat shows recurrent and intense drought periods. Desiccation tolerant plants found in these areas show a typical comportment, which includes leaf rolling or folding concomitant with changes in coloration.

Desiccation tolerant species of vascular plants are particularly common among cryptogams [4]. Among angiosperms, few genera have been found to be desiccation tolerant. The known desiccation tolerant angiosperms are mainly from south and southwestern Africa [7,8,9,10]. Some well recognized species belong to the monocotyledonous *Cyperaceae, Velloziaceae* and *Poaceae*. In Brazil few desiccation tolerant species were characterized. Reports and papers refer to *Selaginella convoluta* (Arn.) Spring. [17, 19], the fern *Anemia anthriscifolia*, and the angiosperm *Xerophyta plicata* Spreng [6, 15]. However, a survey of the cryptogams on rock outcroppings in southeastern Brazil suggests that there are many ferns with poikilohydric behavior [5]. The few known Brazilian desiccation tolerant plants are typical of rock outcroppings from the coast of the southeastern region (e.g. Rio de Janeiro) and northeastern "caatinga" (rocky desert). As an exception, the fern *Anemia anthriscifolia* occurs in

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the "cerrado" formation (a type of neotropical savanna). Outside Brazil, the other neotropical angiosperm known to have desiccation tolerance is the fern *Satureja gilliesii*, found in Chile [16].

Our interest in desiccation tolerant plants was motivated by their rarity, practically unknown ecology, and the lack of knowledge about their role in Brazilian rock outcropping vegetation. Preliminary observations of this vegetation indicate that a considerable proportion of the species may be desiccation tolerant. In southeastern Brazil, rock outcroppings with typical vegetation are very frequent near highly urbanized areas. This may represent a potential source of disturbance, mainly by factors such as fire and intentional denudation. Moreover, considering the narrow distribution of rock outcropping species, they can be threatened with extinction. Here we give a survey of potentially desiccation tolerant plants associated with the rock outcropping vegetation of southeastern Brazil.

Materials and Methods

Surveyed areas

Localities were selected by the occurence of rock outcroppings with representative vegetation under low disturbance impact. The type of bedrock included sandstone, quartzite, ferric laterite, gneiss and granite. The main areas belong to the southeastern region of Brazil, including the states of Sao Paulo, Rio de Janeiro, Espirito Santo and Minas Gerais and are situated between 20°50',and 27°54' latitude and 40°43' and 47°39' longitude. Two species from central (Brasilia-DF, 15°46' S) and northern (Carajas-PA, 05°22' S) Brazil were also included, as material was available during the dry period.

Plant Material, Leaf Water Status and Chlorophyll Analyses

During drought periods plants occuring in rock outcroppings were checked for leaf rolling and/or changes in coloration. Plants showing these properties were collected and identified. Leaf samples and entire plants were collected and transported in dry state to the laboratory. Entire plants were removed with soil, potted and maintained in a greenhouse for at least 2 months until the experiments were performed. When available in the field, seeds were also collected. The ability to endure desiccation was investigated under controlled conditions of low air humidity or at room temperature (around 75% relative humidity). Samples consisted of seedlings obtained by sowing on wet filter paper, leaves and entire plants.

The leaf water saturation deficit (WSD) was calculated as described by Barrs [3]:

$$WSD = 100 - \left\{ \frac{(LFW)-(LDW)}{(LSFW)-(LDW)} \times 100 \right\}$$

where: LFW is the leaf fresh weight; LDW is the leaf dry weight and LSFW means leaf saturated fresh weight after 24h under water.

Chlorophyll a and b contents of leaf samples were measured in acetone extracts according to Arnon [2]. Controlled conditions of relative humidity were ob-

Table 1. Surveyed areas with rock substrate characteristics and altitude.

Code	Locality	Substrate	Altitude
I	Itanhangá, Rio de Janerio -RJ	granite	0-200 m
II	Imbuí, Rio de Janerio -RJ	granite	0-200 m
III	Itacoatiara, Rio de Janerio -RJ	granite	0-200 m
IV	Pedra Bonita, Rio de Janerio -RJ	granite	700 m
V	Urca, Rio de Janerio -RJ	granite	0-200 m
VI	Ilha de Santana, Marcaé -RJ	granite	0-100 m
VII	Pedra do Oratório, Araras -RJ	granite	1000 m
VIII	Pedra Dubois, Madalena -RJ	granite	1200 m
IX	Monte Aga, Piuma -ES	granite	0-500 m
X	Serra da Moeda, MG	granite	1000 m
XI	Serra do Rola Moça, MG	ferric laterite	1500 m
XII	Serra do Cipó, MG	quartzite	1500 m
XIII	Brasília, DF	fine sand	300 m
VXIV	Carajás, PA	ferric laterite	>300 m
XV	Pedra Grande, Atibaia -SP	granite	>1000 m
XVI	Cuscuzeiro, Analândia -SP	sandstone	>1000 m
XVII	Itatiaia, Itatiaia -RJ	granite	>1500 m

tained by concentrated solutions of salts [22] or sulfuric acid [20] mantained in closed containers under room temperature which ranged from 21°C to 27°C.

