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Temperature and light requirements for germination of species of Velloziaceae from different Brazilian rocky outcrops

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ABSTRACT

Germination is the first step to successful plant establishment. The range of factors that promote germination varies among species. Light and temperature requirements for the germination of species of Velloziaceae were investigated. Seeds of *Barbacenia flava*, *B. markgrafii*, *B. purpurea*, *B. williamsi*, *Vellozia alata*, *V. compacta*, *V. glochidea* and *V. plicata* were collected from rocky outcrops located in different Brazilian states and were incubated for germination at 10 to 40 °C in light or dark conditions. Seed mass and length were measured for each species. In general, all species exhibited a high germination percentage at temperatures of 15-40 °C in the light, with the optimal temperature being 25-30 °C for species of *Barbacenia* and 30 °C for species of *Vellozia*. *Barbacenia flava*, *V. compacta* and, particularly, *B. markgrafii*, germinated in the dark. In contrast, *B. purpurea* exhibited an absolute requirement for light and the most restricted range of temperature to germinate. Germination responses and seed traits were related to the microclimate where the species were collected, and germinability in darkness is likely a common trait for species of Velloziaceae from the *Espinhaço* Range.

Keywords: *Barbacenia,* darkness, granitic outcrops, inselbergs, ironstone outcrops, optimal temperature, quarzitic outcrops, *Vellozia*

Introduction

Seed germination is one of the most important steps in the life cycle of a plant and it depends on a combination of seed traits and environmental factors (Bewley *et al.* 2013). Besides water and oxygen, light and temperature are considered important requirements for germination onset (Baskin & Baskin 1998). Seed size and mass can strongly influence germination requirements and timing, mainly with regard to light. In general, small seeds require light to germinate (Bewley *et al.* 2013). Light signals germination to begin (and the termination of dormancy) by interacting with the phytochrome and the control of the main phytormones involved in germination, specifically the germination inductor gibberellin and the dormancy maintainer abscisic acid (Finch-Savage & Leubner-Metzger 2006). The role of temperature in seed germination is related to membrane permeability, which improves enzyme activity and increases respiratory metabolism, and thus the rate of germination (Bewley *et al.* 2013).

It is common that, for some species, a combination of environmental factors determines the timing of seed germination (Baskin & Baskin 1998). The manner by which seeds respond to combinations of factors can be phylogenetically conserved and highly dependent on their niches (Donohue *et al.* 2010). Some peculiar environments, such as rocky outcrops, possess soil with sets of characteristics that contribute to endemism (Dayrell *et al.* 2016; Hopper *et al.* 2016; Silveira *et al.* 2016). Therefore, species from rocky outcrops would be expected to have a requirement for specific cues for germination.

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Specific botanical families occur on most rocky outcrops. For example, species of the family Velloziaceae are found on rocky outcrops or sandy soils, which explains their xeromorphic characteristics (Salatino *et al*. 2001). The majority of the described species of Velloziaceae are endemic to Brazil (Giulietti *et al*. 2005), and most of these are found in the Central Plateau (Mello-Silva 1995; Mello-Silva *et al*. 2011). For these reasons, and due to niche disruption by anthropogenic activities, some members of this family were included in the Brazilian list of endangered species (Fundação Biodiversitas 2008) or found to be in need of additional information regarding their life cycle and distribution to deserve more attention from conservation authorities (MMA 2008).

We investigated seed germination of eight species of Velloziaceae from different Brazilian rocky outcrops (with substrates varying among quartzite, granite and ironstone and climates varying from tropical to tropical altitudinal mesothermic) located in multiple different Brazilian states. We aimed to determine the light and temperature requirements for germination in relation to local occurrence and the particular traits of each species in order to understand the process of seedling recruitment. This study provides useful information for developing future efforts and strategies for biodiversity conservation, mainly regarding species of Velloziaceae, and the restoration of the rocky outcrops.

