

## Germination characteristics of *Syngonanthus* seeds (*Eriocaulaceae*) in *campos rupestres* vegetation in south-eastern Brazil

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### Abstract

The present study evaluated the size and germination characteristics of seeds of seven species of *Syngonanthus* (distributed among four sections) that occur in different microhabitats in *campos rupestres* vegetation in Minas Gerais State, to determine if (1) the germination responses of the various species characterize a single germination pattern for the genus; and (2) there is a correlation between the germination characteristics and the geographic distribution as well as the microhabitat of the different species. The experiments were undertaken with recently collected seeds exposed to a 12-h photoperiod and continuous darkness, at constant temperatures of 10–40°C (at intervals of 5°C) in germination chambers. The results indicated the existence of a pattern of reduced seed size and light requirements for germination within the genus. The geographic distribution of different species of the genus cannot be explained by the responses of seed germination to different temperatures, but suggests some relationship to their edaphic microhabitats. Therefore, germination characteristics of the populations studied may have been selected to colonize specific environments at different soil water conditions.

**Keywords:** dormancy, geographic distribution, light, seed size, soil water status, temperature

### Introduction

The *Eriocaulaceae* are perennial or, rarely, annual plants that vary in height from 0.5 cm to 2.0 m (Andrade, 2007); they have pantropical distributions but are

concentrated in the Neotropical region (Giulietti and Hensold, 1991). The Cadeia do Espinhaço mountain range in Minas Gerais State, Brazil, is considered to be the principal centre of diversity for this family, and more than 90% of its species are endemic (Giulietti *et al.*, 2005). The family is characterized by its rosette habit, from which scapes emerge bearing inflorescences of the capitulate type. The genus *Syngonanthus* Ruhland is represented by approximately 200 species (Mabberley, 1987), and was divided by Ruhland (1903) into five sections based on floral characteristics: *Syngonanthus* Ruhland, *Carphocephalus* (Koern.) Ruhland, *Chalarocaulon* Ruhland, *Eulepis* (Bong. ex Koern.) Ruhland and *Thysanocephalus* (Koern.) Ruhland. A number of species of this genus are popularly known as 'sempre-vivas' (ever-living plants) and have significant commercial value (Giulietti *et al.*, 1988). Endemism and the intensive harvesting of these plants for commercial purposes have resulted in some species being classified as threatened with extinction (Giulietti *et al.*, 1988). The different species occur in regions of *campos rupestres* of the Cadeia do Espinhaço Range with distinct soil water conditions, such as sandy soils, bogs and/or swampy areas, and at altitudes that vary between 800 and 2000 m (Giulietti *et al.*, 2000). The occurrence of these plants across various habitats is reflected in physiological, anatomical and morphological adaptations that vary from species to species, allowing them to survive under even very adverse environmental conditions (Angosto and Matilla, 1993; Menezes and Giulietti, 2000). As such, the chances of a non-dormant seed developing into a healthy seedling will depend on the environmental conditions it can tolerate during germination (Sheldon, 1974).

Germination is one of the most critical stages in the life cycle of any plant (Kigel, 1995; Villalobos and Peláez, 2001), and two of the most important environmental factors influencing (or controlling) this process are light and temperature (Baskin and Baskin, 1988; Bewley and Black, 1994; Benech-Arnold

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and Sánchez, 1995). Germination patterns reflect the habitat, life strategy, phylogenetic relationships and the geographical distribution of a given species (Schütz and Rave, 1999; Ellison, 2001). Strategies and life cycles are generally similar among congeneric species and differences in their germination behaviour may reflect adaptations to the habitats in which they are found (Specht and Keller, 1997; Van Assche *et al.*, 2002).

Considering their phylogenetic proximity and the occurrence of species in different microhabitats throughout the region of *campos rupestres* vegetation, the germination characteristics and seed size of seven species of *Syngonanthus* were evaluated in the present study under laboratory conditions to test if (1) the germination responses of these different species allow us to characterize a particular germination pattern for the genus; and (2) there is a correlation between the germination characteristics and the geographic distribution as well as the microhabitat of the different species.

