



Physiological ecology of seed germination for the columnar cactus *Stenocereus queretaroensis*

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Responses of seed germination to temperature, water potential, time after harvest, and light were investigated for *Stenocereus queretaroensis*, a columnar cactus native to west central Mexico. Germination was optimal between 20°C and 30°C, and the germination percentage decreased as the water potential was lowered from 0.00 to -1.0 MPa. Maximal germination of 85% occurred for seeds that were 11 – 28 months old. Germination required light but became light saturated at a photosynthetic photon flux over 10 days of only 0.15 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (equivalent to a fluence of 67 mmol m^{-2}). Germination was apparently phytochrome mediated, as evidenced by its relative spectral sensitivity (greatest at 660 nm). The environmental requirements for breaking seed dormancy for *S. queretaroensis* are finely tuned to those typical of the rainy season in its native habitat.

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Introduction

Successful establishment of plant species is often dependent on the timing for germination resulting from seed responses to environmental cues (Vázquez-Yanes & Orozco-Segovia, 1996). For example, seeds may readily germinate following an early summer rain, but fail to respond to winter rains when air temperatures are lower (Larcher, 1980). Indeed, seeds often respond to specific combinations of light, temperature, and soil moisture that are most favorable to their establishment (Baskin & Baskin, 1998). In a desert environment with limited and sporadic rainfall, favorable conditions may not occur every year (Nobel, 1988; De la Barrera, 1997). Hence, the duration of seeds in a seed bank also can be an important long-term aspect of plant success.

Positive photoblasticism, the requirement of light to trigger the interruption of seed quiescence, provides competitive advantages to many plant species and can help determine the structure of a community (Vázquez-Yanes & Orozco-Segovia, 1996; Baskin & Baskin, 1998; Gallagher & Cardina, 1998; Restrepo & Vargas, 1999). For instance, seeds may respond to changes in the spectral composition or the amount of

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light resulting from canopy disturbance or to increases in the photosynthetic photon flux (PPF, wavelengths of 400 – 700 nm) when a buried seed is exposed (Orozco-Segovia & Vázquez-Yanes, 1990). Response to light quality provides pioneer species with the ability to sense the formation of gaps within the canopy, enabling their establishment (Orozco-Segovia, 1989; Restrepo & Vargas, 1999). Response to light quantity can result from secondary seed dispersal (Chambers & MacMahon, 1994) and anthropogenic disturbances, such as tillage (Gallagher & Cardina, 1998), which provide an increased PPF that permits germination and establishment of photoblastic species with seeds in the seed bank.

The temperature optimum for seed germination of cacti is usually approximately 25°C (Nobel, 1988; Rojas-Aréchiga & Vázquez-Yanes, 2000), ranging from 15°C for the columnar cactus *Oreocereus trolü* (Zimmer, 1969a) to 33°C for *Pereskia aculeata* (Dau & Labouriau, 1974), a primitive leaf-bearing cactus. For the latter species (Campbell, 1988) and several columnar cacti (Nolasco *et al.*, 1996, 1997; Rojas-Aréchiga *et al.*, 1997), seeds do not require light to germinate. The opposite is the case for the photoblastic seeds of barrel cacti (genera *Echinocactus* and *Ferocactus*; Rojas-Aréchiga *et al.*, 1997) and some columnar cacti, such as *Carnegiea gigantea* (Alcorn & Kurtz, 1959). Of particular interest is the genus *Stenocereus*, whose species have both photoblastic and light-insensitive seeds. For example, *S. gumosus* is able to germinate in the dark (López-Gómez & Sánchez-Romero, 1989), *S. thurberi* has both photoblastic (McDonough, 1964) and light-insensitive (Nolasco *et al.*, 1997) phenotypes, and *S. griseus* (Martínez-Holguín, 1983), *S. queretaroensis* (Pimienta-Barrios & Nobel, 1995; Muñoz-Urías *et al.*, 2000), and *S. stellatus* (Rojas-Aréchiga *et al.*, 2001) are all photoblastic.