Materials and methods

Plant material, collection areas and seed characterization

Fruits of *Barbacenia flava* Mart. ex Schult. & Schult.f. and *Vellozia alata* L.B.Sm. were collected in Serra do Cipó National Park; *B. markgrafii* Schulze-Menz in Biribiri State Park; *B. williamsi* L.B.Sm. in Serra do Curral; and *V. compacta* Mart. in Serra do Rola Moça State Park. All these localities are in the state of Minas Gerais and are part of the *campos rupestres* (rocky grasslands) of *Cadeia do Espinhaço*, which has a climate classified as Cwb, by the Köppen system, which is characterized as tropical altitudinal mesothermic with a rainy spring-summer and a dry autumn-winter (Köppen 1900; Alvares *et al*. 2013). Annual precipitation is around 1200 mm and is concentrated during the spring-summer season. Temperature ranges between 15 (average minimum in the coldest season) and 25 °C (average maximum in the warmest season) and the mean elevation is 900m above sea (revised by Silveira *et al*. 2016).

Fruits of *B. purpurea* Hook. were collected at *Pedra da Urca*, an inselberg located in the municipality of Rio de Janeiro (state of Rio de Janeiro), which has a climate classified as Af, by to Köppen system (Köppen 1900; Alvares *et al*. 2013), which is characterized as warm tropical with low temperature fluctuations and high humidity throughout the seasons. Annual precipitation is around 1300 mm and temperature ranges between 20 and 30 °C (INMET 2014).

Fruits of *V. glochidea* Pohl were collected in *Serra dos Carajás* (municipality of Parauapebas, state of Pará) whose climate is Aw according to Köppen system (Köppen 1900; Alvares *et al*. 2013), which is characterized as tropical with low temperature fluctuations and dry winters (precipitation < 100mm). The annual precipitation is above 2000 mm and temperature ranges between 21 and 25 °C (Corrêa 2011). *Vellozia plicata* Mart. was collected in an inselberg in Vitória city (Espírito Santo), which is classified as Am, by the Köppen system (Köppen 1900; Alvares *et al*. 2013), which is characterized as tropical with low temperature fluctuations and less-dry winters (precipitation > 100 mm). Temperature ranges between 23 and 30 °C and annual precipitation is around 1100 mm (INMET 2014).

Fruits were removed from the plants in at least 100 matrices per species located in rocky outcrops at the moment of seed dispersion (December to March for all species). Then the fruits were broken, processed to separate the seeds, and the seeds measured for length and dry mass (Tab. 1). For each species, 100 seeds were measured for length and 25 to 50 seeds were weighed before and after drying at 105°C for 24 hours (MAPA 2009). The seeds were used immediately in subsequent germination experiments. The results of germination tests were also considered to measure seed viability.

Germination experiments

Germinability was tested under constant temperatures in light and dark conditions. Four replicates of 25 seeds were used for each temperature and light/dark treatment. Seeds were placed in Petri dishes with a double layer of germination paper moistened with nystatin solution (0.1%) to control fungal infestation (nystatin was previously tested and found to have no effects on germination). Petri dishes were kept moistened with nystatin solution during the entire experiment to avoid losses due to desiccation. The Petri dishes were distributed among germination chambers set at 15, 20, 25, 30, 35 and 40 °C under a photoperiod of 12 hours (40 µmol photon $m^{-2} s^{-1}$) or in darkness (wrapped in aluminum foil and placed within black plastic bags). The seeds were evaluated daily for 30 days, with the criterion of germination being radicle protrusion of 2 mm. The Petri dishes kept under dark conditions were evaluated daily in a dark room under green light because it is considered safe for observation of darkness treatments (Vieira *et al*. 2017a). The resulting data were used to calculate germination percentage and mean germination time. The optimal temperature for seed germination was considered the temperature that promoted the highest germination percentage in the shortest time (*sensu* Labouriau 1983).

Table 1. Sample locality, type of substrate, length and dry mass (means ± SD) of four species of *Barbacenia* and *Vellozia* seeds collected in Brazilian States, Minas Gerais (MG), Rio de Janeiro (RJ), Pará (PA) and Espírito Santo (ES).

