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Distinct germination responses may contribute to the distribution pattern of two *Moquiniastrum* species in different phytophysiognomies from the Brazilian savanna

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ABSTRACT

Understanding how germination traits can influence the distribution pattern of adult plants is still an important issue for seed ecologists and biologists. Here, we evaluated if seed germination responses to abiotic factors may be related to the occurrence of two *Moquiniastrum* species in different phytophysiognomies from the Brazilian savanna. To evaluate if germination responses are distinct between species, seeds of *M. barrosoae* (common to typical savanna) and *M. polymorphum* (common to typical and forested savanna) were set to germinate under different constant (5 to 40 °C) and alternating (15–30, 20–30, 25–30 and 25–35 °C) temperature regimes in light and dark conditions, different red:far-red ratios (0.1, 0.5, 2.0 and 7.2 R:FR) of light, and water availability (0 to −1.0 MPa) in controlled experiments. Seed germination responses were distinct between species, with *M. polymorphum* presenting higher germinability over a wider temperature range, with lower light requirement for germination, less sensitivity to alteration of R:FR ratios and higher tolerance to water limitation compared to *M. barrosoae*, which presented more specific environmental requirements to seed germination. Therefore, we demonstrate that seed germination responses may contribute to the distribution pattern observed in adult plants, since the more widely distributed species (*M. polymorphum*) presented higher germinability over a broader range of environmental conditions, which may enable this species to occur in different phytophysiognomies compared to the species with the more restricted distribution area (*M. barrosoae*).

1. Introduction

Seed germination is one of the first traits expressed during the life cycle of plants, and has the potential to be strongly subjected to natural selection, because plants need to overcome the germination and seedling stage before they can express other adaptive characteristics in their life (Donohue et al., 2010). Accurate germination cuing can enable germination under optimal conditions for seedling survival and growth. So, seed germination traits may play an important role in the distribution pattern of plant species, because successful germination can be related to habitat preference (Donohue et al., 2010; Grubb, 1977; Leyer and Pross, 2009; Pearson et al., 2002).

A number of studies have investigated the relationship between germination traits and the species distribution pattern; some of them have failed to find such a relationship (e.g. Silveira et al., 2012; Thompson et al., 1999; Thompson and Ceriani, 2003). However, other studies reported that germination traits may be related to distribution patterns in plants, where species with wider distribution patterns present higher germinability in different conditions compared to species with narrower distribution (Luna and Moreno, 2010; Marques et al., 2014; Ranieri et al., 2012).

Environmental factors such as water availability, temperature regimes, luminosity and quality of light are key aspects that control seed germination. Suitable water availability is needed to initiate germination in non-dormant seeds, and different responses to water stress can reflect adaptation to drought (Baskin and Baskin, 2014). Temperature is the main factor regulating seed dormancy and germination (Probert, 2000); light can also influence dormancy, germinability and germination time of many species (Pearson et al., 2002; Smith, 2000).

The Brazilian Neotropical savanna (Cerrado) covers approximately 2 million km^2 (Eiten, 1972). In its domain, there is

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considerable seasonality, with the rainy and dry seasons well defined (Franco, 2002). Soils are acidic, with low content of organic matter and nutrients and high amounts of aluminum (Furley and Ratter, 1988).

The vegetation landscape of the Cerrado consists of different phytophysiognomies. The typical savanna (cerrado *sensu stricto*) is an open physiognomy and comprises a mix of scattered shrubs and trees often 3–8 m tall with more than 30% crown cover, with a rich herbaceous layer. The forested savanna (cerradão) is predominantly composed of trees often 8–12 m tall or even taller with crown cover of 50–90%, casting a considerable shade (Oliveira-Filho and Ratter, 2002). Although these two vegetation types can occur in the same area, they are structurally and floristically distinct (Pinheiro and Durigan, 2012). Some plant species of the savanna can occur in different vegetation types, but others are unique to one or only a few physiognomies, such as many non-arboreal species, which are restricted to open environments (Pinheiro and Durigan, 2012; Rossatto et al., 2008).

Different vegetation types impose distinct selective pressure on recruitment and germination, with forested savanna (closed canopy) possessing lower light intensity and lower red:far-red ratio (Salazar et al., 2012), milder temperatures (Kissmann et al., 2012) and higher soil water availability (Assis et al., 2011) than the typical savanna, which has a more open physiognomy.

In southern peripheral areas of the Cerrado, the sympatric Asteraceae species *Moquiniastrum barrosoae* (= *Gochnatia barrosii*) and *M. polymorphum* (= *G. polymorpha*) co-exist. However, they present a distinct distribution pattern in the mosaic of the Cerrado vegetation (Rossatto and Kolb, 2012). *Moquiniastrum polymorphum* has a wider distribution, occurring both in the more open and in the more closed vegetation types (typical or forested savanna and riparian forests), while *M. barrosoae* has a narrower distribution, occurring only in open areas of Cerrado (typical savanna or grasslands) (Durigan et al., 1999, 2004a).