Stenocereus queretaroensis, one of eight congeneric columnar cacti native to Mexico (Gibson, 1990), occurs in low deciduous forests (Rzedowski, 1983) of the west central Mexican states of Colima, Guanajuato, Jalisco, Queretaro, and Zacatecas (Pimienta-Barrios & Nobel, 1994). It produces attractive edible fruits on vertical branches that can be over 5 m tall (Bravo, 1978; Pimienta, 1999). The following hypotheses were tested for the seeds of *S. queretaroensis*: (1) optimal temperatures for germination are similar to those occurring in the field during summer, whereas lower winter temperatures inhibit seed germination; (2) the water potential required for seed germination approximates that measured at field capacity for the sandy loam in which *S. queretaroensis* grows; (3) seeds are viable for multiple years; (4) germination is triggered at low PPF; and (5) positive photoblasticism is a phytochrome-mediated response, with seeds being especially sensitive to blue and red light.

Material and Methods

Plant material

Ripe fruits of *S. queretaroensis* Weber (Buxbaum) were obtained from Techaluta (20°5'N latitude, 103°32'W longitude, 1380 m a.s.l.), Jalisco, Mexico, in May of 1998, 1999, 2000, and 2001. After being removed from the pulp, the seeds were rinsed in tap water and then dipped into a sodium hypochlorite solution (1% v/v) for sterilization. The seeds were dried at 25°C, sent to the University of California, Los Angeles, California, U.S.A., and then stored in the dark at 25°C and 42% relative humidity for various periods before being placed in sterilized aqueous solutions.

Germination, scored as radicle protrusion from imbibed seeds, was assayed by incubating seeds in covered plastic Petri dishes 55 mm in inner diameter and 15 mm in height to which two layers of sterile filter paper had been added. The Petri dishes were routinely placed in Conviron E-15 environmental chambers (Controlled

Environments, Pembina, ND, U.S.A.) at a constant air temperature of 25°C with a 12-h day and a 12-h night. The photosynthetic photon flux (PPF, 400 – 700 nm, determined with a LI-190S quantum sensor, LI-COR, Lincoln, NE, U.S.A.) at seed level was routinely $150 \mu\text{mol m}^{-2} \text{s}^{-1}$ during the daytime, leading to $6.5 \text{ mol m}^{-2} \text{ d}^{-1}$, and 75% was provided by F72T12/CW/VHO fluorescent lamps (Sylvania/Osram, Danvers, MA, U.S.A.) and 25% by 100-W incandescent light bulbs (Sylvania/Osram).

Experimental manipulations

To determine the optimal temperature for germination, 12-month-old seeds collected in May 1999 were incubated under various day/night air temperature regimes from 15/5°C to 45/35°C, approximately matching the range of temperatures naturally experienced by *S. queretaroensis* in the field (Pimienta-Barrios & Nobel, 1994). Germination was monitored every 24 h until no further changes were observed (generally 14 days). Similarly, time courses for germination were assessed for such seeds that were incubated in polyethylene glycol (PEG 8000, Sigma, St. Louis, MO, U.S.A.) solutions of various water potentials from 0.00 to -1.0 MPa . The amount of PEG 8000 utilized for each solution was calculated with SPMM (Michel & Radcliffe, 1985) for a temperature of 25°C; water potential was also directly verified with an SC10X thermocouple psychrometer (Decagon Devices, Pullman, WA, U.S.A.).

