

Effects of Temperature on Seed Germination in Six Species of Mexican *Cactaceae*



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Summary

Germination studies were conducted on six Sonoran Desert species from the genera *Ferocactus*, *Pachycereus* and *Stenocereus*, with the objective of optimising laboratory propagation techniques in support of conservation programmes. Germination was light-dependent in four species and light-independent in the two other species. The optimum temperature for germination level was 26°C, although c. 31°C resulted in the shortest mean times for germination (MTG) of c. 2–9 d across species. The range of constant temperatures permissible for 50 % of total germination was widest in the *Pachycereus* spp. (from 6–11°C to 43°C) and narrowest in *Stenocereus gummosus* (from 21°C to 31°C). Alternating temperature treatments of 33/19°C and 26/16°C did not generally increase germination levels above that of their respective constant temperature controls. Except for *Pachycereus* spp., alternating temperatures of 21/11°C and 23/9°C improved germination compared to the control (16°C), as the warm temperature phase was above the minimum temperature for germination. This latter observation may explain earlier, variable reports on the effects of alternating temperatures on cactus seed germination.

Introduction

The *Cactaceae* comprises about 100 genera and 1,500 species (Barthlott and Hunt, 1993). Mexico is the main centre of cactus diversity with around 48 genera and 570 species (c. 38% of the total in the family), of which c. 78% are endemic (Hernández and Gómez-Hinostrosa, 2002). The species are distributed across the three main desert regions of the country, the Chihuahuan Desert, the Sonoran Desert and the Tehuacán-Cuicatlán Valley. Whilst the species in the Chihuahuan Desert tend to be small and cryptic, the other two regions have a prevalence of arborescent species.

It has been estimated that between one third and one half of Mexican cacti (i.e., up to c. 285 species) are rare and threatened with extinction (Hernández and Godínez, 1994; NOM-059-ECOL-2001, Diario Oficial de la Federación [Official Diary of the Government of Mexico], March 6, 2002). There is particular concern for *Ferocactus peninsulæ* (var. *santa-maria*) and *Stenocereus eruca*, plus representatives of key genera, such as *Ariocarpus* (7 species), *Aztekium* (2 species), *Coryphantha* (18 species), *Echinocereus* (21 species), *Peniocereus* (8 species) *Mammillaria* (118 species), *Thelocactus* (9 species) and *Turbiniacarpus* (27 species) (Anderson *et al.*, 1994; NOM-059-ECOL-2001).

The main threats to species are illegal harvesting, often for the export market, and conversion of habitat for agriculture, goat raising, road construction and mining (Hernández and Gómez-Hinostrosa, 2002). An additional threat may be the over exploitation of fruit at the local level, thereby potentially reducing

opportunities for population survival and/or growth. Species in the tribe *Pachycereeae* are particularly sought after, with seven species of *Stenocereus* in cultivation for this purpose. Wild fruits are harvested from three other *Stenocereus* species (including *S. gummosus*) and from *Pachycereus pringlei* and *P. pecten-arboriginum* (Nobel, 1994; Dubrovsky, 1998). *Ferocactus peninsulae*, which is endemic to Baja California, is used in candy production (Dubrovsky, 1998) and cattle feeding (Vega-Villasante *et al.*, 1997).

Cacti are particularly sensitive to habitat disturbance as they have slow growth rates, long life cycles and low recruitment (Nobel, 1988). Recruitment will depend on a number of factors, including the environmental requirements for germination and seedling establishment. Generally, temperature extremes do not favour germination in cacti, i.e., below 12°C and above 28°C (Fearn, 1981; Rojas-Aréchiga and Vázquez-Yanes, 2000). The impact of alternating temperature on cactus seed germination can be negative, neutral or positive depending on study and species (Godínez-Alvarez and Valiente-Banuet, 1998; Rojas-Aréchiga and Vázquez-Yanes, 2000), although the causes of this variation have not been elucidated. The magnitude of diurnal temperature fluctuations can be influenced by microsite conditions. For example, nurse plants generally provide protection against excessive direct solar radiation. This may result in a lower level of temperature fluctuation and greater moisture availability, both of which may favour germination and seedling growth. Columnar (arborescent) cacti tend to provide more shade than barrel cacti and to favour such conditions. Consequently, seed germination and seedling establishment of barrel cacti might be expected to be more tolerant of temperature extremes.