In this way, we hypothesized that the distribution pattern of the two *Moquiniastrum* species over the different Cerrado phytophysiognomies is related to their distinct germination responses. To test this hypothesis, we sought to answer the following questions: (i) do the two *Moquiniastrum* species differ in their germination responses under key environmental factors, i.e. temperature, light requirement, light quality and water availability? (ii) does the more widely distributed species (*M. polymorphum*) have higher germinability over a broader range of environmental conditions? (iii) do seed germination responses contribute to the distribution pattern observed in adult plants?

2. Material and methods

2.1. Study site

Mature cypselae (hereafter referred to as seeds) were collected at the Assis Ecological Station (AES; 22° 33′ 65″ to 22° 36′ 68″ S, 50° 22′ 29″ to 50° 23′ 00″ W), a conservation area located in the western region of the state of São Paulo, Brazil. The climate at the AES according to the Köppen classification is between Cwa and Cfa, being characterized as subtropical, with rainfall concentrated from October to May and the dry season from June to September. The average annual rainfall and temperature recorded for a period of 20 years (decades 1970–1990) are 1400 mm and 21.8 °C, respectively. Elevations are ranging from 500 to 588 m (Secretaria do Meio Ambiente, 2010). The soils are predominantly weathered dystrophic oxisoils (Juhász et al., 2006). The main vegetation of the study site consists of savanna physiognomies, where the forested savanna predominates (Durigan et al., 1999), which is a sclerophyllous woodland with 8–15 m tall trees, with 20 m^2/ha of basal area and 1800 individuals/ha (dbh $\geq$ 5 cm), creating a canopy cover of about 90%. In the AES the typical savanna vegetation also occurs, which is characterized by shrub vegetation with scattered trees and a discontinuous canopy cover (about 45% of tree cover), with 10 m^2/ha of basal area and 900 individuals/ha (dbh $\geq$ 5 cm) (Pinheiro and Durigan, 2009; Secretaria do Meio Ambiente, 2010).

2.2. Study species and seed collection

Moquiniastrum barrosoae (Cabrera) G. Sancho is an erect shrub (about 2 m tall) that occurs predominantly in the typical savanna, being restricted to more open phytophysiognomies. In contrast, *Moquiniastrum polymorphum* (Less.) G. Sancho is a generalist tree (about 6–15 m tall), occurring both in open areas (typical savanna) and in closed physiognomies (riparian forest and forested savanna) (Durigan et al., 1999, 2004a). Seeds were collected from many individuals ($n \geq 12$) for a suitable genetic sample of each species during dispersion peak, in October 2012 for *M. barrosoae* and January 2013 for *M. polymorphum*. Seeds of all individuals were mixed to form a single seed sample for each species.

2.3. Seed mass

Seeds of both species were dried for 48 h at 80 °C. Dry seed mass was determined by weighing the individual seeds (*M. barrosoae* n = 107; *M. polymorphum* n = 100) with a 0.1 mg precision balance.

2.4. Environmental features

We selected the two vegetation types where the species studied, the typical and the forested savannas, are more common. Measurements of superficial soil temperature (°C; 1 cm depth) and irradiance of light ($\mu mol\ m^{-2}\ s^{-1}$) were performed at around 08:00 and 12:00, in October 2012 and January 2013. These measurements were taken in five randomized replicates for each vegetation type, with 5 m between each other. The temperature was measured using an instant-read digital thermometer (Incoterm®) and the irradiance of light was measured near the soil surface with a spherical quantum sensor (Li-250A, Biosciences, Lincoln, USA).

Precipitation and environmental temperature data from the study area were obtained from the online database of the Information Integrated Center of Agrometeorology (CIIAGRO) of the São Paulo State government.

2.5. Temperatures and light effects on germination

To evaluate the effect of temperature and light on germination, seeds were subjected to constant temperatures of 5, 10, 15, 20, 25, 30, 35 and 40 ± 1 °C, and alternate temperatures of 15–30, 20–30, 25–30 and 25–35 ± 1 °C, under both light (12-h photoperiod of white light, 60 $\mu mol\ m^{-2}\ s^{-1}$) and continuous darkness. Four replicates of 25 seeds were placed on four sheets of filter paper moistened with distilled water in germination boxes. For dark treatments the germination boxes were wrapped in aluminum foil.

2.6. Different red:far-red ratios on germination

To evaluate germination responses to red:far-red (R:FR) ratios of light, seeds were subjected to four treatments of light with different R:FR ratios: (i) 7.2 R:FR ratio, obtained with white light; (ii) 2.0 R:FR ratio, obtained from the white light that passed through two red and two blue cellophane foils wrapping the germination boxes; (iii) 0.5 and (iv) 0.1 R:FR ratios, obtained by passage of incandescent light (two 25 W and two 60 W bulbs) through plastic film like insulfilm® with different levels of light filtering wrapping the germination boxes (Simão et al., 2008). All treatments were performed with four replicates of 25 seeds placed on four sheets of filter paper moistened with distilled water in germination boxes, under light intensity at seed level of approximately 60 μmol m^{-2} s^{-1} and alternating temperatures of 25–30 ± 1 °C (optimal temperature regime) with 12-h photoperiod. The measurement of R:FR ratios were obtained with a LI-1800 spectroradiometer (Li-cor, USA).