Seed longevity was determined in November 1998 and May 1999 for seeds collected in May 1998 and in August 2001 for seeds collected in all 4 years by observing germination during 14 days. The effect of PPF was assessed for 12-month-old seeds collected in May 1998 by varying the amount of PPF incident on them from 1.3×10^{-4} to $154 \mu\text{mol m}^{-2} \text{ s}^{-1}$, using layers of grayish polyethylene film and/or white paper to cover the Petri dishes. In addition, an action spectrum of germination was determined by incubating such seeds at various photon fluxes of monochromatic light from 5×10^{-4} to $5 \times 10^{-2} \mu\text{mol m}^{-2} \text{ s}^{-1}$, obtained by shining white light through B-1 interference filters (Baird-Atomic, Cambridge, MA, U.S.A.) that had a full-bandwidth at the half-maximum for transmission of 8 nm. An LI-200SA LI-COR pyranometer was utilized to measure photon fluxes of wavelengths greater than 700 nm (the LI-190S quantum sensor was used at shorter wavelengths). The same photon flux was obtained for each wavelength by varying the distance from the filters to the light source. The number of seeds that germinated under various radiation quantities and qualities was determined 10 days after water imbibition.

Five replicates of 100 seeds each were routinely used for each measurement. Statistical analyses were performed with SigmaStat (SPSS, San Rafael, CA, U.S.A.). Data are means ± 1 S.E.

Results

Seeds of *S. queretaroensis* did not germinate when incubated for 14 days at day/night air temperatures of 15/5°C (Fig. 1). The time courses for germination varied at higher incubation temperatures ($p < 0.05$), except for 25/25°C vs. 35/25°C (pairwise Tukey tests, following a Friedman repeated measures ANOVA on ranks). Also, the onset of germination was hastened by higher temperatures, occurring at 3.6 ± 0.2 days after imbibition at 25/15°C, 2.8 ± 0.4 days at 25/25°C ($p < 0.05$ compared to 25/15°C), 2.0 ± 0.0 days and 2.4 ± 0.2 days, respectively, at 35/25°C and 45/35°C (both significantly earlier than at 25/25°C, $p < 0.05$). Final germination averaged 84% of the seeds at 25/15°C, 25/25°C, and 35/25°C but only 31% at 45/35°C (Fig. 1).

The time course for germination of *S. queretaroensis* differed for seeds incubated at 0.00 and -0.01 MPa compared with those at -0.10 and -1.0 MPa ($p < 0.05$ from

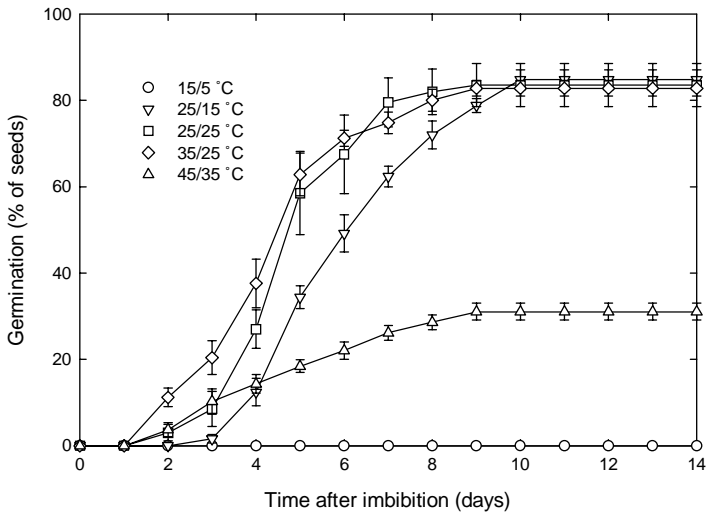


Figure 1. Time course for the germination for seeds of *Stenocereus queretaroensis* incubated at the indicated day/night air temperatures. Data are means \pm 1 S.E. ($n = 5$ Petri dishes with 100 seeds each).

pairwise Tukey tests, following a Friedman repeated measures ANOVA on ranks; Fig. 2). Final germination was higher at higher water potentials ($p < 0.001$ from a one-way ANOVA followed by pairwise Tukey tests). Specifically, germination was 50% for seeds incubated at -1.0 MPa, increasing to 62% at -0.1 MPa ($p = 0.02$), and an average of 75% at -0.01 and 0.00 MPa ($p < 0.05$; Fig. 2).