Here we report laboratory germination of six species (four arborescent, one possessing horizontal stems than lie on the ground [procumbent stems], and one barrel) from the Sonoran Desert, in support of restoration ecology and plant reintroduction programmes. Such programmes often depend on an initial propagation step in the laboratory for which knowledge of the optimum conditions for germination is important.

Materials and Methods

Mature fruits of six Mexican species were collected in 1995 from the Sonoran desert in Baja California, Mexico by staff of Centro de Investigaciones Biológicas del Noroeste. The species were: *Ferocactus peninsulæ*, *Pachycereus pecten-aboriginum*, *Pachycereus pringlei*, *Stenocereus eruca*, *Stenocereus gummosus* and *Stenocereus thurberi* (for authorities, see Table 32.1). Seeds were separated by dissection of the fruit. After washing with tap water and distilled water, to remove any remaining mucilage, the seeds were surface sterilised (immersion in 10% (v/v) sodium hypochlorite for 5 min), washed again and then dried on absorbent paper. Seeds were placed in paper bags and stored under room conditions until being received at the Royal Botanic Gardens, Kew, Wakehurst Place in August 1995. On receipt, seed equilibrium relative humidity at 21°C was determined by a Rotronic Hygroskop BT-RS1 hygrometer and found to be c. 45%. Seed dry weight was also measured after oven drying (103°C, 17 h) of 15 individual seeds per seed lot. The seed lots were sealed in aluminium foil laminate bags and held at 15°C until use.

For germination, three replicates of 25 seeds were sown on 1% (w/v) agar-water in 9 cm-diameter Petri dishes. The exception to this was an initial screen for germination at 26°C in the light and darkness, when 50 seeds (2 × 25) per treatment were used (see Results and Discussion). Dishes were incubated at constant temperatures at 5°C intervals from 6°C to 36°C and at 43°C. Seeds were also incubated at alternating temperatures of 21/11°C, 23/9°C, 26/16°C and 33/19°C, all on a 12/12 h daily cycle. Seeds were generally incubated (see Results) for 12 h d⁻¹ in warm, white fluorescent light at an intensity of c. 15 μmol m⁻²s⁻¹. During alternating temperature treatments, the light period coincided with the warm temperature phase. In the initial screen for germination, darkness was achieved by wrapping dishes in aluminium foil, and germination was recorded under safe green light (Pritchard and Manger, 1990). Germination was assessed as radicle emergence outside the seed by at least 1 mm. The effects of light and darkness on germination were compared statistically using a 2-sample test for equality of proportions, carried out using S-Plus 2000 software (MathSoft Inc.). Germination was recorded regularly (sometimes more than once a day, depending on species) and the mean time for germination (MTG) was calculated as:

$$\text{MTG} = \Sigma(t.n) / \Sigma n$$

where t is the time in days, starting from the day of sowing, and n is the number of seeds completing germination on day t .

Results and Discussion

Seeds of all the six species studied here germinated in the light to levels ranging from 32 to 94% (Table 32.1). *Stenocereus thurberi* germinates best under shade conditions, at light levels similar to those used in this study (Nolasco *et al.*, 1997), as do seeds of *Ferocactus peninsulae* (Romero-Schmidt *et al.*, 1992). Thus, seeds of arborescent cacti, like *Stenocereus*, and barrel cacti, like *Ferocactus*, can require light for germination. Similarly, the arborescent *Carnegiea gigantea* (Engelm.) Britton & Rose (*Cereus giganteus* Engelm.) and *Lemaireocereus thurberi* (Engelm.) Britton & Rose (*Cereus thurberi* Engelm.) have light sensitive seeds (McDonough, 1964). In contrast, the two arborescent species of *Pachycereus* (*P. pecten-aboriginum* and *P. pringlei*) also germinated in the dark, at levels that were statistically indistinguishable from those observed in the light (Table 32.1). These findings support an earlier observation on *P. pringlei* germination (Nolasco *et al.*, 1996). Overall, the results suggest that there is no simple link between light requirement for seed germination and the plant's life form (arborescent, procumbent or barrel), at least under the conditions used here. As a consequence of these findings, all further germination tests included 12 h d⁻¹ light.