## Materials and methods

### Study area

The Cadeia do Espinhaço Range has been declared a Biosphere Reserve by Unesco (Unesco, 2005). It covers an area approximately 1000 km long (generally N–S) by 50–100 km wide through the states of Minas Gerais and Bahia (Brazil) (Menezes and Giulietti, 2000). The regional climate is considered tropical altitudinal mesothermic (Cwb in the classification of Köppen). The dry season occurs during the austral winter and lasts 6–7 months, followed by the summer rainy season, lasting 5–6 months. The average annual precipitation rate is approximately 1600 mm (Marques

*et al.*, 2000). The classification of the habitats of species as seasonally xeric, mesic and wetland, was solely based on the soil water status during the year. In the seasonally xeric environments the soil is sandy and allows for more water drainage and therefore the species are subject to water deficit during the dry season. The mesic habitat remains moist throughout the year, with humidity close to saturation of the soil during the rainy season, and the wetland habitat is permanently flooded.

### Species studied

Capitula of seven species of *Syngonanthus* – *S. aciphyllus* (Bong.) Ruhland, *S. anthemidiflorus* (Bong.) Ruhland, *S. bisulcatus* (Korn.) Ruhland, *S. caulescens* (Poir.) Ruhland, *S. gracilis* (Bong.) Ruhland, *S. verticilatus* (Bong.) Ruhland and *S. vernonioides* – were collected in areas of *campos rupestres* vegetation in the Cadeia do Espinhaço Range in Minas Gerais State, south-eastern Brazil. Information concerning the geographic distribution of the species, as well as additional collection data is provided in Table 1. Collections of capitula were undertaken during the months of July/August (with the exception of *S. vernonioides*, collected in November) when these structures were mature and their seeds were dispersed. The capitula were subsequently triturated in a blender and sieved to separate the seeds (Oliveira and Garcia, 2005).

### Seed size

Data concerning the length (mm) and width (mm) of the seeds was based on a sampling of 100 individuals, and data of dry mass (mg) was based on a sampling of 400 seeds distributed over four lots of 100 seeds. As the seeds of *S. gracilis* were very light, however, four lots of

**Table 1.** List of species, their geographical distributions and data concerning the location of collections of the studied populations

Sections/species	Geographical distribution	Geographic coordinates	Altitude (m)	Habitat
Section <i>Carphocephalus</i>				
<i>S. caulescens</i>	América do Sul	19°22'56"S/43°35'43"W	819	Wetland
Section <i>Eulepis</i>				
<i>S. aciphyllus</i>	Itacambira/Chapada do Couto to Serra do Cipó	18°05'23"S/43°20'41"W	848	Seasonally xeric
<i>S. bisulcatus</i>	Serra de Grão-Mogol to Serra do Cipó	19°20'27"S/43°35'07"W	1022	Mesic
Section <i>Syngonanthus</i>				
<i>S. anthemidiflorus</i>	Diamantina to Serra do Cipó	19°23'08"S/43°35'34"W	811	Seasonally xeric
<i>S. gracilis</i>	América do Sul	20°25'48"S/43°29'60"W	1580	Seasonally xeric
<i>S. verticilatus</i>	Serra de Grão-Mogol to Serra do Cipó	19°15'35"S/43°33'05"W	1330	Mesic
Section <i>Thysanocephalus</i>				
<i>S. vernonioides</i>	Small part of Serra do Espinhaço	18°33'47"S/43°38'35"W	1300	Seasonally xeric

150 seeds were used to determine their average dry mass. The seeds were dried to a constant weight at 105°C and then weighed using an analytical balance. Fresh seeds were digitally photographed and their length and width measurements were calculated using Quantikov Image Analyzer software (Pinto, 1996).