2.7. *Water limitation on germination*

The effect of water limitation was applied by five different concentrations of polyethylene glycol 6000 (PEG 6000), yielding water potentials ranging from −0.2 to −1.0 MPa (with −0.2 MPa intervals), and compared to a control group (0 MPa) containing only distilled water. The osmotic potential of the aqueous solutions of PEG 6000 was calculated according to Villela et al. (1991). For each osmotic potential treatment five replicates of 20 seeds placed on four layers of filter paper in petri dishes (90 mm diameter) were used, moistened with 12 mL of the different solutions including the control treatment. The petri dishes were sealed with transparent PVC film to maintain humidity and were kept at a constant temperature of 25 ± 1 °C and 12-h photoperiod of white light (60 μmol m^{-2} s^{-1}).

2.8. *Germination parameters and statistical analysis*

In all the experiments, germination was evaluated daily for 30 days (when germination was terminated) and the seeds were considered germinated after the radicle reached 1 mm in length. For the dark and R:FR ratios treatments, germination was checked under green safety light. We previously tested the effect of green light on germination, and there was no effect on the number of germinated seeds compared with seeds maintained 30 days under continuous dark conditions.

For each replicate, in all experiments, we calculated final germination percentage (germinability; $G\% = \left(\left(\sum n_i N^{-1}\right) \times 100\right)$) and mean germination time ($\mathrm{MGT} = \left(\sum n_i t_i\right)\left(\sum n_i\right)^{-1}$), where Σn_i is the amount of germinated seeds in relation to the number of seeds (N) placed to germinate and n_i is the number of germinated seeds within the time interval t_{i-1} and t_i (Ranal and Santana, 2006).

For the experiments of temperature and light on germination, we also calculated the light requirement index (LRI = Gl/(Gd + Gl)), where Gl is the germination percentage in light, and Gd is the germination percentage under dark conditions. LRI ranges from zero (germination occurring only under dark conditions) to one (total light requirement). LRI data were pooled from all temperatures (Marques et al., 2014; Milberg et al., 2000).

Data in percentage were arcsine transformed prior to statistical analysis. All data were primarily tested for normality (Shapiro-Wilk test, $P = 0.05$) and homogeneity of variances (Cochran test, $P = 0.05$). When the dataset did not meet these criteria data were $\log_{10}$ transformed before being submitted to the factorial ANOVA followed by Tukey test ($P < 0.05$); LRI and seed dry mass data were analyzed by *t*-test. Environmental conditions were analyzed with Mann-Whitney test. Only the original data are presented in tables and figures.

3. Results

3.1. *Seed mass*

Moquiniastrum barrosoae presented larger dry seed mass (mean ± standard error, 1.48 ± 0.02 mg) compared to *M. polymorphum* (1.27 ± 0.02 mg) (t-value = 6.42, df = 205, $P < 0.01$).

Table 1

Temperature and shading (mean ± standard error; n = 5) on the soil surface in different vegetation types where the two *Moquiniastrum* species occur at the Assis Ecological Station, state of São Paulo, Brazil, in different months when their seeds were shed. Different letters indicate significant differences between means in lines (Mann-Whitney test, $P < 0.05$).

	Typical savanna	Forested savanna
	Temperature on the soil surface (°C)	
October		
Morning	26.0 ± 0.0 a	24.0 ± 0.0 b
Midday	29.2 ± 0.9 a	26.2 ± 0.2 b
January		
Morning	25.3 ± 0.9 a	23.0 ± 0.0 b
Midday	32.7 ± 1.4 a	27.0 ± 0.3 b
	Shading on the soil surface (%)	
October		
Morning	74.9 ± 9.5 b	98.0 ± 0.6 a
Midday	75.3 ± 7.8 b	97.2 ± 0.1 a
January		
Morning	75.6 ± 13.3 b	98.9 ± 0.5 a
Midday	79.1 ± 8.5 b	98.1 ± 0.9 a

Table 2

Two-way ANOVA results for the effects of temperature (T), light (L) and their interaction (T × L) on germinability (G) and mean germination time (MGT) of *Moquiniastrum* species. df: numerator and denominator degrees of freedom; ns: not significant.