Final germination after 14 days of incubation varied with seed age ($p < 0.001$ from a one-way ANOVA; Fig. 3). It was maximal at 85% for seeds stored between 12 and 28

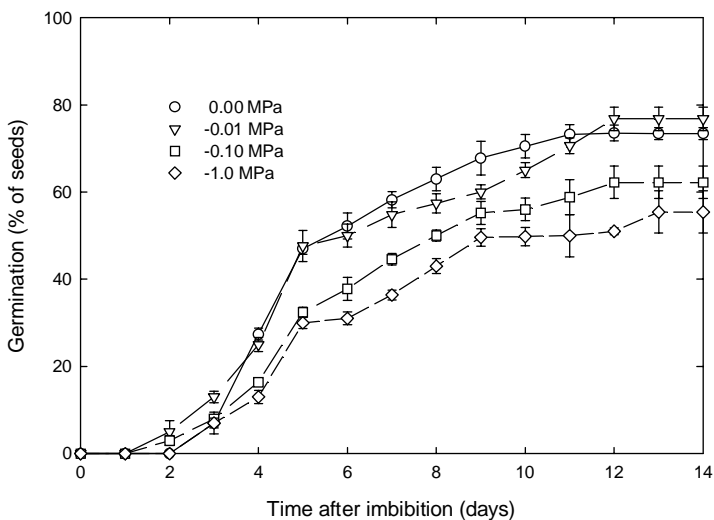


Figure 2. Effect of osmotic pressure on the time course for seed germination of *S. queretaroensis* at a day/night air temperature of 25°C . Data are means \pm 1 S.E. ($n = 5$ Petri dishes with 100 seeds each).

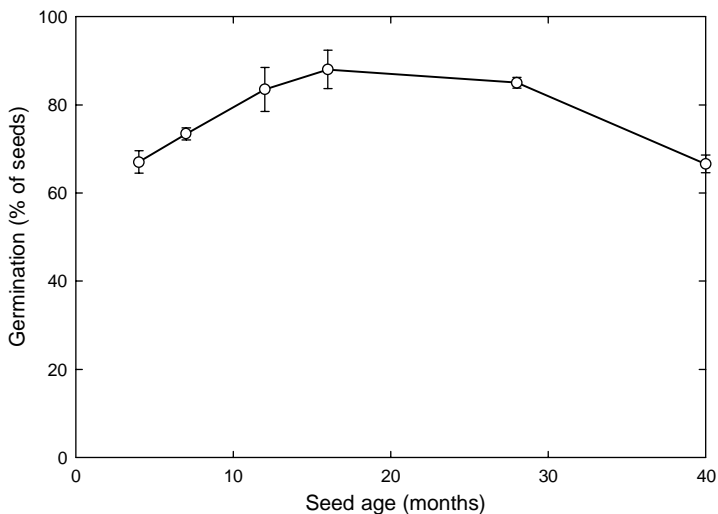


Figure 3. Final germination for seeds of *S. queretaroensis* stored in the dark for the indicated periods at 25°C and incubated at a day/night air temperature of 25°C for 14 days. Data are means \pm 1 S.E. ($n = 5$ Petri dishes with 100 seeds each).

months ($p < 0.01$ compared to 4- and 7-month-old seeds and $p = 0.0025$ compared with 40 month-old seeds; Fig. 3).