Species	Sample locality	Coordinates	State	Substrate/soil	Altitude (m)	Lenght (mm)	Dry mass (mg)
Barbacenia flava	Parque Nacional da Serra do Cipó	19º12'-19º34'S 43º27'-43º38'W	MG*	Quartzite outcrops	900	2.11 ± 0.28	1.21 ± 0.09
Barbacenia markgrafii	Parque Estadual de Biribiri	18º14'53''-18º02'15''S 43º39'57"-43º29'36"W	MG*	Quartzite outcrops	1200	1.16 ± 0.23	0.18 ± 0.005
Barbacenia purpurea	Pedra da Urca, Rio de Janeiro	22°57'5''S 43°9'50''W	RJ	Granite outcrops	220	1.54 ± 0.19	0.20 ± 0.004
Barbacenia williamsi	Serra do Curral, Belo Horizonte	19°57'39"S 43°54'35"W	MG*	Ironstone outcrops	1200	2.05 ± 0.34	0.13 ± 0.004
Vellozia alata	Parque Nacional da Serra do Cipó	19º12'-19º34'S 43º27'-43º38'W	MG*	Quartzite outcrops	900	2.62 ± 0.31	3.76 ± 0.32
Vellozia compacta	Parque Estadual da Serra do Rola Moça	20°02'34.6"S 44°0'23.2"W	MG*	Ironstone outcrops	1300	1.05 ± 0.14	0.20 ± 0.02
Vellozia glochidea	Serra de Carajás	6°6'29"S 50°18'16"W	PA	Ironstone outcrops	900	2.29 ± 0.32	1.24 ± 0.18
Vellozia plicata	Vitória	20°19'20''S 40°20'17''W	ES	Granite outcrops	0	2.03 ± 0.32	0.15 ± 0.03

*Espinhaço Mountain Range

Statistical analysis

Data of germination percentage and mean germination time were submitted to GLM two-way ANOVA considering "temperature" and "light or darkness conditions" as factors. When significant, the differences between means were compared by Newman-Keuls post-hoc test with the *P* value set at 5 % probability. Germination percentage in light and darkness and mean germination time in both conditions were also used in a multivariate cluster analysis (UPGMA) based on the Euclidian distance in percentage

Results

Temperature and light requirements for germination in Velloziaceae

In general, all species of Velloziaceae studied here exhibited high germination percentages under light and at most of the temperatures tested (Fig. 1). Regarding the species of *Barbacenia*, in the light *B. flava* had more than 90 % of its seeds germinate from 15 to 35 °C, but none of its seeds germinated at 10 and 40 °C. In the dark, the highest germination percentages for *B. flava* seeds were at 30 and 35 °C (optimal temperatures, Fig. 2), with no statistical differences between germination percentage of light and dark at 35 °C (Fig. 1). *Barbacenia markgrafii* exhibited germination in all temperatures in the light and from 15 to 40 °C in the dark, but the percentages were higher in the light, with the exception of 30 °C for which no differences were found in relation to the dark (Fig. 1). For this species the optimal temperatures were 25 and 30 °C in the light and 30 °C in the dark (Fig. 2). *Barbacenia purpurea* exhibited 93 to 99 % germination from 15 to 30 °C in the light, with 25 °C being the optimal temperature (Fig. 2), and no germination at 35 and 40 °C (light); there was no germination by this species at any temperature in the dark (Fig. 1). For *B. williamsi*, germination was above 94 % from 15 to 30 °C, diminishing at 35 and 40°C, in the light; less than 10 % germinated in the dark (Fig. 1). For this species, the optimal temperatures for germination in the light were 25 and 30 °C (Fig. 2).