	M. barrosoae				*M. polymorphum*			
	G		MGT		G		MGT	
	df	*F*	df	*F*	df	*F*	df	*F*
	Constant temperatures							
T	7,48	189.1***	3,23	12.9***	7,48	347.7***	4,30	754.0***
L	1,48	83.1***	1,23	29.5***	1,48	5.5*	1,30	9.9**
T × L	7,48	11.9***	3,23	5.1*	7,48	12.0***	4,30	18.0***
	Alternating temperatures							
T	3,24	81.6***	2,18	21.8***	3,24	121.3***	2,18	80.1***
L	1,24	78.6***	1,18	2.1ns	1,24	24.0***	1,18	0.03ns
T × L	3,24	11.9***	2,18	8.4**	3,24	1.9ns	2,18	2.3ns

df: numerator and denominator degrees of freedom; ns: not significant.

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.001$.

3.2. *Environmental features*

Both species disperse their seeds during the rainy season, when average temperatures (October–January) varied between 16 and 20 °C (minimum), 23 and 25 °C (average) and between 28 and 31 °C (maximum) (Fig. 1).

In the study area, the temperatures on the ground level were always higher in typical savanna (≥2 °C), while the vegetation shading values were always higher in the forested savanna, reaching 98% (Table 1).

3.3. *Temperatures and light effects on germination*

There was a significant interaction between constant temperatures and light conditions for both species (Table 2). Both species germinated in temperature ranges of 10–35 °C in light and 10–30 °C in dark conditions. Constant temperatures of 20 and 25 °C in light provided higher germinability (≥88%) and lower mean germination time (≤15.3 days) compared to the other constant temperature regimes in *M. barrosoae*. In *M. polymorphum* constant temperatures of 20 and 25 °C in light and 20 °C in dark provided higher germinability (≥97%) and lower mean germination time (≤5.6 days) compared to the other constant temperature regimes (Fig. 2).

Moquiniastrum polymorphum presented higher germinability (above 60%) in a wider thermal breadth (10–30 °C in light and 10–25 °C in the dark) while in *M. barrosoae* this range was 15–30 °C

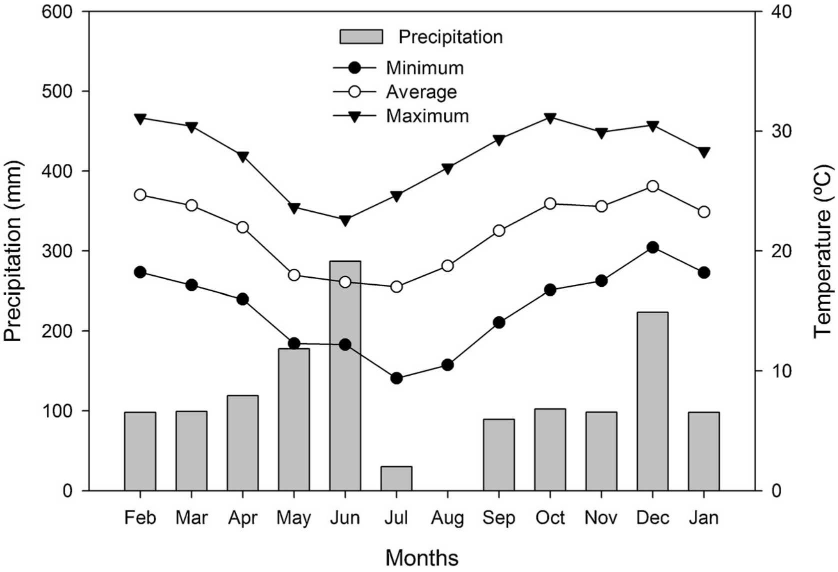

Fig. 1. Temperatures and monthly precipitation from February 2012 until January 2013 in the study area at Assis, state of São Paulo, Brazil.

