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Germination Characteristics of Four Argentinean Endemic *Gymnocalycium* (Cactaceae) Species With Different Flowering Phenologies

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ABSTRACT: We analyzed germination percentages and germination rates at four temperature treatments (5/15, 10/20, 15/25 and 20/35 °C) and in light or darkness in four endemic species of the genus *Gymnocalycium* with different flowering phenologies from the Córdoba Mountains (Argentina). *Gymnocalycium bruchii* flowered and dispersed its seeds very early in the season in comparison to the other three species. No seeds germinated in darkness or at the coldest temperature regime. For all species except *G. bruchii*, germination was higher at the two warmest treatments. *Gymnocalycium bruchii* germination was maximum at the second warmest temperature (15/25 °C) and did not germinate at all at the highest temperature treatment (20/35 °C). Germination varied strongly among species, from about 80% in *G. quehlium* to 20% in *G. monvillei*. Germination rate (t_{50}) varied more strongly among temperature treatments (from 15 to 7 days in the coldest and warmest treatments respectively) than among species. The lack of germination of *G. bruchii* at 20-35 °C could be related to its early flowering phenology.

Index terms: Argentina, cactus seeds, light, seed germination, temperature responses

INTRODUCTION

Knowledge of plant characteristics such as sexual reproduction (i.e. flowering phenology and germination) is crucial to our understanding of causes of rarity and for conservation of rare and endemic species (Kaye 1999; Quilichini and Debussche 2000). Germination is often considered a key element in plant life history strategy. The germination requirements of species can determine the timing of germination and hence seedling survival and establishment (Bell et al. 1995; Funes and Venier 2006). In slow-growing species, such as cacti, seed germination and establishment are critical phases of their life cycle (Bowers and Pierson 2001; Contreras and Valverde 2002). Sometimes seedling establishment is very low, although seed production can be rather high (Godínez-Álvarez et al. 2003). Low seedling establishment is caused by animal predation, both to seeds and seedlings, as well as desiccation (Flores et al. 2004). Cactus seedlings are stem succulents, but with a much lower surface/volume ratio than adult plants, which make them prone to desiccation (Cervera et al. 2006). Differences in germination characteristics have also been considered important for plant species coexistence (Flores and Jurado 1998; Daws et al. 2002), especially for species morphologically very similar to congeneric species (Daws et al. 2002; Ramírez-Padilla and Valverde 2005).

It has been demonstrated that different cactus species have different optimal temperatures to germinate. This pattern has been attributed to geographic distribution. For example, species from tropical areas

germinate better at higher temperature than species from temperate or cold areas (Rojas-Aréchiga and Vázquez-Yañes 2000). However, less known is what occurs at the community level where different species coexist (Rojas-Aréchiga et al. 1998). Coexisting species of the same genus usually differ in their reproductive biology, for example in phenology, in order to avoid competition for pollinators and interbreeding (McIntosh 2002, 2005). If coexisting species differ in their phenology, they will also differ in the timing of seed dispersal.

Germination response to light differs among cactus species (Rojas-Aréchiga and Vázquez-Yanes 2000). Rojas-Aréchiga et al. (1998) found that globular cactus species need light to germinate while columnar species germinate well in darkness. However, McDonough (1964) found that two columnar species, *Carnegiea gigantea* and *Lemaireocereus thurberi*, require light to germinate. Other authors found that light requirements depend on temperature (Dau and Labouriau 1974; Arias and Lemus 1984). However, there is no information in the literature about light requirements in *Gymnocalycium* species.

