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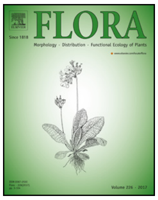

Seed germination of *Xyris* spp. from Brazilian campo rupestre is not associated to geographic distribution and microhabitat

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A B S T R A C T

Xyridaceae comprises the seventh largest monocot family in Brazil, with *Xyris* L. being the largest and most representative genus there. The most important center of diversity for this genus is the Espinhaço Range in southeastern Brazil, where these plants grow in rocky open fields (*campo rupestre*), usually on humid or boggy soils. The present work examined the seed germination of *Xyris* species to evaluate the relationships between the germination requirements and their geographic distribution patterns and the distinct micro-habitats they occupy. Laboratory tests were carried out to evaluate light, temperature, and oxygen restriction effects on the germination of eight *Xyris* species occurring in the Espinhaço Range. All eight species had small seeds that were intolerant of high temperatures ($\geq$35 °C) when imbibed, absolute light requirements for germination, and were able to germinate under hypoxic conditions. The effects of temperature on seed germination do not explain the patterns of geographic distribution nor the endemism seen among the species examined here. Additionally, the occurrence of *Xyris* species in soils with different water retention capacities cannot be attributed to the capacity of their seeds to germinate under conditions of hypoxia, as the seeds of species that occur on well-drained soils also germinated under low-oxygen condition.

1. Introduction

Research in seed biology is essential for understanding the processes of establishment and succession and the natural regeneration of plants (Vázquez-Yanes and Orozco-Segovia, 1993; Jiménez-Alfaro et al., 2016). Species within the same genus generally show similar strategies and life cycles, but their different germination requirements appear to reflect specific adaptations to the habitats they occupy (Specht and Keller, 1997; Van Assche et al., 2002). From this perspective, comparative studies focusing on the germination requirements of phylogenetically related species can demonstrate how germination is regulated by environmental factors and if these requirements reflect the natural conditions of the habitats of each species.

The time and place of seed germination represent central components in the life cycles of all plant species, also the successful establishment of a seedling is almost invariably dependent on the rapid exploitation of temporarily favorable environments (Grime et al., 1981; Casal and Sánchez, 1998). Light and temperature stand out among the principal factors that can affect seed germination (Baskin and Baskin, 1988). Light is almost always essential for the germination of small seeds (Milberg et al., 2000), and seed mass is a fundamental characteristic in many aspects of plant ecology (Moles et al., 2005). Temperature is generally the most important factor in the perception of favorable environmental conditions for seedling development, and is often responsible for the synchronization of germination induction (Baskin and Baskin, 1988; Probert, 2000).

Another important factor influencing successful germination is the concentration of oxygen available to the seeds. The physiological processes necessary for germination require the presence of O_2 (Bewley et al., 2013) and restrictions of their availability can negatively affect germination in many species (Okamoto and Joly, 2000). Excess water can alter soil structure and inhibit gas diffusion, so that any oxygen present in the soil will be consumed in the aerobic metabolic processes of roots and microorganisms, resulting in conditions of reduced soil oxygen tension (Blom and Voesenek, 1996). Germination generally requires relatively high atmospheric levels of O_2 and tolerance to different environmental oxygen concentrations can vary significantly among plant species (Kozlowski, 1997), although some species can germinate underwater and under conditions of hypoxia (Hilhorst and Karssen, 2000).

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Xyridaceae is the seventh-largest family of monocotyledons in Brazil, with the genus *Xyris* L. being the most well represented and widely distributed taxon there. In addition to its species richness, the genus *Xyris* displays a high degree of endemism, with approximately 100 species being found only in Brazil (Giulietti et al., 2005). Many of these species are threatened with extinction, principally due to the loss of natural habitats and the indiscriminate harvesting of their reproductive structures for use in handicrafts (Silveira et al., 2016). Species of *Xyris* are predominantly found in swamps and wetlands, but can also occur in sandy substrates that are poorly drained but periodically dry (Wanderley, 2011).

This study investigated the germination requirements of eight species of *Xyris* of Brazilian *campo rupestre* with different geographical distributions and occupying distinct microhabitats with different soil water retention. The seeds of these species are described here in terms of their morphologies and the effects of light, temperature and waterlogged conditions on their germination processes. In light of the phylogenetic proximity of the species studied, we addressed the following questions: are the sizes of the seeds associated with specific germination traits that show distinct patterns within the genus? Are the geographic distributions of the species regulated by temperature ranges favorable to their germination? Is the capacity to germinate in a waterlogged environment dependent on the species considered, and does it represent a limiting factor in terms of the microhabitats that can be colonized?