### Germination

Germination tests were performed in germination chambers under a 12-h photoperiod ( $30 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) and continuous darkness at constant temperatures from 10 to 40°C at intervals of 5°C. *S. vernonioides* was not tested at 10°C due to its very low germinability at 15°C. For the germination tests, the seeds were placed in Petri dishes lined with a double layer of filter paper dampened with a nystatin solution ( $100,000 \text{ UI ml}^{-1}$ ) (Oliveira and Garcia, 2005) that maintained a high humidity in the dishes for the entire duration of the experiments. The dark treatment was obtained by wrapping the Petri plates in aluminium foil and black polyethylene bags. The germination of these seeds was evaluated under green light. A total of 200 seeds distributed over four replicates of 50 seeds was used in all light and temperature treatments. Germination was defined as radicle emergence and was verified on a daily basis using a stereomicroscope. The samples were observed until the germination response became constant.

### Statistical analyses

All of the data were submitted to non-parametric statistical analyses as they did not demonstrate normality using the Shapiro–Wilk test nor homogeneity using the Brown–Forsythe test (JMP software package, 2002; SAS Institute Inc., Cary, North Carolina, USA). Germination rate was calculated ( $V = 1/\text{MT}$ , where  $\text{MT} = \Sigma(Dn)/\Sigma n$ ; where  $n$  is the number of seeds that germinate on day  $D$ , and  $D$  the number of days from the beginning of the germination experiment (Labouriau, 1983). The optimal germination temperature was defined as that temperature showing the greatest germinability associated with the greatest germination velocity (Labouriau, 1983). The germinability and average velocity data were compared using the Kruskal–Wallis test, followed by pair comparisons using the Conover test at a 5% significance level (Conover, 1999). The statistical analyses were performed using BrightStat software (Stricker, 2008).

## Results

### Seed size

The different species of *Syngonanthus* produced very small elliptical seeds that were reddish brown when

mature. Sizes varied significantly among the various species, ranging from 0.38 to 0.79 mm in length, and from 0.21 to 0.42 mm in width, and had dry weights between 0.014 and 0.095 mg (Table 2). The seeds of *S. vernonioides* had the largest values for all three parameters; the seeds of *S. gracilis* and *S. aciphyllus* had the shortest lengths; the species *S. verticilatus* and *S. gracilis* had the smallest widths; and the seeds of *S. gracilis* the lowest dry weights.