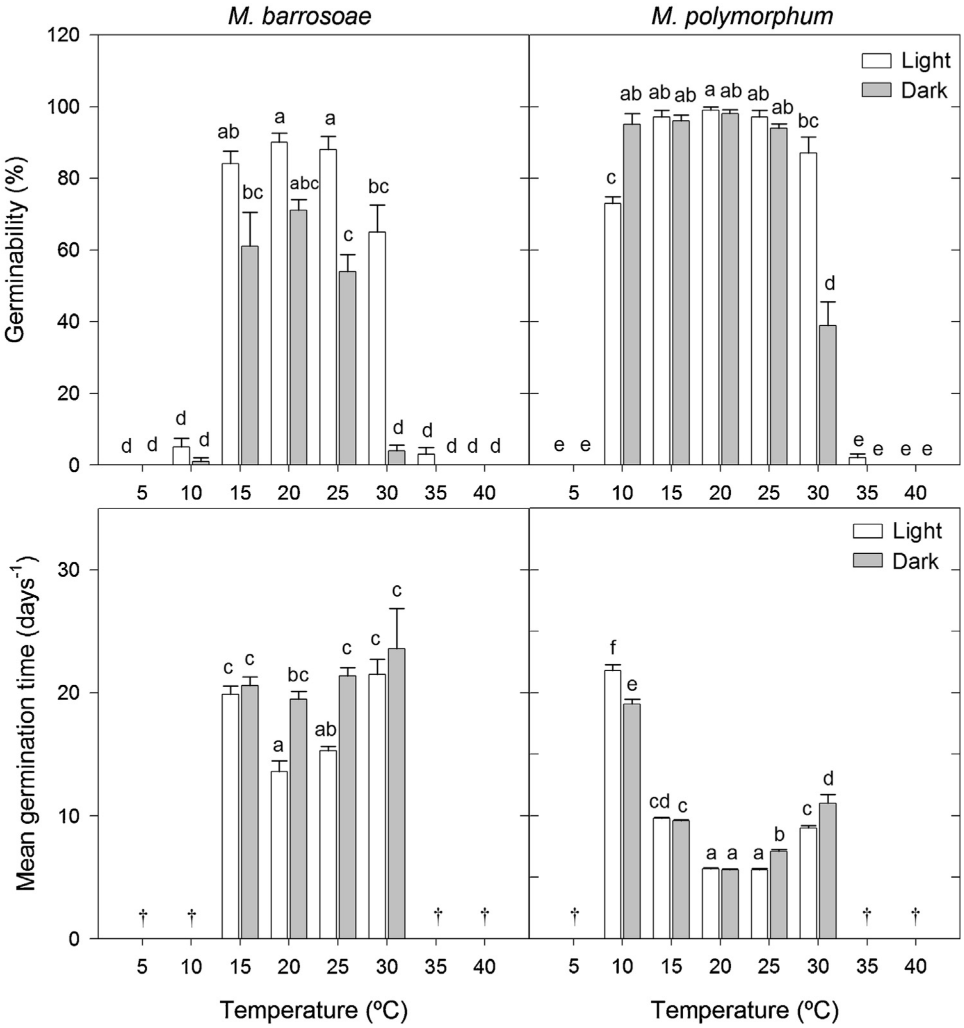

Fig. 2. Mean germinability and mean germination time (± standard error; n = 4) of seeds of *Moquiniastrum* species in different constant temperatures and light conditions. Different letters indicate significant differences among means (Tukey test; $P < 0.05$). †Not calculated.

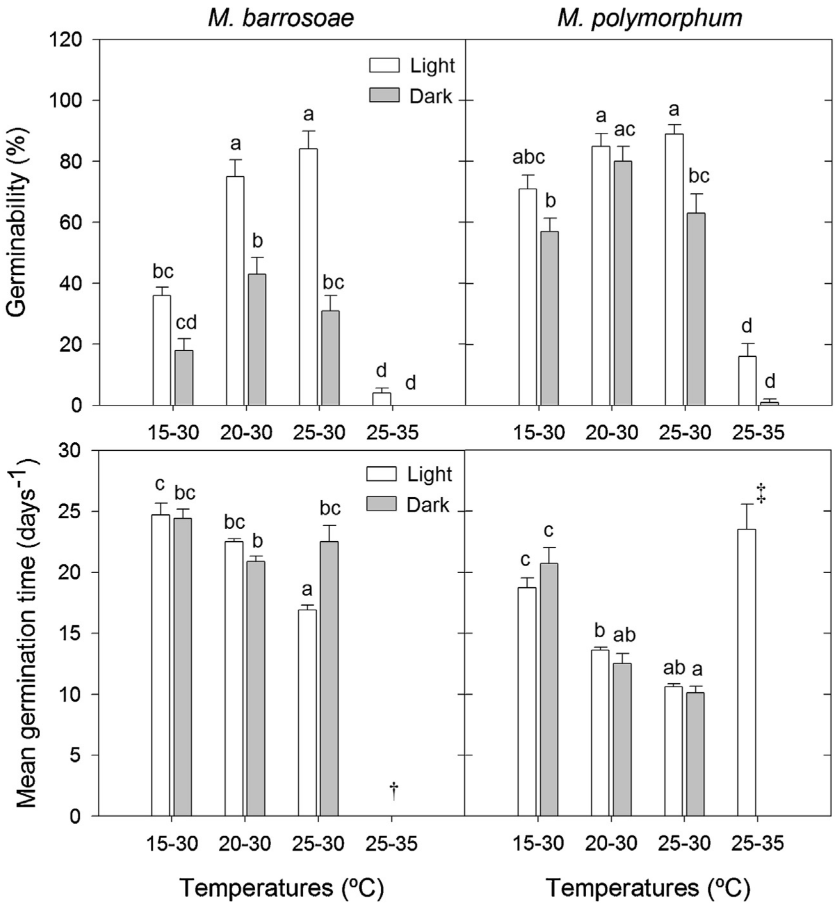

Fig. 3. Mean germinability and mean germination time (± standard error; n = 4) of seeds of *Moquiniastrum* species at different alternating temperatures and light conditions. Different letters indicate significant differences among means (Tukey test; $P < 0.05$). †Not calculated. ‡Not included in factorial ANOVA test.