2. Materials and methods

2.1. Study area and species

The present study was undertaken in the Rio Preto State Park (PERP) in the state of Minas Gerais in southeastern Brazil (43°18′21″W; 18°14′03″S). PERP is located in the central portion of the Espinhaço Mountain Range (*campo rupestre*) that extends for 1100 km in a generally north-south direction (10°–20° S) with altitudes varying from 1000 to 2000 m. The regional climate is characterized by mild and humid summers (October to April) and cooler and drier winters (June to August), with short transition periods during the months of May and September (Antunes, 1986).

Eight species of *Xyris* with distinct geographic distributions and microhabitat preferences were selected (Smith and Downs, 1968; Giulietti et al., 1996; Giulietti et al., 2009) (Figs. 1 and 2). Floral scapes with well-developed spikes containing seeds that were sufficiently mature for dispersal were collected. The spikes were harvested randomly within the populations of the different species and efforts were made to collect the largest possible numbers of individuals (one population per species, at least 50 individuals).

2.2. Seed characteristics and germination

Data concerning the length (mm) and width (mm) of the seeds were based on a sampling of 100 seeds, using a digital caliper. The data of water content and dry mass (mg) was based on a sampling of 400 seeds distributed into four lots of 100. Freshly seeds were weighted and dried to a constant weight at 105 °C and then reweighed using an analytical balance.

Germination tests were performed in germination chambers under a 12-h photoperiod (30 μmol m^{-2} s^{-1}) and continuous darkness at constant temperatures from 10 to 35 °C at intervals of 5 °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 UI/mL) 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 aluminum foil and black polyethylene bags, and the germination of these seeds was evaluated under green light. A total of 200 seeds distributed four replicates of 50 were used in all light and temperature treatments. Germination was defined as the radicle emergence and was verified on a daily basis using a stereomicroscope. The samples were observed until the germination response stabilized (7 days without germination). Seeds exposed to temperature treatments of 10, 15 and 35 °C (under a 12-h photoperiod) that did not germinate after 60 days were transferred to 25 °C conditions and observed for an additional 20 days.

To test the effect of waterlogged (considered as hypoxia), four repetitions of 50 seeds were placed in Petri dishes containing a 7 mm deep column of distilled water. This test was undertaken in a growth chamber under white light (30 μmol m^{-2} s^{-1}; 12-h photoperiod) at 25 °C. Germination was evaluated every 10 days until the seed responses stabilized.

2.3. Statistical analyses

All of the data was submitted to non-parametric statistical analyses as it did not demonstrate normality using the Shapiro–Wilk test or homogeneity using the Brown-Forsythe test (JMP software package; SAS Institute Inc. 2002). Mean germination time was calculated ($MT = \Sigma(GnTn)/\Sigma Gn$); where MT is the mean time required for maximum germination; Gn is the number of seeds germinate at time Tn (Edmond and Drapala, 1958). The optimal germination temperature was defined as that temperature showing the greatest germinability associated with the greatest germination velocity (Labouriau, 1983). Germination and mean time data were analyzed by GLM and the means were compared using the Newman-Keuls post-hoc test. The hypoxia and normoxia data were compared using the Mann-Whitney (5% significance level) (Zar, 1984).

3. Results

The eight species of *Xyris* studied had very small seeds, with *X. coutensis* and *X. aurea* having the largest dimensions and *X. peregrina* and *X. jolyi* the smallest (Table 1). In spite of the fact that all of the species had very low individual dry seed mass (<0.16 mg), the seeds of *X. jolyi* weighed approximately 13 times more than those *X. coutensis* (Table 1). Variations in water contents were more discrete (ranging between 10.9 and 13.1% for *X. bialata* and *X. peregrina* respectively).

None of the seeds of the species studied germinated in the darkness at any of the temperatures tested. The most favorable temperature range for germination varied among the species investigated, being from 10 to 30 °C for three species, from 15 to 30 °C for four species, while one species demonstrated a very restricted germination range of 20–30 °C (Fig. 3), although the germination percentage of *X. laxifolia* at 30 °C was lower than 20–25 °C (13.5% and 80% respectively, Fig. 4). In spite of the variations observed among the different optimal temperature ranges, 25 °C was included within the optimal temperature range for germination among seven of the eight species examined (Fig. 3).

Under light and conditions of optimal temperatures, germinability was above 60% in all species except for *X. coutensis* (whose germination response was below 33% under all tested conditions) (Fig. 4). No germination was observed among the seeds of any species at 35 °C, even after the subsequent transfer to 25 °C conditions. At the time of the transfer (from 35 to 25 °C) all of the seeds demonstrated visible signs of deterioration (such as leakage of seed content and darkening of the tegument). The seeds of *X. bialata*, *X. peregrina* and *X. spinulosa* demonstrated germinability of 81.5%, 77.5%, and 54.5% respectively after transfer from 10 °C to 25 °C. However, the transfer of *X. laxifolia* seeds from 10 and 15 °C to

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