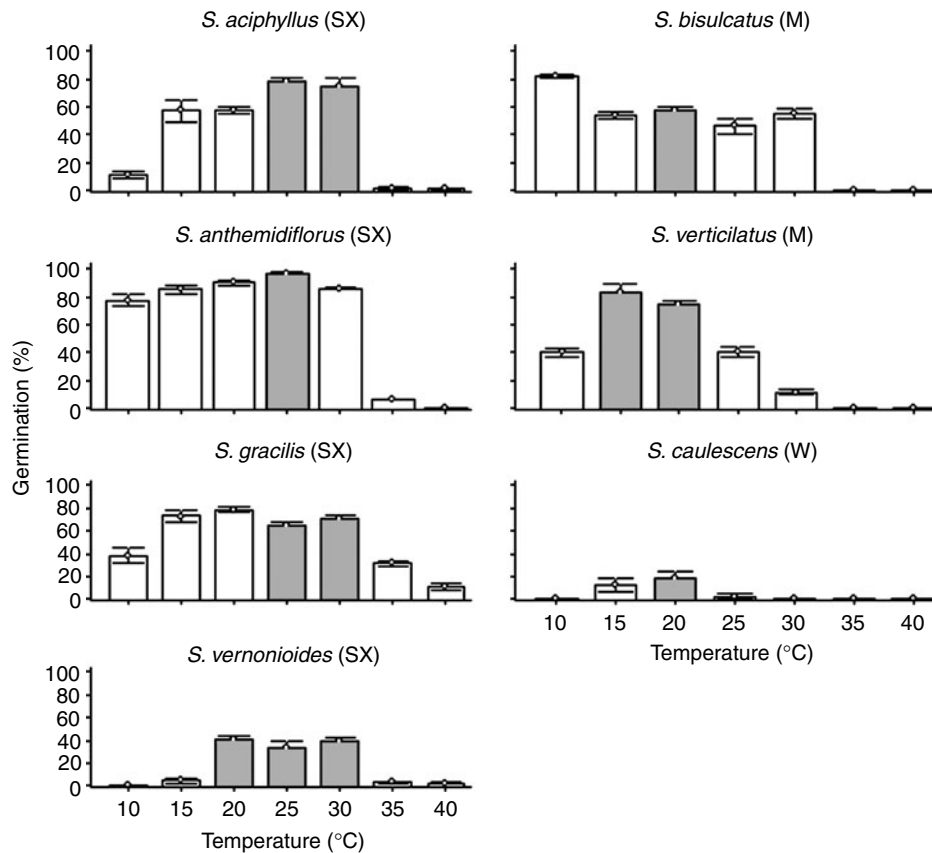
### Germination characteristics

The seeds of six of the species studied germinated exclusively in the presence of light and within a relatively wide temperature range (Fig. 1); only the seeds of *S. gracilis* demonstrated low germinability in continuous darkness (maximum of 22% at 35°C). In general, the seeds of species from seasonally xeric habitats germinated within the range of 10–40°C, albeit to only low percentages at the highest temperatures (Fig. 1). The germinabilities of *S. gracilis* and *S. aciphyllus* were significantly lower at 10°C. *S. vernonioides* had low germinability in the range of 20–30°C, and at 15°C its germinability was less than 10% (Fig. 1).

The seeds of species from mesic habitats germinated between 10 and 30°C and germination was completely inhibited at temperatures of 35 and 40°C (Fig. 1). *S. caulescens*, the only species from a wetlands environment, germinated only within the temperature range of 15–25°C, and even then with very low germinability (maximum of 19%) (Fig. 1). The seeds of *S. aciphyllus*, *S. gracilis* and *S. verticilatus* displayed highest germination velocity in the temperature range from 25 to 30°C; the seeds of *S. anthemidiflorus* germinated most rapidly at 25°C and the germination velocity of *S. bisulcatus* was greatest at 20°C (Fig. 2). The germination velocity of these five species was lowest at both the lowest (10 and 15°C) and highest (35 and 40°C) temperatures. The germination velocity of *S. caulescens* was constant in the range from 15 to 25°C; it was likewise constant for *S. vernonioides* in the range of 20–30°C, but reduced at extreme temperatures (Fig. 2). The optimal temperature for germination

**Table 2.** Seed sizes: length, width and dry weight (average  $\pm$  standard error) of seven species of *Syngonanthus*

Species	Length (mm)	Width (mm)	Dry mass (mg)
<i>S. aciphyllus</i>	0.38 $\pm$ 0.03	0.22 $\pm$ 0.02	0.015 $\pm$ 0.0005
<i>S. anthemidiflorus</i>	0.49 $\pm$ 0.04	0.25 $\pm$ 0.03	0.022 $\pm$ 0.00 075
<i>S. gracilis</i>	0.39 $\pm$ 0.02	0.21 $\pm$ 0.02	0.012 $\pm$ 0.00 040
<i>S. vernonioides</i>	0.79 $\pm$ 0.08	0.42 $\pm$ 0.05	0.095 $\pm$ 0.0047
<i>S. bisulcatus</i>	0.46 $\pm$ 0.04	0.26 $\pm$ 0.03	0.020 $\pm$ 0.00 077
<i>S. verticilatus</i>	0.46 $\pm$ 0.04	0.21 $\pm$ 0.02	0.014 $\pm$ 0.0016
<i>S. caulescens</i>	0.48 $\pm$ 0.03	0.29 $\pm$ 0.03	0.024 $\pm$ 0.00 057



**Figure 1.** Final germination percentages of the seeds of seven species of *Syngonanthus*; 12-h photoperiod, at constant temperatures of 10–40°C. Error bars indicate standard error; shaded bars indicate optimal temperature. SX, seasonally xeric; M, mesic; W, wetland habitat.

was also habitat dependent, being between 25 and 30°C for species from seasonally xeric habitats, and 15 and 20°C for species from mesic and wetland habitats.