The genus *Gymnocalycium* (Cactaceae) is native to southern South America. There are around 70 species distributed in Argentina, Brazil, Bolivia, Paraguay, and Uruguay (Pilbeam 1995). All species have a globose body, and can be solitary or colonial. The Córdoba Mountains (central Argentina) are an important diversity center for the genus with around 17 species, most of them endemic (Zuloaga and Morrone 1996). In the Sierras Chicas range, four

Gymnocalycium species coexist. Previous field observations showed that these four species differ in the timing of flowering, ranging from early spring to mid and late summer. Although *Gymnocalycium* species are cultivated worldwide, there is a lack of information about basic aspects of their biology and ecology (Gurvich et al. 2006). Such knowledge is, of course, essential for both in situ and ex situ conservation programs (Flores et al. 2006). The aim of this study was to analyze total germination and germination rate at different temperature regimes, in darkness and light, of four *Gymnocalycium* species endemics of the Sierras Chicas Mountains, Córdoba, Argentina.

MATERIALS AND METHODS

Study species and area

We studied four globose cactus species of the genus *Gymnocalycium* which coexist in the Sierras Chicas range of the Córdoba Mountains (Gurvich et al. 2006): (1) *G. bruchii* (Speg.) Hosseus var. *bruchii*, (2) *G. capillaense* (Schick) Hosseus, (3) *G. monvillei* (Lem.) Britton et Rose subsp. *monvillei*, and (4) *G. quehlianum* (F. Haage ex Quehl) Vaupel ex Hosseus. All species are endemic to the Córdoba Mountains (Zuloaga and Morrone 1996). The study site is located in the "Parque la Quebrada" natural reserve (31° 07' 51" W, 64° 25' 04" S). The altitude is approximately 1200 m.a.s.l., and the climate is temperate with a mean annual temperature of 13.5 °C and a mean annual precipitation of around 850 mm. Frosts are common during the winter and the rains are concentrated to the warm season (October to April).

Reproductive phenology

Data on reproductive phenology was taken for a broader study of species phenology and reproductive output actually in course (M.A. Giorgis, unpubl. data). In that study, at least 33 individuals of each species were marked and their phenology was measured weekly during the 2004-2005 growing season. For the purposes of this study, only the peak date of fruit ripening was used to

relate it to the germination characteristics of the species.

Seed collection and germination experiment

Seeds were collected at the same site where phenology was measured. Mature fruits were collected during spring-summer 2004-2005 for at least 15 individuals of each species. Seeds were separated from the fruits, cleaned, pooled, and stored in paper bags at ambient temperature until the experiment began.

The germination experiment was performed between February and March 2005. Seeds of the four species were subjected to a combination of two light and four temperature treatments. Light treatments were: light (12/12 h daily photoperiod of about 38 $\mu\text{mol m}^{-2} \text{s}^{-1}$ cool white fluorescent light tubes) and continuous darkness (dishes wrapped with a layer of aluminum foil). The temperature treatments were 5/15, 10/20, 15/25 and 20/35 °C (12/12 h daily thermo period). Three replicates (Petri dishes of 9 cm diameter) were used, and in each dish fifty seeds were placed on filter paper and incubated for 15 days. When it was necessary, Petri dishes were moistened with distilled water (3 ml). Protrusion of the radicle was the criterion for germination. Germination of seeds incubated in dark was checked at the end of the experiment.

Statistical analysis

Under some treatments, no germination was found (under darkness, under the coldest temperature; for one species, also under the warmest temperature). These treatments were excluded from the statistical analyses because germination rate could not be calculated and because the large number of zero values for germination percentage made it difficult to meet statistical assumptions. Thus, we could not perform two-way ANOVAs with species and temperature as factors. Instead, each species by temperature combination was considered as a treatment (i.e., 11 treatments), and final percentages of seed germination and germination rate (t_{50}) were

compared through one way ANOVA. All analyses included a LSD Fisher a posteriori test. Before analysis, percents were arcsin-transformed to stabilize variances (Sokal and Rohlf 1995).

RESULTS

The different species showed marked differences in their reproductive phenology. *Gymnocalycium bruchii* was the species with the earliest flowering that takes place at the beginning of the spring, followed by *G. quehlianum*, *G. monvillei*, and finally *G. capillaense*. All species but *G. quehlianum* presented one flowering peak with short phenological amplitude. In contrast, *G. quehlianum* shows a large flowering range, with a relative constant number of flowers. For fruits of all species, maturation takes around 5 weeks, so the peak of dispersion of *G. bruchii* was around the 19th October, at mid-spring. All the other species had their dispersion peak later in the season, which coincides with the beginning of the summer (Figure 1).