Seeds incubated in the dark for 10 days did not germinate. Increases in PPF steadily increased germination ($p < 0.05$; Tukey test following an ANOVA; Fig. 4) from 5% at $57 \mu\text{mol m}^{-2}$ ($1.3 \times 10^{-4} \mu\text{mol m}^{-2} \text{s}^{-1}$ for 10 days) to 81% at 67 mmol m^{-2}

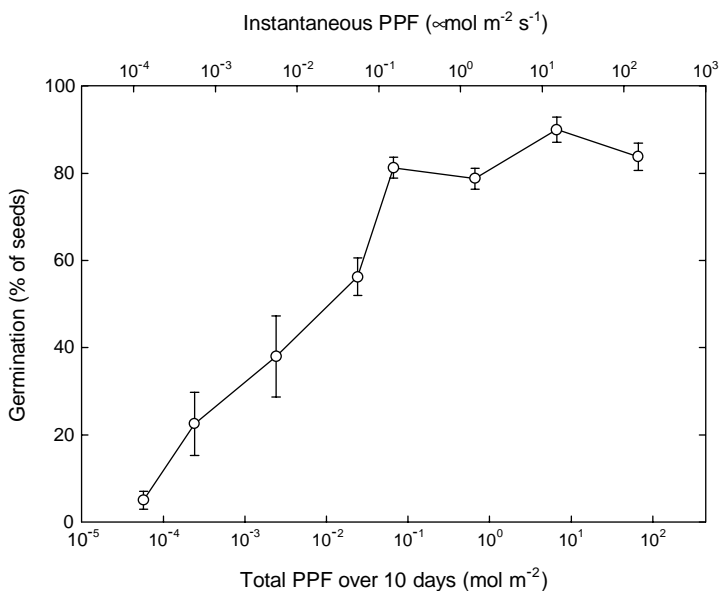


Figure 4. Effect of PPF level on seed germination for *S. queretaroensis* incubated at a day/night air temperature of 25°C for 10 days. Data are means \pm 1 S.E. ($n = 5$ Petri dishes with 100 seeds each).

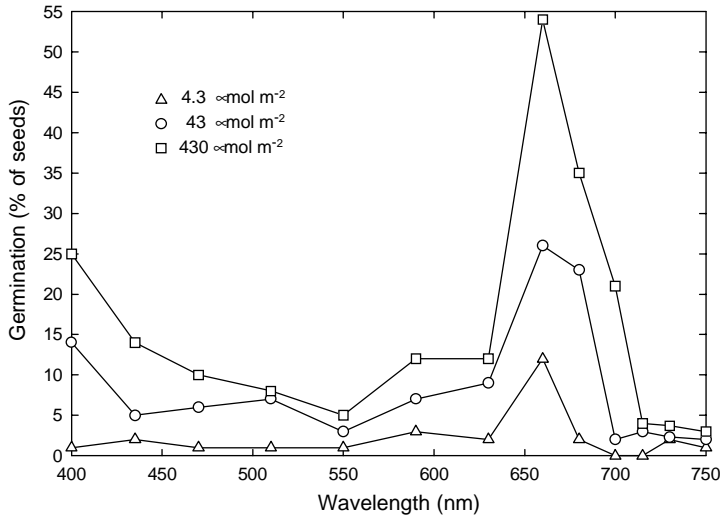


Figure 5. Action spectrum for seed germination of *S. queretaroensis* incubated at a day/night air temperature of 25°C for 10 days. Data are percentages of seeds ($n=100$) germinating at the indicated monochromatic photon fluxes (43 $\mu\text{mol m}^{-2}$ corresponds to a PPF of $0.92 \times 10^{-4} \mu\text{mol m}^{-2} \text{s}^{-1}$ for 10 days).

($0.15 \mu\text{mol m}^{-2} \text{s}^{-1}$ for 10 days). Further increases in PPF did not increase germination within the 10-day incubation period (Fig. 4). For seeds incubated under monochromatic light, a higher photon flux also induced a higher germination percentage; a ten-fold increase in photon fluence from 4.3 to 430 $\mu\text{mol m}^{-2}$ (0.092×10^{-4} – $9.2 \times 10^{-4} \mu\text{mol m}^{-2} \text{s}^{-1}$ for 10 days) resulted in an approximate doubling of the germination percentage (Fig. 5). Seeds were sensitive to blue (wavelengths near 400 nm) and especially to red (near 660 nm) light, the latter leading to 54% germination at only 23 mmol m^{-2} ($5 \times 10^{-2} \mu\text{mol m}^{-2} \text{s}^{-1}$ for 10 days; Fig. 5).