Regarding the species of *Vellozia*, *V. alata* exhibited high germination in the light from 20 to 40 °C, and no germination at 10 and 15 °C. Germination was no greater than 16 % for this species in the dark from 25 to 40 °C (Fig. 1). Germination was fastest in the light at 30 °C, which was considered the optimal temperature (Fig. 2). The seeds of *V. compacta* exhibited high germination in all temperatures tested, except for 10 °C in the light, with the optimal temperatures being 25 and 30 °C (Fig. 2). In the dark, germination percentage increased gradually from 25 to 40 °C (Fig. 1) for this species. For *V. glochidea*, germination was less than 70 % in the light, with no germination at 10°C. In the dark, this species exhibited germination only at 35 and 40 °C (Fig. 1). The optimal temperatures for germination of *V. glochidea* was 25 and 30 °C (Fig. 2). For *V. plicata*, germination in the light was null at 10 °C, low at 15 °C and optimal at 30 °C (Fig. 2). In the dark, germination of *V. plicata* occurred from 30 to 40 °C, being higher at 40 °C (Fig. 1).

The influence of seed traits on germination

The greatest seed mass and length were for *V. alata* (Tab. 1), although seeds of all species of Velloziaceae studied were relatively small (low mass and short length). The variables germination percentage in the light, germination percentage in the dark, seed mass and seed length, grouped the species