## Discussion

The seeds of the seven species of *Syngonanthus* investigated were all very small (*sensu* Hughes *et al.*, 1994; Ekstan *et al.*, 1999), with dry mass and lengths less than or equal to 0.1 mg and 1 mm, respectively. Generally, very small seeds do not contain sufficient nutritional reserves to complete embryonic development and germinate independently, as occurs in species of *Orchidaceae* and *Orobanchaceae* (Hilhorst, 2008). However, in spite of their very small size, the seeds of *Syngonanthus* have sufficient nutritional reserves to complete germination.

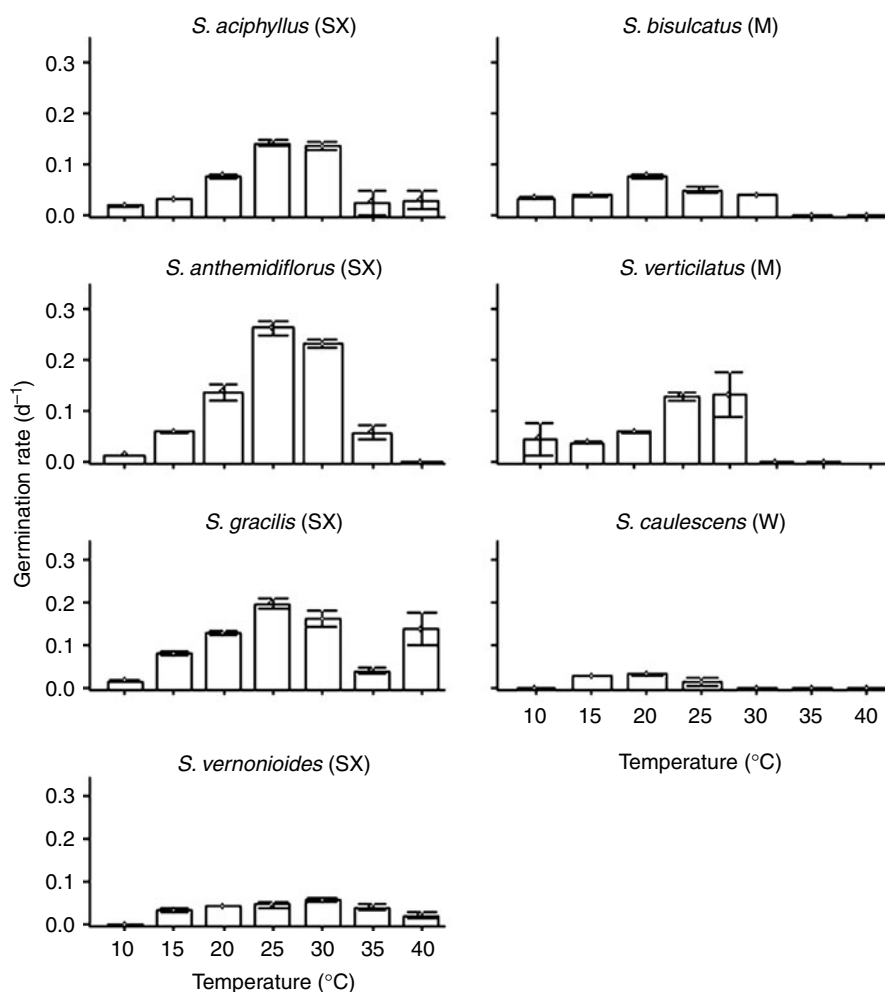
The seeds showed a light requirement for germination, a characteristic generally associated with small seeds (Thompson and Grime, 1983; Bewley and Black, 1994; Milberg *et al.*, 2000) and open habitats (Leishman and Westoby, 1994; Milberg *et al.*, 2000). Small and positively photoblastic seeds have been reported in other studies with species of *Eriocaulaceae*, *Xyridaceae*

and *Velloziaceae* – families typical of *campos rupestres* vegetation and open environments exposed to high-intensity solar illumination (Mercier and Guerreiro-Filho, 1989; Sá e Carvalho and Ribeiro, 1994a, b; Scatena *et al.*, 1996; Garcia and Diniz, 2003; Abreu and Garcia, 2005; Oliveira and Garcia, 2005; Garcia *et al.*, 2007; Schmidt *et al.*, 2008).