Selected healthy seedling were maintained at low humidity levels of 10% and 0% in glass vessels for over one month. Survival was recorded by the ability of the seedlings to reattain growth. At least 100 healthy plantlets were tested in 4 replicates. Non-desiccated controls were left under conditions of saturated humidity for a minimum of one month. Leaf sections were left at low humidity of aprox. 10% (over $CaCl_2$) from 2 weeks to several months. Survival was observed by placing leaf cuts in distilled water and checking for the chlorophyll levels (in poikilochlorophyllous plants) or the absence of leakage of leaf contents. Each species was evaluated by two replicates of 40 leaf sections or entire leaflets. Potted plants were allowed to dry for up to 6 months, leading to equilibrium with variable greenhouse humidities. Recovery of desiccated leaves, and resumption of growth, were considered to indicate plant survival. Several samples, consisting of single or grouped plants were tested.

Results and Discussion

Localities and site descriptions are listed on Table 1. A total of 30 species with properties indicating desiccation tolerance were found (Table 2). The species belong to the cryptogams *Polypodiaceae, Pteridaceae, Schzaeaceae* and *Selaginellaceae*, all of which are homeochorophyllous, and to the angiosperms *Cyperaceae, Poaceae* and *Velloziaceae*. The only homeochlorophyllous angiosperm found was *Microchloa indica.* Not all of the test for desiccation tolerance could be applied to each species due to the limited availability of plant material. However, all species tested showed at least one of the traits of desiccation tolerance. Plantlets and potted mature plants regularly exhibited 100% recovery after exposure to low relative humidities. Although leaf sections reacted in the same way some species revealed lower recovery capacity.

Chlorophyll contents of desiccated leaves of poikilochlorophyllous plants were always zero. In contrast, recovered leaves showed variable contents, probably due to differences in initial leaf characteristics and rehydration time needed for total activation of physiological processes (data not shown). Leaf sections of *Trilepis lhotzkiana* sometimes showed difficulty to reattain chlorophyll,although whole plants were capable of full recovery. In the field, some species exhibited signals of incomplete recovery of leaf structure. This was always observed as preservation of the dry state on the tips of the leaves. Once removed and subjected to full rehydration under laboratory conditions, unrecovered leaf tips reattain the normal state. An unexpected behavior was found in the Velloziaceae *Aylthonia gentianoides*, which exhibits desiccation-intolerant leaves in mature plants. Despite this sensitivity of adult plants to drought, seedlings typically show desiccation tolerance. In mature plants the leaves were regenerated by sprouting of the apical meristem, which apparently endures desiccation.

Whole plants of *Microchloa indica* (Poaceae), the homeochlorophyllous angiosperm, sometimes failed to survive desiccation. A number of dehydrated leaves failed to recover when desiccation was attained at the laboratory. Full recovery of desiccated plants was rapidly followed by the formation of new leaves, which were frequently desiccation intolerant. More commonly the leaf bases were the only revivescent parts in this plant.

The survey done during drought periods revealed that most of the vegetation established over rock outcrops on shallow soil clumps shows desiccation tolerant comportment. Other potentially desiccation tolerant plants were found living over pebbles and crevices. Considering the preliminary nature of this work, and the knowledge about the occurrence of desiccation tolerant plants in other parts of the world, the number of species showing desiccation tolerance in the surveyed areas is striking.

Observation of the comportment of desiccation tolerant plants in the field may suggest distinctive intesities and frequencies of desiccation that could be related to the degree of sun exposure and soil depth. Plants from shaded habitats or deep soil were found to be desiccated less often than plants exposed, or rooted in, thin soil layers. Tolerant angiosperms more commonly occur in the sunny and more frequently drought-prone habitats and tolerant cryptogams are more common in shaded sites. An exception was found in species of the genus *Selaginella,* occuring in exposed sites.