It is notable that the two *Pachycereus* species had heavier seeds (5 to 10 mg) than the other species (1 to 2 mg) investigated (Table 32.1). This finding lends support to the notion, based on an analysis of 54 species with seeds of variable mass (0.032 to 22 mg), that large-seeded species are generally less dependent on light for germination (see Millberg *et al.*, 2000). Indeed, seedlings from large seeds tend to be capable of emerging from a greater depth than light can penetrate.

1. Effects of Constant Temperatures

The effects of constant temperature on the final germination level (%) and on the mean time to germinate (MTG) are shown in Figure 32.1.

The temperature range for maximum germination varied between seed lots/species (Figure 32.1). *Pachycereus pringlei* had the widest response to temperature, germinating to 53% and 83% at the most extreme temperatures used, i.e., 6°C and 43°C respectively, compared to a maximum of about 90% for all temperatures from 16°C to 36°C (Figure 32.1A). The lower quality seed lot of *P. pecten-aboriginum* also germinated at all temperatures but with only 4 to 10% at 6 to 11°C. All other temperatures resulted in about 25% germination compared with an absolute maximum of 33% (Figure 32.1A). Seeds of the other species generally reached maximum germination in the temperature range of 21 to 31°C (Figure 32.1B). Seeds that did not germinate at the highest temperature tended to rot in the germination test, probably indicating high-temperature induced

Table 32.1 Effects of light and darkness on seed germination at 26°C for six Mexican cacti (n = 50 seeds per treatment, with a comparison between treatments [χ^2 , (P)]). Seed weights are also shown

Species [common name]	Seed dry weight (mg; n = 15)	Germination in dark (%)	Germination in light (%)	χ^2 (P)
<i>Ferocactus peninsulae</i> (F.A.C. Weber) Britton & Rose [Townsend barrel cactus; biznaga]	2.17	0	92	81.52 (<0.001)
<i>Pachycereus pecten-aboriginum</i> (Engelm.) Britton & Rose [cardón barbón]	10.20	38	40	0 (1)
<i>Pachycereus pringlei</i> (S. Watson) Britton & Rose [cardón]	5.06	90	94	0.136 (0.71)
<i>Stenocereus eruca</i> (T. Brandegees) A.C. Gibson & K.E. Horak [creeping devil cactus]	1.24	0	32	16.74 (<0.001)
<i>Stenocereus gummosus</i> (Engelm.) A.C. Gibson & K.E. Horak [pitaya agria]	1.07	0	68	48.53 (<0.001)
<i>Stenocereus thurberi</i> (Engelm.) Buxb. [organ pipe cactus; pitaya dulce]	1.12	0	66	46.31 (<0.001)

ageing of the seeds. Overall, the results support previous observations that tropical arid land species, including cacti, tend to have maximum germination in the 20 to 30°C temperature range (Baskin and Baskin, 1998; Fearn, 1974, 1981; Gutterman, 1993; Rojas-Aréchiga and Vázquez-Yanes, 2000).