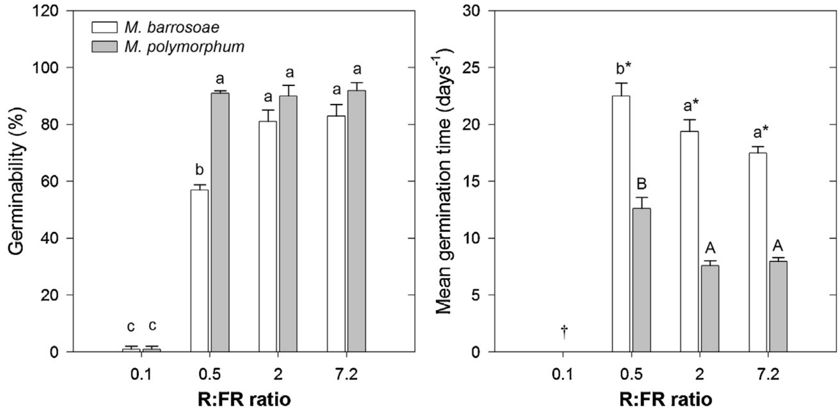

Fig. 4. Mean germinability and mean germination time (± standard error; n = 4) of seeds of *Moquiniastrum* species in different red:far-red (R:FR) ratios. Different letters indicate significant differences among means. For mean germination time, lowercase letters compare the different R:FR ratios for *M. barrosoae* seeds and uppercase letters compare the different R:FR ratios for *M. polymorphum* seeds. *Indicates significant difference between the species in the same R:FR ratio (Tukey test; $P < 0.05$). †Not calculated.

in the light and 15–25 °C in the dark (Fig. 2). Positive photoblastism (germinability in light > germinability in dark conditions) at 25 °C (*M. barrosoae*) and 30 °C (both species), and negative photoblastism (germinability in dark > germinability in light) at 10 °C for *M. polymorphum* (Fig. 2) were observed.

Alternating temperatures had significant effects on germinability and mean germination time in both species, while the light had influence only on germinability under these conditions. In addition, the interaction between alternating temperatures and light conditions was significant only for *M. barrosoae* (Table 2).

The alternating temperatures of 25–30 °C in light-exposed seeds provided higher germinability and lower mean germination time compared to the other alternating temperature regimes in *M. barrosoae*. For *M. polymorphum*, higher germinability and lower mean germination time occurred at alternating temperatures of 25–30 °C in light and 20–30 °C in light and dark conditions (Fig. 3). *M. polymorphum* showed higher germinability (above 70%) in a larger number of alternating temperature regimes (15–30, 20–30 and 25–30 °C in the light) than *M. barrosoae*, which showed the same performance only at 20–30 and 25–30 °C (Fig. 3). Positive

Table 3
Two-way ANOVA results for the effects of R:FR ratios (R) or water limitation (W), with the species (S) and their interaction (R × S or W × S) on germinability (G) and mean germination time (MGT) of *Moquiniastrum* species.

Source	G		MGT	
	df	*F*	df	*F*
	R:FR ratios			
R	3,24	426.7^{***}	2,18	20.5^{***}
S	1,24	42.7^{***}	1,18	244.6^{***}
R × S	3,24	13.5^{***}	2,18	1.2^{ns}
	Water limitation			
W	5,48	126.8^{***}	3,30	121.0^{***}
S	1,48	19.5^{***}	1,30	714.1^{***}
W × S	5,48	7.1^{***}	3,30	3.8^{*}

df: numerator and denominator degrees of freedom; ns: not significant.
* $P < 0.05$.
*** $P < 0.001$.

photoblastism was observed in 20–30 and 25–30 °C regimes for *M. barrosoae*, and only in the 25–30 °C regime for *M. polymorphum* (Fig. 3).

The LRI was higher in *M. barrosoae* at both constant and alternating temperatures than in *M. polymorphum*. At constant temperatures the LRI (± SE) was 0.71 ± 0.02 for *M. barrosoae* and 0.59 ± 0.05 for *M. polymorphum* (t-value = 4.02, df = 6, $P < 0.01$), and at alternating temperatures, the LRI was 0.73 ± 0.07 for *M. barrosoae* and 0.61 ± 0.06 for *M. polymorphum* (t-value = 2.55, df = 6, $P < 0.05$).

3.4. Different R:FR ratios on germination

There was a significant interaction between R:FR ratios and species for germinability. For mean germination time, the R:FR ratios and species effects were significant without interaction (Table 3). For *M. barrosoae*, germinability was reduced by R:FR ratio of 0.5 and inhibited by 0.1 ratio, presenting germination of only 1%. Germinability of *M. polymorphum* was affected only by R:FR ratio of 0.1. The R:FR ratio of 0.5 increased mean germination time for both species, however, *M. barrosoae* had always higher mean germination time compared to *M. polymorphum* (Fig. 4).