No seeds germinated in darkness under any temperature treatment. For the light treatments, total germination varied strongly among species and temperature regimes (Figure 2). At the coldest treatment (5/15 °C), there was no germination. *Gymnocalycium bruchii* also failed to germinate at the warmest (20/35 °C) treatment. The other species attained their highest germination at the two warmest temperature regimes (15/25 and 20/35 °C). In general terms, *G. quehlianum* had the highest germination percentage, followed by *G. capillaense*. *Gymnocalycium bruchii* germinated well only at 15/25 °C. *Gymnocalycium monvillei* germinated poorly at all temperature regimes (Figure 2).

Germination rate varied strongly among treatments but weakly among species (Figure 3). For all species, germination rate decreased steadily as temperature increased. At the species level, there was only one significant difference; at the 20/35 °C treatment, *G. capillaense* germinate faster than *G. monvillei*.

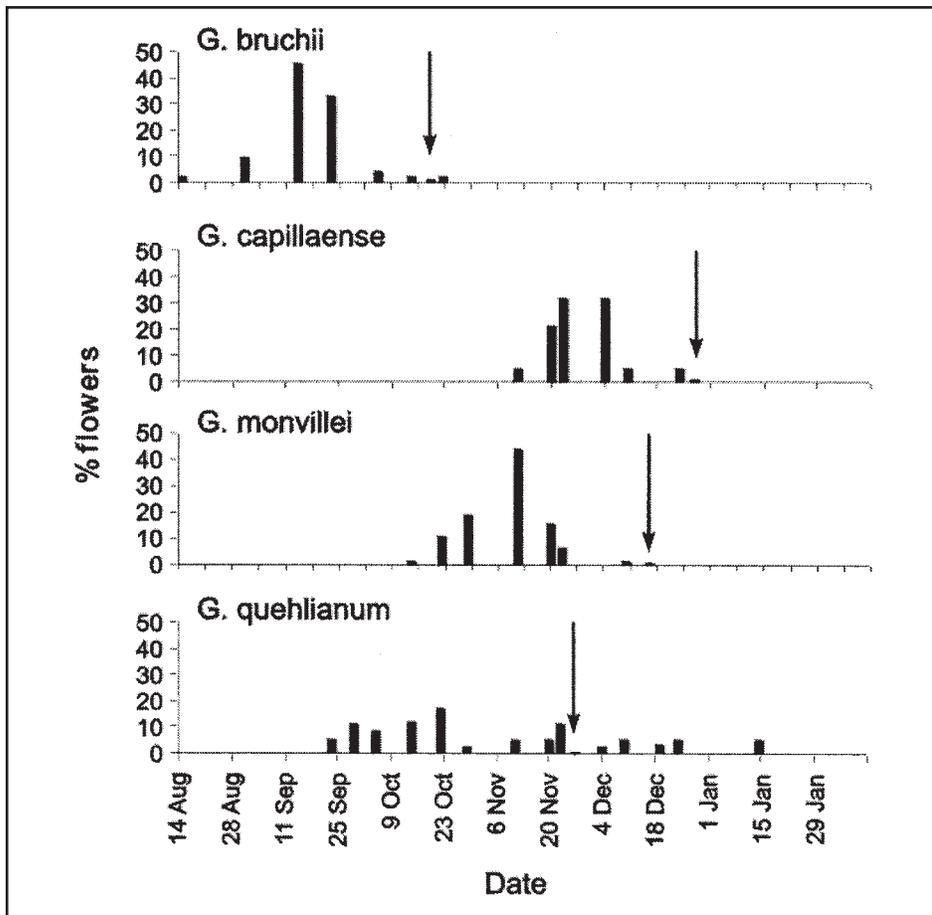


Figure 1. Flowering phenology of the species studied. The length of the bars indicates the % of flowers in a particular census data in relation to all flowers produced for that species. The arrows indicate the date of the peak of seed dispersal. For each species at least 33 individuals were followed during the 2004-2005 growing season.