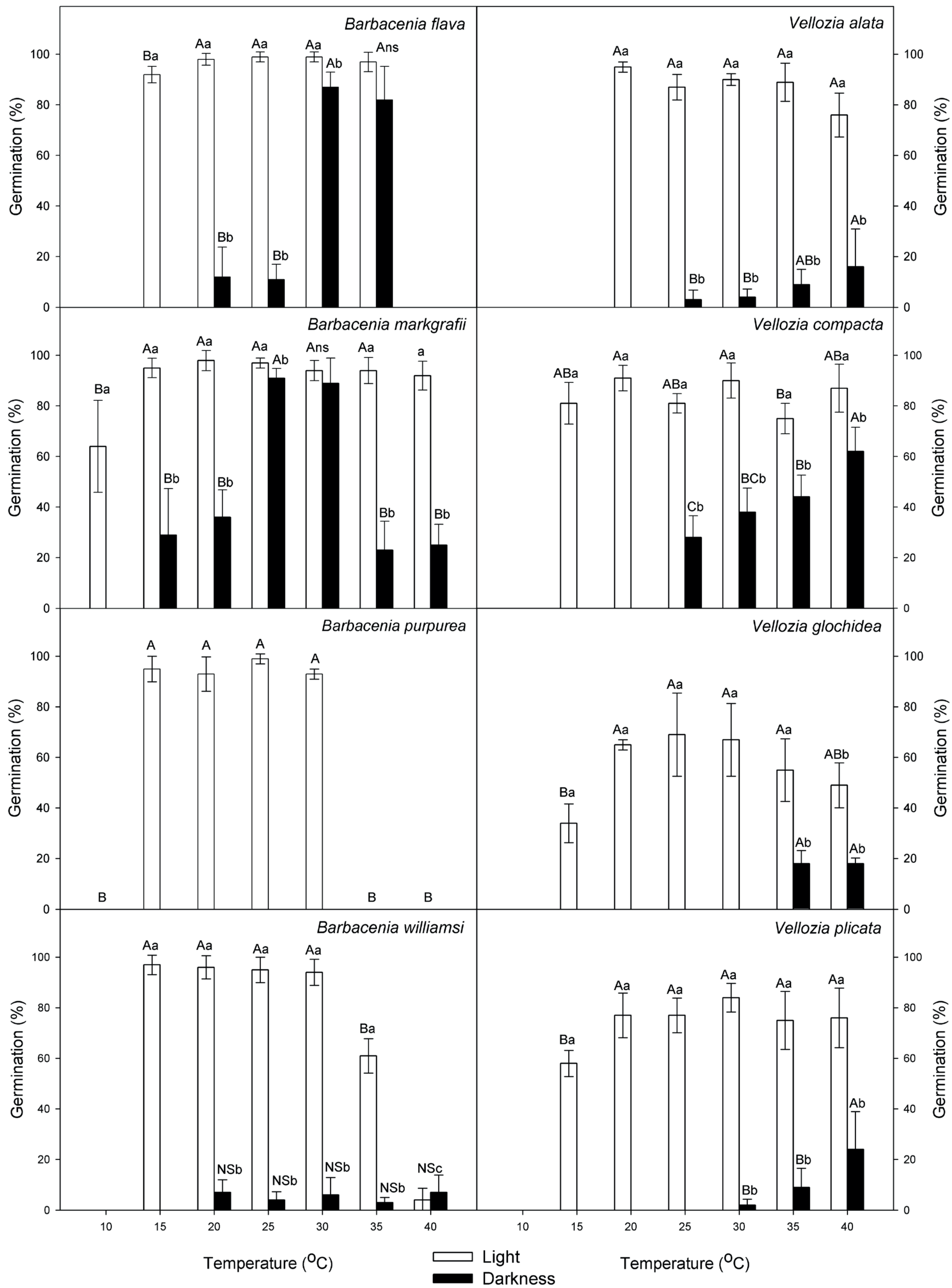

Figure 1. Germination percentage of *Barbacenia* (left) and *Vellozia* (right) species at 15, 20, 25, 30, 35 and 40°C in the light (white bars) and in the dark (black bars). Bars are mean ± standard deviation of 4 replicates. Uppercase compares different temperatures in light or darkness conditions and lowercase compares light and darkness conditions in the same temperature. NS, non-significant.

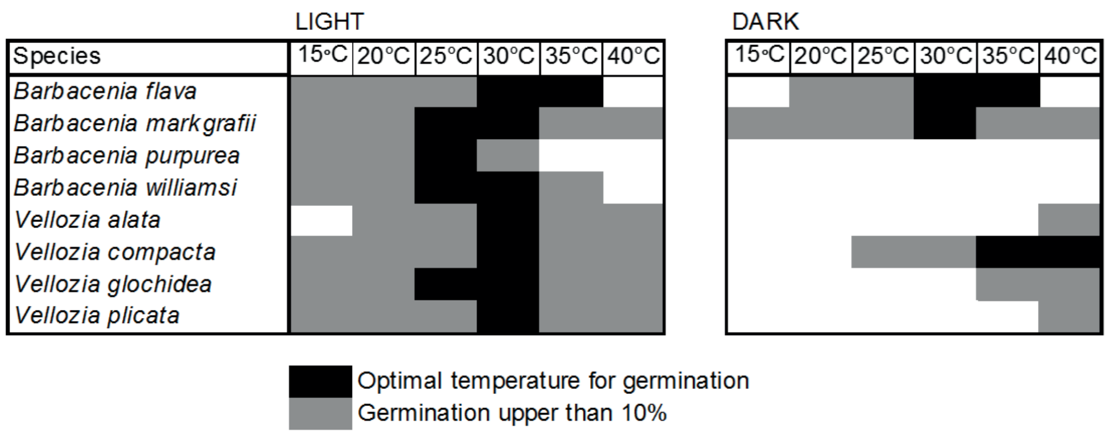

Figure 2. Optimal (in black) and average (gray) ranges of temperature for germination of *Barbacenia* and *Vellozia* species in the light and in the dark. The optimal germination temperature was defined as that temperature showing the greatest germinability associated with the greatest germination velocity.