Compared to other cacti, the Mexican species investigated here appear to have a wider temperature range for germination, extending to both higher (four species) and lower (one species) temperatures (Table 32.2). In comparison, none of the nine species studied by Fearn (1974; 1981) reached germination levels of more than 50% (of the maximum observed) below 11°C. The absolute daily minimum and maximum temperatures in the region of La Paz, B.C.S., Mexico are c. 3°C and 43°C (Meteorological Office, 1980; Nolasco *et al.*, 1997), i.e., close to the temperature range for *Pachycereus* germination (Figure 32.1, Table 32.2). Whilst there may be a strict relationship between the geographical distribution of a species and the temperature limits for germination, this is not necessarily true for cacti (Table 32.2; Fearn, 1974) or other species (see Baskin and Baskin, 1998). Ecology at the microscale, rather than the macroscale, will be the major determinant of seed performance in the field.

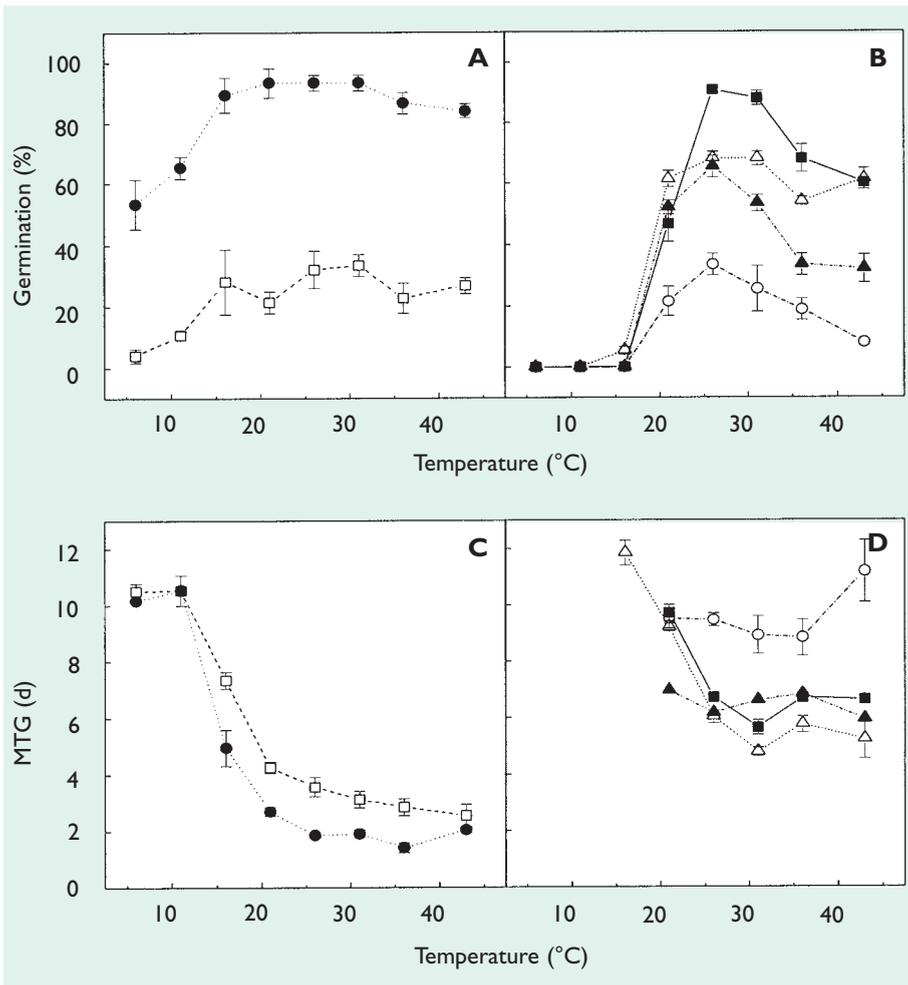


Figure 32.1 Effects of constant temperature on seed germination (A, B) and mean time for germination (MTG) (C, D) for *Ferocactus peninsulae* (■), *Pachycereus pecten-aboriginum* (□), *Pachycereus pringlei* (●), *Stenocereus eruca* (○), *Stenocereus gummosus* (▲), *Stenocereus thurberi* (△). Bars represent the s.e. of the mean.