Discussion

For *S. queretaroensis* a constant temperature of 25°C led to similar maximal germination as day/night air temperatures of 35/25°C or 25/15°C, but germination was slower at 25/15°C. No germination occurred at day/night temperatures averaging 10°C, as is also the case for 17 out of 31 other cactus species of various life-forms (Zimmer, 1969a; Dau & Laboriau, 1974; Rojas-Ar chiga *et al.*, 1998). Elevated day/night temperatures of 45/35°C reduced germination of *S. queretaroensis* by 50%, comparable to the reduced germination found at supra-optimal temperatures for other columnar cacti (Zimmer, 1969a; Rojas-Ar chiga *et al.*, 2001). Temperature optima of other cacti are 15°C for *Oreocereus trollii*, 17°C for *Pachycereus hollianus*, 15–25°C for *Astrophytum myriostigma*, *Cereus peruvianus*, and *Oreocereus celsianus*, 20°C for *Cleistocactus strausii* and *Espositoa lunata*, 20–25°C for *Cleistocactus jujuyensis* and *Trichocereus pasacana*, 20–30°C for *Neobuxbaumia tetetzo*, and 25–30°C for *Cephalocereus chrysacanthus* (Zimmer, 1969a; Rojas-Ar chiga *et al.*, 1997).

Final germination percentage for *S. queretaroensis* was reduced 23% for seeds incubated at a water potential of -1.0 MPa compared with those incubated at 0.00 MPa. A similar reduction occurs for seeds of *Pachycereus pringlei* incubated at -1.3 MPa (Nolasco *et al.*, 1996). Germination after 15 days was reduced by 30% for

seeds of *Stenocereus thurberi* incubated in soil receiving 40% by mass of water compared with soil receiving 50% (Nolasco *et al.*, 1997). In contrast, germination for *Neobuxbaumia tetetzo* increases as soil water potential decreases to -0.66 MPa, and germination for *Pachycereus hollianus* is maximal at -0.44 MPa (Flores & Briones, 2001). The germination percentages for *S. queretaroensis* were reduced for water potentials measured for a soil of similar texture after just 7 days of drought (Nobel & Cui, 1992).

Seed germination for various plant species tends to increase within the first few months after dispersal as a result of breaking dormancy, remains maximal for up to several years, and then eventually decreases (Baskin & Baskin, 1998). Indeed, the germination percentage of *S. queretaroensis* doubles for 12-month-old seeds compared to 38% for recently collected, freshly matured seeds (Muñoz-Urias *et al.*, 2000). In the present study its germination percentage reached an average of 85% between 12 and 28 months of storage; seeds stored for 40 months had a 20% lower germination. Seed germination for *Stenocereus stellatus* is 15% higher for 41-month-old seeds than for 6-month-old seeds (Rojas-Aréchiga *et al.*, 2001). Seed germination remains maximal during 4 years of storage for *Eulychnea castanea* and *Neoporteria subgibbosa* and during 7 years for *O. celsianus* (Zimmer & Schultz, 1975). Eventual reduced germination may result from seed deterioration or from the onset of secondary dormancy (Baskin & Baskin, 1998; Khurana & Singh, 2001).