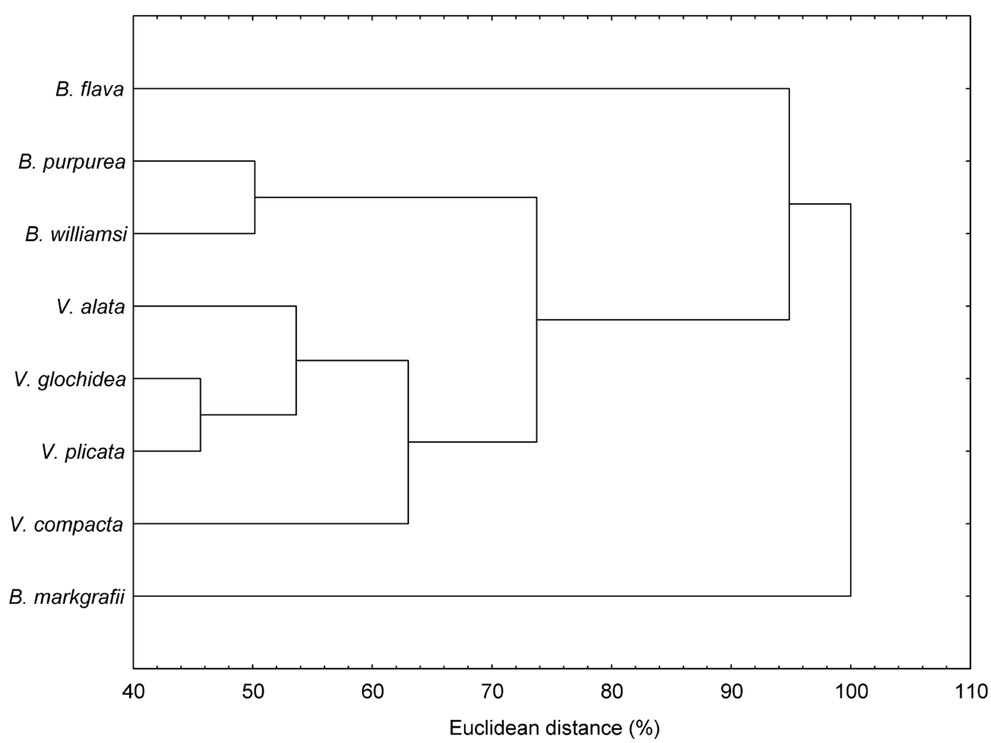

Figure 3. Grouping analysis of Velloziaceae species based on the germination percentage in light, dark and seed traits (mass and length).

as shown in Figure 3. The lowest level of dissimilarity was between *V. glochidea* and *V. plicata*, followed by *B. purpurea* and *B. williamsi*. *Barbacenia markgrafii* exhibited the greatest level of dissimilarity with the other species (Fig. 3).

Discussion

We report the distinct light and temperature requirements for seed germination of eight species from two genera of Velloziaceae: *Barbacenia* and *Vellozia*. The requirement of light for germination has been reported for other species of Velloziaceae (Garcia & Diniz 2003; Garcia *et al.* 2007; Munné-Bosch *et al.* 2011; Soares-da-Mota & Garcia 2013; Vieira *et al.* 2017a), and was confirmed here. Based on length and mass, the seeds studied here are considered small relative to other known species. The requirement for light by small seeds prevents germination when the seeds are too deep in the soil for seedlings to reach the surface due to limited nutrients stored in seed tissues (Pons 1992;

Schütz & Rave 1999). The wide range of temperatures that were found suitable for germination, 15 to 40 °C, in almost all species is an important adaptation to environments in which the temperature can range 20 °C during the course of a year (Orozco-Almanza *et al*. 2003), as happens with the rocky outcrops where the studied species of Velloziaceae occur.

If the range of temperature in which seeds can germinate is large, it means the level of dormancy is very low or nonexistent (Baskin & Baskin 1998). Therefore, the species studied here did not show primary dormancy, which suggests that recruitment from seeds is widely spread over different microhabitats. Based on the optimal temperature for germination, 25-30 °C for *Barbacenia* and 30 °C for *Vellozia* (Fig. 2), and the timing of dispersion in early summer (when temperatures reach above 25 °C in the environments where the species studied here were collected), there could be a synchrony of germination after dispersion. Moreover, it is probably not a coincidence that the optimal temperature range for germination of all the studied species is the same as the temperature range of the microenvironments where they were collected. As revised by Donohue *et al*. (2010), the width of the germination niche and the species ecological or geographic range are, in some cases, closely related even if they are out of their wild environment. Indeed, spring-summer is the rainy season in all microclimates and environments in which the species were collected, indicating a wide window of climatic conditions (including high water potential of the soil and adequate temperature) for seed germination and seedling establishment. Seeds that remain could still be recruited in the next rainy season, when the minimal environmental conditions (at least water and adequate temperature) for germination coexist. Furthermore, species of Velloziaceae have been reported to build persistent soil seed banks (Munné-Bosch *et al*. 2011; Garcia *et al*. 2017) without, however, performing dormancy cycles (Garcia *et al*. 2017), reinforcing the hypothesis of recruitment over time. Interestingly, seeds of some species, especially *B. markgrafii*, *B. flava* and *V. compacta*, germinated in the dark (Fig. 1). Regarding the species of *Vellozia* studied here, we observed increasing germination percentage with increasing temperatures in the dark. Recently, Vieira *et al*. (2017b) demonstrated that germination in the dark by species of *Vellozia* submitted to high temperature (40 °C) was related to a decrease in abscisic acid (ABA) levels due to ABA catabolism, while at low temperature (25 °C) the *de novo* synthesis of ABA was promoted. Our results, and those from Vieira *et al*. (2017b), point out a unique trait of some species of Velloziaceae germination at warm temperatures independently of light.