Germination rate at constant temperatures was quickest in the temperature region of 26–43°C for the majority of species (Figure 32.1 C, D). Shortest MTG were ≤ 2 d for *Pachycereus pringlei*, c. 3 d for *Pachycereus pecten-aboriginum*, c. 5 d for *Stenocereus thurberi*, c. 6 d for both *Ferocactus peninsulae* and *Stenocereus gummosus* and, finally, c. 9 d for *Stenocereus eruca*. In all cases, germination was relatively rapid, which presumably increases the likelihood of rapid establishment in an environment with intermittent precipitation (Dubrovsky, 1996, 1998).

Table 32.2 A comparison of temperature ranges for germination to > 50% of the maximum and distribution ranges for selected cacti

Species	Distribution ‡	Temp (°C)
<i>Carnegiea gigantea</i> (Engelm.) Britton & Rose	N. Mexico/S. Arizona, USA	16 – 28 #
<i>Ferocactus peninsulae</i>	Baja California, Mexico	21 – 43 *
<i>Ferocactus hamatacanthus</i> (Muelenpf.) F. Knuth ssp. <i>sinuatus</i> (A. Dietr.) N.P. Taylor	Texas	15 – 31 #
<i>Frailea pumila</i> (Lem.) Britton & Rose.	Argentina/Paraguay	12 – 40 #
<i>Gymnocalycium spegazzinii</i> Britton & Rose	N. Argentina	15 – 38 #
<i>Echinopsis atacamensis</i> (Philippi) Friedr. & Rowl. ssp. <i>pasacana</i> (A. Web.) G. Navarro	N. Argentina/S. Bolivia; 1,000–4,000 m	12 – 32 #
<i>Lophocereus schottii</i> (Engelm.) Britton & Rose	Sonora and Baja California, Mexico/S. Arizona	18 – 28 #
<i>Pachycereus pecten-aboriginum</i>	Sonoran Desert, Mexico	11 – 43 *
<i>Pachycereus pringlei</i>	Sonora and Baja California, Mexico	6 – 43 *
<i>Parodia chrysacanthion</i> (K. Schum.) Backeb.	N. Argentina	11 – 28 #
<i>Rebutia xanthocarpa</i> f. <i>salmonea</i> (Backeb.) Buining & Donald	N. Argentina; 1,000 m	12 – 23 #
<i>Stenocereus eruca</i>	Baja California, Mexico	21 – 36 *
<i>Stenocereus gummosus</i>	Sonoran Desert, Mexico	21 – 31 *
<i>Stenocereus thurberi</i>	Sonora and Baja California, Mexico	21 – 43 *
<i>Thelocactus setispinus</i> (Engelm.) Anderson	N. Mexico/Texas	15 – 31 #

Distribution data are from Fearn, 1974 (‡) or H. Nolasco, pers comm; germination data from Fearn, 1974 (#) or this study (*). N.B. Fearn (1974) used *Hamatocactus setispinus*, *H. sinuatus* and *Helianthocereus pasacana* for *Thelocactus setispinus*, *Ferocactus hamatacanthus* ssp. *sinuatus*, and *Echinopsis atacamensis* ssp. *pasacana* respectively.

MTG for *Ferocactus peninsulae* at 26°C and 31°C were similar to that reported by Dubrovsky (1996) for seeds at 29°C, i.e., c. 6 d. In contrast, both *Stenocereus thurberi* and *Pachycereus pecten-arboriginum* germinated faster in this study than in the earlier one by Dubrovsky (1996). A contributory factor may have been differences in the total viability of the seed lots, as this measure is known to be related to germination rate in *Stenocereus thurberi* and *Ferocactus peninsulae* (Yang, 1999). The use of agar-water rather than filter paper as the germination substrate, and the use of different light levels between studies may have also contributed to these varying germination responses.