DISCUSSION

We initially hypothesized that coexisting species of *Gymnocalycium* with different flowering phenologies should have different germination requirements. This appeared to be the case. *Gymnocalycium bruchii* flowered only in spring and germinated only at temperatures typical of spring; the other three species, which flowered during late spring and summer, germinated at a wide range of temperatures, but achieved their highest germination at the warmest temperature regimes. It is difficult to explain why *G. bruchii* failed to germinate at the warmest temperature regime. An explanation could be related to the habitat preferences of this species. *Gymnocalycium bruchii* inhabit more vegetated patches, dominated by tussock grasses covering around 100% of the ground, in comparison to the other species that inhabit rocky

outcrops with more severe environmental conditions (Gurvich et al. 2006). The dense canopy of the grasses could ameliorate the temperature conditions, creating a favorable environment for the germination of *G. bruchii* even if temperatures are high. Further experimental work is necessary to understand this pattern through the measurement of micro-environmental variables (i.e., temperature, photosynthetic active radiation) and field germination experiments. All other species disperse their seeds during late spring and the beginning of the summer, which correlates with the fact that their optimal temperature to germinate is 15/25 and 20/35 °C.

For all species, optimal germination was between 15/25 and 20/35 °C, which agrees with the literature about cactus species (Rojas-Aréchiga and Vázquez-Yañes 2000). This pattern is in accordance with the rainy

season of the area, and indicates that there is a coupling between germination and the humid season. Similar results were found by Funes and Venier (2006) for three *Acacia* species in a chaquenan system in central Argentina and by Bell et al. (1995) for Mediterranean species of Australia. The total germination varied markedly among species. *Gymnocalycium monvillei* had the lowest germination while *G. quehlianum* had the highest one. The germination of *G. monvillei* is low even compared with other cactus species, particularly of the subfamily Opuntioideae, which have low germination values (Godínez-Alvarez and Valiente-Banuet 1998; Mandujano et al 2005). This species has the highest seed production of the four study species (i.e., the mean number of seeds per fruit is 1680, while the species with second highest production is *G. quehlianum* with 360 seeds per fruit; M.A. Giorgis, unpubl. data); high seed production perhaps compensates for its low germination.

Germination rate differed among temperatures but not among species. It is well known that germination rate increases as temperature increase (Rojas-Aréchiga and Vázquez-Yañes 2000). Germination rates found in this study were similar to those reported for other cactus species of the subfamily Cactoideae (Flores et al. 2006), which germinate rather fast. This fast germination has been viewed as a strategy to couple germination with favorable conditions (particularly rains), which is important for species establishment, particularly in arid and semiarid systems with unpredictable rains. Even when our study area cannot be considered as semiarid, cactus grow in rather dry microhabitats (Gurvich et al. 2006), where water deficits probably occur for short time periods, even during the rainy season.

None of the species germinated in the darkness. This agrees with other studies in globose cactus, which found that seeds need light to germinate (Flores et al. 2006) and in contrast to columnar cactus that can germinate in darkness (Rojas-Aréchiga et al. 1997; Rojas-Aréchiga and Vázquez-Yañes 2000). Light requirements in cactus should be directly related to seedling morphology. Cactus seedlings, and particularly those of