One might find the occurrence of such an extreme strategy like desiccation tolerance unexpected in areas situated besides very humid environments such as a tropical rain forest. Even in localities situated far from the rain forest, the pluviosity does not characterize a dry climate. Thus, the dry conditions are related to substrate-lacking soil, which causes extreme and unpredictable dry periods. Desiccation tolerance can be considered a proper strategy for such conditions as it permits survival for long spells without any water and can be displayed at any time when the environment dries out. The complete recovery of the active state to full growth is achieved rapidly when water is available. During periods of water availability, desiccation tolerant plants behave as common drought avoiding plants, accruing the advantages of this strategy [15].

It is also interesting to note that some of these plants may perform the role of pioneers in local lithoseres, as suggested by African rock outcroppings [8, 13]. In the surveyed areas, the pioneer character appears to be remarkable for *Trilepis* species and has to

Table 2. List of surveyed species showing at least one evidence for desiccation tolerance.

Species	Occurence (numbers refers to Table 1)	Seedlings	Plant Material Leaves	Whole plants
SELAGINELACEAE				
Selaginella convoluta (Arn.) Spring.	I, II, VIII,IX	+	+	
Selaginella sellowii Hieron.	I, III, IV, V	+	+	+
SCHIZEACEAE				
Anemia flexuosa (Sav.) Sw.	I		+	
Anemia villosa Humb.&Bonpl.	I to VII		+	+
PTERIDACEAE				
Doryopteris collina (Raddi) J.Sm.	I to VIII, X, XI, XII, XV		+	+
Doryopteris ornithopus (Mett. ex H. et B.)	XII, XVI		+	
Hemionitis tomentosa (Lam.) Raddi.	V, XVI		+	
VELLOZIACEAE				
Aylthonia gentianoides (Goeth. & Henr.) Menezes	XII	+		+–
Barbacenia flava Mart. ex J.A. & J.H. Schult.	XII	+		+
Barbacenia fragrans Goeth. & Henr.	XVI			+
Pleurostima fanniae Menezes	VIII	+	+	+
Pleurostima gouneleana (Beauv.) Menezes	XVII			
Pleurostima purpurea (Hook.) Raf.	II, III, V	+	+	+
Pleurostima seubertiana (Goeth. & Henr.) Menezes	VII	+	+	
Pleurostima spectabilis (Smith & Ayensu) Menezes	IX	+		
Vellozia albiflora Pohl	VII, X, XI,	+	+	+
Vellozia candida Mikan	I to IV, VIII	+	+	+
Vellozia caruncularis Mart & Seubert	X, XI, XII			+
Vellozia compacta Mart. & Schult.	X		+	+
Vellozia glochidea Pohl	XIV	+		
Vellozia nanuzea L.B. Smith & Ayensu	XVI	+		
Vellozia squamata Pohl	XIII	+		
Vellozia variabilis Mart. ex J.A. & J.H. Schult	XVI	+		
Vellozia variegata Goethart & Henrard	VII	+	+	
Xerophyta plicata (Mart.) Spreng.	VI to IX	+	+	+
POACEAE				
Microchloa indica Beauv.	XI	+	+–	+
CYPERACEAE				
Trilepis ciliatifolia Koyama	VIII	+		
Trilepis lhotzkiana Nees	I to IV, X, XII. XVI	+	+	+
Trilepis microstachya H. Pfeiff.	VII			+
Trilepis sp.	VII to IX	+	+	+

(+) positive; (–) negative; ( ) not tested

be clarified in further research. In granitic outcroppings in Nigeria, Hambler [12, 13] observed desiccation tolerance and the pioneer role of *Afrotrilepis*, a genus related to the South American *Trilepis* which can be considered an "ecological counterpart" of *Afrotrilepis*. There are also many similarities between reported characteristics of *African Velloziaceae* and the species found in Brazil, concerning habitat, growth-formation and desiccation tolerance [11, 18]. We expect to find a kind of ecological correspondence between the species referred to in this paper and species mentioned for African rock outcroppings.

In summary, we believe that desiccation tolerance should be the most important strategy for exploitation of rocky habitats in the tropics and we expect to find a greater number of desiccation tolerant species in the surveyed regions as more localities are examined in the future. Assessment of the ability of plants to endure desiccation in the seedling state is a new approach in the study of this strategy of drought survival. We consider the capacity of revivescence shown by the seedling as the best evidence for the ecological advantage of desiccation tolerance for plant establishment. Thus, this work provides material for a wide range of research lines on desiccation tolerance, from community ecology to molecular biology.

Acknowledgements

We are grateful to Prof. Dr Ulrich Lüttge and Prof. Dr Hubert Ziegler for helpful discussions and comments on the manuscript. We also thank Prof. Deia Maria dos Santos for providing us with scientific facilities and our colleagues at the Universidade Federal do Rio de Janeiro for helpful field assistance.

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