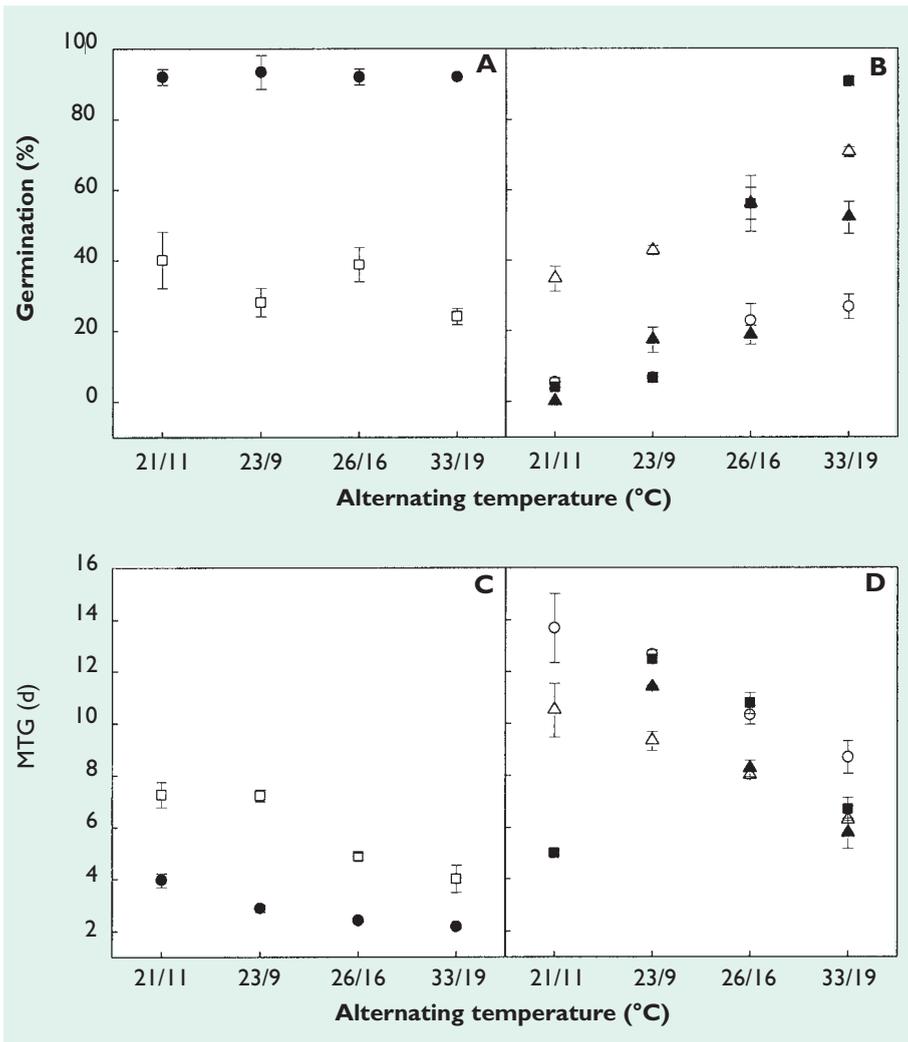


Figure 32.2 Effects of alternating temperature on seed germination (A, B) and mean time for germination (MTG) (C, D) for *Ferocactus peninsulae* (■), *Pachycereus pecten-aboriginum* (□), *Pachycereus pringlei* (●), *Stenocereus eruca* (○), *Stenocereus gummosus* (▲), *Stenocereus thurberi* (△). In (D), there is no data point for *S. gummosus* at 21/11°C. Bars represent the s.e. of the mean.