Temperature is another important environmental factor that controls germination (Baskin and Baskin, 1988; Bewley and Black, 1994; Benech-Arnold and Sánchez, 1995), and seeds germinate within certain temperature ranges that are characteristic of each species (Bewley and Black, 1994). The permissive temperature range for germination can determine the geographic distribution of plants (Thompson, 1973; Labouriau, 1983; Probert, 1992) and reflects the adaptation of the species to the environments in which they occur naturally (Schütz and Rave, 1999).

*S. gracilis* and *S. caulescens* are widely distributed species in South America. *S. aciphyllus*, *S. anthemidiflorus*, *S. bisulcatus* and *S. verticilatus* are found in many regions of the Cadeia do Espinhaço Range, while *S. vernonioides* is only encountered in a small part of that mountain range. *S. caulescens*, the only species that occurs in a wetland environment, is the most widely





**Figure 2.** Germination rate ( $d^{-1}$ ) of the seeds of seven species of *Syngonanthus*; 12-h photoperiod, at constant temperatures of 10–40°C. Error bars indicate standard error. SX, seasonally xeric; M, mesic; W, wetland habitat.

distributed taxon, but had the most restricted temperature range for germination among the species examined here. Other species of *Eriocaulaceae* (Oliveira and Garcia, 2005), *Xyridaceae* (Abreu and Garcia, 2005) and *Velloziaceae* (Garcia and Diniz, 2003; Garcia *et al.*, 2007) that are widely distributed (or not) within the Cadeia do Espinhaço Range germinate under a wide range of temperatures. Baskin and Baskin (1988) noted that only the germination characteristics of a species could be eliminated as determinant factors in endemism because these are usually quite similar within a given genus even though it may contain both endemic and widely distributed species. Likewise, the data presented here indicates that the temperature ranges for germination cannot explain the geographic distribution of the species in the present study.

The temperature limits for germination and the optimal temperatures that were observed among the species examined here demonstrated a relationship between water resource availability in the microhabitats that they naturally occupy and their germination

responses. *S. bisulcatus*, *S. verticilatus* and *S. caulescens* grow in mesic/wetland environments and did not germinate at the highest temperatures (35 and 40°C; optimal temperatures 15 and 20°C), while *S. aciphyllus*, *S. vernonioides*, *S. anthemidiflorus* and *S. gracilis* are found in seasonally xeric environments and germinated even under the highest temperatures tested (though at low percentages; optimal temperature 25 and 30°C). Similar results have been observed in other studies with *campos rupestres* species. Oliveira and Garcia (2005), for example, noted that high temperatures favoured the germination of *S. elegans* (a species from seasonally xeric environments) but inhibited germination of *S. elegantulus* and *S. venustus*, both from swamp habitats. In addition, Abreu and Garcia (2005) demonstrated that four species of *Xyris*, typical of boggy soils in *campos rupestres* vegetation (Wanderley, 1992), did not germinate at high temperatures. Species of *Syngonanthus* (Oliveira and Garcia, 2005; and the present study) and *Xyris* (Abreu and Garcia, 2005) generally occur in sandy quartzite soils where high soil humidity dampens the amplitudes of

thermal fluctuations and helps maintain relatively low ground temperatures, which is reflected in the low germinability of the seeds of species from mesic/wetland environments at temperatures above 30°C.

The results obtained in the present study demonstrate that, in spite of the variability observed in terms of seed size, all were considered to be very small and positively photoblastic, indicating a pattern for the seeds of the genus *Syngonanthus* in relation to their size and their light requirements for germination. The geographic distribution of different species of the genus cannot be explained by the responses of seed germination at different temperatures, but suggests some relationship to their edaphic microhabitats, and therefore germination characteristics of the populations studied may have been selected to colonize specific environments at different soil water conditions.

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