3.5. Water limitation on germination

There was significant interaction between osmotic potential and species on seed germination (Table 3), and the degree of stress tolerance differed between the species (Fig. 5). From the osmotic potential of −0.4 MPa germinability of *M. barrosoae* decreased when compared to the control treatment (0 MPa), and was very low at −0.6 and −0.8 MPa. Germinability of *M. polymorphum* seeds decreased from −0.6 MPa, but germinability remained high in this condition (66.3%) compared to *M. barrosoae* (6%). In *M. polymorphum*, germination occurred even at potentials of −0.8 and −1.0 MPa, being however, very low in these conditions. Mean germination time increased from −0.2 MPa for *M. barrosoae* and from −0.4 MPa for *M. polymorphum* compared to the control treatment (0 MPa). *M. barrosoae* had always higher mean germination time compared to *M. polymorphum* (Fig. 5).

4. Discussion

Considering the high germinability reached within 30days under optimum conditions (≥88%), our data suggest that mature fresh seeds of the *Moquiniastrum* species studied here are non-dormant (Baskin and Baskin, 2004). Germination of their seeds was controlled by the different environmental factors studied. However, germination responses were distinct between the species; with the widely distributed species (*M. polymorphum*) having higher germinability under a wider range of the environmental conditions tested compared to *M. barrosoae*. Furthermore, our results indicated that the germination traits are related to the species occurrence in the different vegetation types in Cerrado.

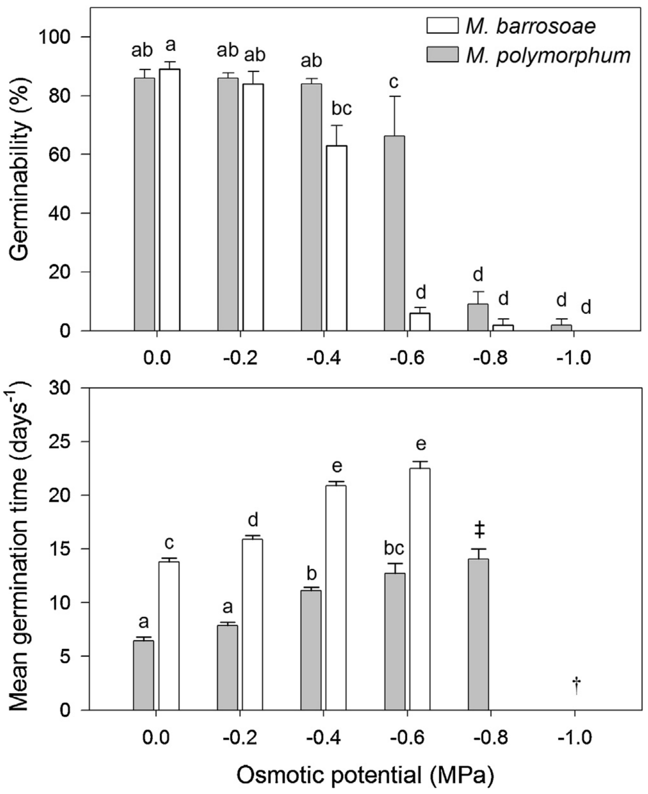

Fig. 5. Mean germinability and mean germination time (± standard error; n = 5) of seeds of *Moquiniastrum* species in different osmotic potential conditions. Different letters indicate significant differences among means (Tukey test; $P < 0.05$). †Not calculated; ‡Not included in factorial ANOVA test.

In this study, constant temperatures of 20 and 25 °C or alternating temperatures of 25–30 °C were the optimal regimes for both species, providing higher germinability in less time. These values are close to the temperature range measured at the soil surface in the different vegetation types studied, and to the mean air temperature at the study site during the period of seed dispersal of both species. This indicates that the germination response to temperature is habitat-specific for the species studied (Baskin and Baskin, 2014; Liu et al., 2013). This kind of result was also found for *Vellozia* species from Brazilian campo rupestre, whose germination occurred in a wide thermal range, including high temperatures (20–40 °C); this was related to higher solar radiation and to larger temperature fluctuations in their extreme environment (Garcia and Diniz, 2003; Garcia et al., 2007).

Although the typical savanna had shown higher temperatures on the soil surface than the forested savanna, the observed variation is still within the germination temperature range of both species. Therefore, this phenomenon is not a limiting factor for the germination of the studied species in these environments. However, *M. polymorphum* presented higher germinability in a wider temperature range, and also more optimal temperature regimes to germination when compared to *M. barrosoae*. Therefore, this feature may ensure advantages for *M. polymorphum* when germinating in the different vegetation types of the Cerrado.