Regarding traits of individual species, *B. markgrafii* showed high germination percentages from the lowest (10 °C) to the highest (40 °C) temperatures tested, including 25 and 30 °C in the dark. These responses, added to seed length and mass, separated this species as more dissimilar from the others, including those of the same genus. On the other hand, *B. purpurea* had the most restricted germination temperature range and, interestingly, did not germinate in conditions of darkness. The population studied was located on an inselberg in the Brazilian littoral zone and had small seeds and photoblastism, which, according to Pearson *et al*. (2002), are in line with pioneer species. This species was very similar to *B. williamsi*, which exhibited high germinability from 15 to 30 °C, as did *B. purpurea*. These differences highlight the wide germinability of species of *Barbacenia* found in the present study, from very restricted to broad temperature and light conditions.

Altogether, our results point-out a common trait among species of Velloziaceae from the rocky outcrops of the *Cadeia do Espinhaço* (Cwb, tropical mesothermic climate): the capacity to germinate in conditions of darkness (see Tab. 1, Fig. 1). Our findings are in agreement with those of Soares-da-Mota & Garcia 2013 and Vieira *et al*. (2017a), whose studied species that germinated in the dark were also collected from *Cadeia do Espinhaço*. Additionally, the lowest dissimilarity level was found between *V. glochidea* and *V. plicata*, both of which exhibited similar germination in the dark at the highest temperatures, and both were collected in a tropical climate (Aw and Am according to Köppen system). Adding the responses of *B. purpurea* to this observation, species from "A" climate (less temperature fluctuations over the seasons, according to Köppen system) seem to have an absolute requirement for light to germinate. Thus, the similarities found among species here might be more related to climate than to the substrate of the rocky outcrops where the species were from.

In conclusion, our findings reaffirmed the requirement of light for germination and the capacity to germinate in conditions of darkness for some species of Velloziaceae. Moreover, we confirmed the absence of primary dormancy in the studied species, which is in line with other studies. We found differences in germination responses among species of *Barbacenia* and *Vellozia*, and among species from different climates and substrates. The similarities found in germination responses may be related to microclimate. Regarding light and temperature requirements for germination, *B. markgrafii* and *B. purpurea* deserve further investigation due to the contrasting differences found between them. Altogether, the high germinability of the seeds of the species of Velloziaceae studied here over a large range of temperatures, including in the dark, point to the possibility of long-term recruitment. Furthermore, germination, and probably seedling establishment, seem to be finely regulated and synchronized by the specific temperature window typical of tropical and tropical mesothermic climates. Considering a scenario of increasing temperatures as a result of climate change, the wide range of germination traits of the species studied here will probably allow their establishment with minimal consequences to their germination niches, as pointed out by Soares-da-Mota

& Garcia (2013). However, changes to the rainy season with prolonged droughts would probably be a major challenge for plant regeneration of these species. Therefore, it is reasonable to expect that altered environmental conditions will probably not change the germination niches of the species of Velloziaceae reported here.

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