Seeds of *S. queretaroensis* exhibited positive photoblasticism, consistent with previous studies on this species (Pimienta-Barrios & Nobel, 1995; Muñoz-Urias *et al.*, 2000) and its congeners, *S. griseus* (Martínez-Holguín, 1983) and *S. stellatus* (Rojas-Aréchiga *et al.*, 2001). Positive photoblasticism is generally regarded as a very low or low ($<10^{-4}$ mol m⁻²) fluence response mediated by phytochrome (Taiz & Zeiger, 1998). Indeed, for *S. queretaroensis* germination could be observed at fluences below 10^{-4} mol m⁻² of white light and was light saturated at 10^{-1} mol m⁻² (equivalent to only about 1 min of full sunlight). Germination was especially sensitive to red light; e.g. 10% germination occurred for 4.3 μ mol m⁻² of red light compared with 100 μ mol m⁻² required for white light (a PPF of 2.1×10^{-4} μ mol m⁻² s⁻¹ for 10 days). Higher germination percentages also resulted for seeds of 8 out of 12 cacti treated with very low levels of red compared with blue light (Zimmer, 1969b). For *S. queretaroensis*, far-red light leads to little seed germination, similar to the case for *Carnegie gigantea* (Alcorn & Kurtz, 1959), as is expected for a phytochrome-mediated reaction (Taiz & Zeiger, 1998; Nobel, 1999).

Species present in seed banks of arid and semi-arid environments are subject to prolonged drought alternating with seasonal or sporadic rains (Nobel, 1988; De la Barrera, 1997). Indeed, the rate of germination for *S. thurberi* increases following cycles of drying and rewetting (Dubrovsky, 1996). As for other species in arid and semi-arid environments (Flores & Briones, 2001), seed germination for *S. queretaroensis* was favored by soil water potentials of 0.0 MPa that occur in its native habitat during the summer, when 90% of the precipitation takes place (Pimienta *et al.*, 1998). Wild populations of *S. queretaroensis* may experience winter temperatures of 8°C or lower (Pimienta, 1999). Lack of germination below 10°C , in addition to low germination percentage at low water potentials, might improve the fitness for this species. In particular, due to limited germination after the infrequent winter rains, few seedlings are exposed to the dry season in the spring, when the highest annual temperatures occur, frequently exceeding 40°C (Pimienta, 1999). Similarly, reduced germination percentages at higher temperatures reduce the risk for seedlings after light rains that occasionally occur during the spring (Pimienta, 1999). Also, some cacti exhibit C₃ photosynthesis during the first 10–20 weeks after germination (Altesor *et al.*, 1992), rendering the seedlings less resistant to dehydration when exposed to high temperatures. In addition, daily net CO₂ uptake by mature *S. queretaroensis* is at its lowest during the spring (Pimienta-Barrios *et al.*, 2000).

Seeds of *S. queretaroensis* germinate during the summer concurrently with a dense cover of annuals (Pimienta, 1999), which attenuates the PPF by over 80% (Hirose & Werger, 1995). The PPF available at the soil surface then averages approximately $6 \text{ mol m}^{-2} \text{ d}^{-1}$ for sites where wild populations of *S. queretaroensis* occur (Pimienta *et al.* 1998). Such a PPF level could trigger germination, but the red to far-red ratio of the light reaching the ground is likely to be low, hence inhibiting germination (Grant, 1997; Nobel, 1999). For the case of seeds present in the seed bank, the soil greatly attenuates the light and tends to transmit at longer wavelengths; e.g. 1 cm of sand transmits 0.01% of incident radiation, 80% of which has wavelengths above 700 nm (Bliss & Smith, 1985). Light-dependent germination for buried seeds would then be triggered only when the soil is disturbed, such as by tillage (Gallagher & Cardina, 1998) or by erosion of the upper soil layer. Also, seeds may be subject to secondary dispersal, ants being a principal vector (Chambers & MacMahon, 1994; Rojas-Aréchiga & Vázquez-Yanes, 2000).

Seed dispersal for *S. queretaroensis* occurs during the spring (Pimienta, 1999), allowing freshly dispersed seeds to afterripen for a few months before the summer rainy season, when they readily germinate. Temperatures from 20°C to 30°C are optimal, which is the range for the mean summer temperatures in the field (Pimienta, 1999). As for barrel cacti and some columnar cacti, light-triggered germination for this species apparently is a low fluence response mediated by phytochrome. In conclusion, the environmental factors triggering germination for *S. queretaroensis* appear to be finely tuned to the summer climate in its native habitat.

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