Seed mass has an important role in several processes, such as seed dispersal and germination (Leishman et al., 2000). In this way, this seed trait may have consequences for the establishment and distribution pattern of the species. For some wind-dispersed species, smaller seeds may achieve greater dispersal distances than larger ones (Greene and Johnson, 1993; Morse and Schmitt, 1985). Moreover, taller species release their seeds at greater heights than shorter species and this may result in greater dispersal distances (Thomson et al., 2011). This means that *M. polymorphum* (smaller wind-dispersed seeds and taller species) may have better dispersal ability than *M. barrosoae* (larger wind-dispersed seeds and shorter species), contributing to its occupancy in a wider range of vegetation types in the Cerrado. For the relationship between seed mass and germination, small-seeded species are more likely to require light to germinate than large-seeded ones (Milberg et al., 2000; Pearson et al., 2002). However, the opposite was observed here, with *M. barrosoae* (larger seeds) presenting higher light requirement to germinate (>LRI values) compared to *M. polymorphum* (smaller seeds). Furthermore, seeds of *M. barrosoae* need R:FR ratio above 0.5 to reach maximum germinability, while for *M. polymorphum* R:FR ratio threshold to reach maximum germinability remains between 0.1 and 0.5.

Both higher light requirement and higher sensibility to the decrease of R:FR ratio for seed germination in *M. barrosoae* may be related to its preference for typical savanna environments, which has more light than the forested savanna. These traits may increase its chances to germinate in sites with suitable radiation levels for the development of its seedlings (Pearson et al., 2002; Vasquez-Yanes and Orozco-Segovia, 1993), since they are shade-intolerant (Durigan et al., 2004b). In turn, the lower light requirement and the lower sensibility as to the decrease of R:FR ratio for *M. polymorphum* germination probably enable this species to germinate in a wider range of light variation in the Cerrado. Although seedlings of *M. polymorphum* are also considered intolerant to shade (Durigan et al., 2004b), its occurrence inside the forested savanna is probably due to effective occupation of gaps. Therefore, light may be an important factor controlling seed germination in savanna communities, and contributes to regulating the distribution patterns, coexistence and species diversity in different habitats, as already observed for tropical forests (Daws et al., 2002; Kobe, 1999; Pearson et al., 2003).

Although both *Moquiniastrum* species shed their seeds during the rainy season, short periods of drought may interfere on seed germination, as the water potential of the soil surface can reach −1.3 MPa in an open savanna or −0.8 MPa in a forested savanna (Kanegae et al., 2000). *Moquiniastrum barrosoae* had lower tolerance to water limitation when compared to *M. polymorphum*. Germination response to water limitation varies among Cerrado species. In *Styrax camporum* germination was affected by −0.1 MPa solutions (Simão et al., 2013); *Bowdichia virgilioides* had germination affected by −0.3 MPa, and its tolerance limit was between −0.6 and −0.9 MPa (Silva et al., 2001). In *Zygophyllum xanthoxilum*, a species from arid environments, seed germination was more sensitive to water limitation than in other species from less dry environments, and this strategy was proposed as an adaptive germination mechanism of native xerophytes, which can reduce seedling mortality after short-term rainfall events (Zeng et al., 2010). In the same way, although the Brazilian Cerrado is a moist savanna, this strategy could help to spread germination in time and avoid germination in inadequate moisture conditions for seedling establishment of *M. barrosoae*. In contrast, the higher tolerance to water limitation of *M. polymorphum* seeds is probably an ecological advantage that propitiates their germination in soil in a wider moisture range, which is in accordance with its wider occurrence in different vegetation types of Cerrado.

In all tested situations, the mean germination time was higher in *M. barrosoae* (≥13.6 days) than in *M. polymorphum* (≥5.6 days). Considering that micro-climatic conditions tend to be more unstable and limiting at typical savanna (Salazar et al., 2012), the strategy of spreading germination through time may increase the chances of seedling survival and establishment, when conditions become suitable. This trait was reported in other typical savanna species (Kissmann and Habermann, 2013; Mendes-Rodrigues et al., 2011; Ribeiro and Borghetti, 2014; Simão et al., 2013). This strategy would also help seedling survival at the beginning of the rainy season (dispersal time of *M. barrosoae*), when rainfall varies in intensity and frequency in the Cerrado region (Oliveira, 2008). The dispersal of *M. polymorphum* seeds occurs later, so its early germination can be a strategy in taking advantage of favorable environmental conditions of the wet period (Borghetti and Ferreira, 2004). Probably, it also enables the fast seedling establishment and the rapid growth of its roots, which can reach deep and moist soil layers before the next dry season.

Our findings are consistent with the regeneration niche hypothesis, which predicts that regeneration stage (including germination traits) can influence adult distribution patterns (Grubb, 1977). Here, we show that the shrub *M. barrosoae* and the tree *M. polymorphum* have different seed germination traits, and the more widely distributed species (*M. polymorphum*) has higher germinability in different environmental factors, which may enable this species to germinate under a wider range of environmental conditions compared to the species with a more restricted distribution area (*M. barrosoae*), which presented more specific environmental requirements for seed germination. These results demonstrate how the germination traits may be related to the distribution pattern of adult plants at local scale, and contribute to the distribution patterns and diversity of Cerrado plant communities.

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