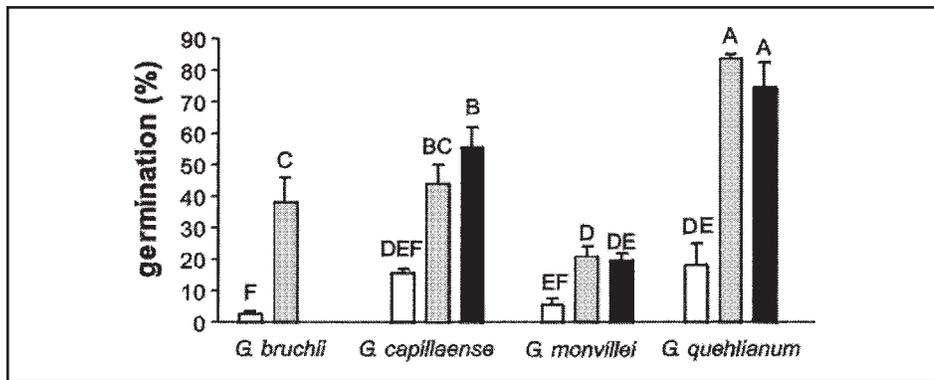


Figure 2. Total germination (%; mean + 1SE) of the species in laboratory conditions. The color of the bars indicates the temperature treatment: white 10/20 °C; grey 15/25 °C; and black 20/35 °C. Letters over bars indicate significant differences (ANOVA test, and LSD *a posteriori* test, $P < 0.05$) among treatments.

the genus *Gymnocalycium*, are spherical or shortly cylindrical, and generally small (in our species seedling height is between 2-4 mm), so they have a limited capacity to reach the light if they germinate buried in the soil. This is different from “typical” plants where seedlings can grow upward through the soil, reaching the surface and hence a favorable growing environment.

Although no field data are available, our results suggest that germination in these species mainly occurs shortly after seed dispersion, which agrees with their reproductive phenology (all species disperse during the growing season) and also with germination characteristics of other cereoid cactus (Pimienta-Barrios and Del Castillo 2002). A rapid germination after dispersion

would minimize seed predation (Crawley 2000). However, further studies are needed, particularly concerning the longevity of seeds and their capacity to form seed banks (Bowers 2000, 2005).

Our work also provides essential information for ex situ conservation programs. As many other cacti species, and particularly globose species (Flores et al. 2006), *Gymnocalycium* is a genus very popular among hobbyists, so the collection on natural populations is high (Gurvich et al. 2006). A good alternative is to develop ex situ conservation programs, such as growing plants from seeds in nurseries (Boyle and Anderson 2002; Flores et al. 2006).

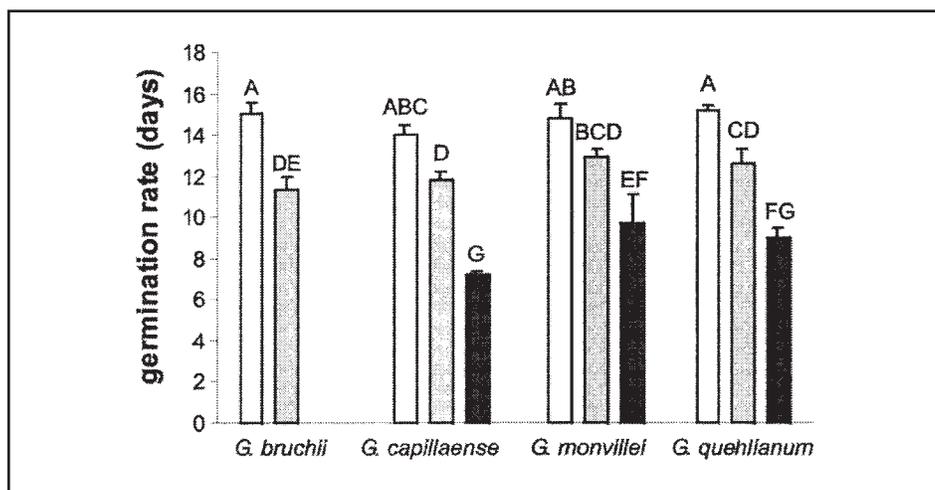


Figure 3. Germination rate (days; mean + 1SE) of the species in laboratory conditions. The color of the bars indicates the temperature treatment: white 10/20 °C; grey 15/25 °C; and black 20/35 °C. Letters over bars indicate significant differences (ANOVA test, and LSD *a posteriori* test, $P < 0.05$) among treatments.

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