2. Effects of Alternating Temperatures

The effects of alternating temperature on germination level and rate are shown in Figure 32.2. There was no change in final germination of *Pachycereus pringlei* (c. 92%) across the four alternating temperature regimes compared to their constant temperature controls (Figure 32.2A cf. 32.1A). In *Pachycereus pecten-aboriginum*, germination varied only slightly (24–40%) with alternating temperature, being higher at 21/11°C and 26/16°C and lower at 23/9°C and 33/19°C (Figure 32.2A). Moreover, there was little change in germination rate of the two *Pachycereus* spp. at alternating temperatures compared to their respective constant temperature controls (c.f. Figure 32.1 and 32.2). This is probably because both species appeared to have a minimum temperature for germination < 10°C and a maximum not < 40°C, meaning that all temperature combinations fell within the permissible range of temperatures for germination for these two species. Nonetheless, germination rate in *Pachycereus* did vary across the alternating temperatures; the warmer the temperature maximum, the quicker the MTG by about 2–3 d (Figure 32.2C). Thus germination rate was fastest under conditions where the accumulation of thermal energy was greatest, i.e., the mean daily temperature was higher. Similarly, MTG in the other four species was shorter (by about 5 d), the greater the temperature of the warm temperature phase in treatments, from 23/9°C to 33/19°C. Whilst the benefits of warmer alternating temperatures appeared smaller for the *Pachycereus* species compared to the others, the relative improvements were similar across all species, i.e., MTG was lowered by about 40% (Figures 32.2C and D).

In contrast to the *Pachycereus* species though, the final germination level in the other four species consistently increased as the upper temperature of the alternating temperature was raised from 21°C to 33°C (and the mean temperature from 16°C to 26°C), i.e., from 4% to 91% for *Ferocactus peninsulæ*, from 5% to 27% for *Stenocereus eruca*, from 0% to 52% for *Stenocereus gummosus* and from 35% to 71% for *Stenocereus thurberi* (Figure 32.2B).

As with the *Pachycereus* species, there were few differences in the final germination and germination rate for the other four species at 33/19°C compared to 26°C, or at 26/16°C compared to 21°C, except for *S. gummosus* for which germination was much lower at 26/16°C than at 21°C. For the latter alternating temperature regime though, MTG values for all six species were < 1.4 d at variance with their respective, corresponding constant temperature control, suggesting that the main effect of such a low temperature phase on *S. gummosus* related to the proportion of seeds germinating rather than the rate of those seeds capable of germination.

At the lower alternating temperature treatments of 21/11°C and 23/9°C, the low temperature phases were far below the apparent lowest temperatures for germination in the three species of *Stenocereus* and for *Ferocactus peninsulæ* (Figure 32.1). Although there was no or very little germination at the constant temperature of 16°C (Figure 32.1B), some germination was observed at

21/11°C and 23/9°C (Figure 32.2B). Moreover, germination increased, if in some, slightly, in all four species when sown at 23/9°C compared to 21/11°C (Figure 32.2B) and MTG was generally shorter (Figure 32.2D). Presumably, these seeds did not progress towards germination at temperatures below 16°C, i.e., during the lower temperature phases of 9°C and 11°C. However, during the higher temperature phases at 21°C or 23°C, they could progress towards germination and, assuming the cooler temperatures were neutral in effect (Ellis and Barret, 1994), germination at 23°C should be greater and/or faster than at 21°C.

Alternating temperatures are thought to favour the germination process of diverse plant families growing in arid zones (Mahmoud *et al.*, 1983), including some cacti (Fearn, 1974; 1981). However, seeds of *Ferocactus latispinus* var. *spiralis* and *Echinocactus platyacanthus* f. *grandis* may or may not benefit from alternating temperatures, depending on the study, whilst germination in a range of cacti, including *Opuntia* sp., was seen not to be favoured by such treatment compared with constant temperatures (Baskin and Baskin, 1977; Potter *et al.*, 1984; Rojas-Aréchiga *et al.*, 1998; Rojas-Aréchiga and Vázquez-Yanes, 2000), perhaps for the reasons offered above. Studies on cactus seed germination would benefit from more detailed modeling of the germination response, particularly in relation to: 1) estimates of the minimum temperature for the progression of germination, T_b , and 2) whether cumulative thermal time accurately describes the observed effects of temperature (García-Huidobro *et al.*, 1982).

In conclusion, whilst seed germination in the six Mexican cacti investigated has variable upper and lower temperature limits and different responses to alternating temperatures, rapid propagation of all species can be achieved when seeds are incubated at 26°C or 31°C in the light.

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