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Seed response to temperature of Mexican cacti species from two life forms: an ecophysiological interpretation

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Abstract

The effect of seven different constant temperatures and five ranges of alternating temperatures on seed germination of seven species of cacti from Puebla, México was analyzed. Six cacti species germinated in a wide range of temperature. Columnar cacti were more tolerant to low temperatures and germinated in a wider range of temperature than barrel cacti. One of the barrel cacti studied (*Ferocactus recurvus*) only reached full germination at 25 °C. Temperature fluctuations did not produce significant effects on germination compared to the results obtained at constant temperatures. This may reveal differing ecophysiological adaptations with respect to temperature requirements during the establishment conditions for each life form. Columnar cacti may become established mainly under the shade of desert shrubs, whereas barrel cacti maybe can also become established in open areas, beneath the shade of small rocks or soil irregularities. In both cases, temperature fluctuations are attenuated by the shade, but mean temperatures may be higher in the second condition than beneath the shade of plants.

Introduction

Natural selection has favored environmental cueing mechanisms initiating seed germination in conditions that decrease the probability of encountering inadequate growth conditions following germination (Angevine & Chabot 1979). In general, temperature is one of the most important environmental factors regulating germination timing and velocity (Probert 1992). Therefore, germination of non-dormant seeds in a range of temperatures can be related to ecological or geographical distribution along different climatic regions (Thompson 1970, 1973). Studies with seeds from arid zones have demonstrated that temperature, either constant or alternating, plays an important role in seed germination (Went 1948, 1949; Juhren et al. 1956; Mott 1972, 1974; Hess 1975). This has been particularly underlined for summer and winter desert annuals (Kigel 1995).

Most desert plants germinate in a wide range of temperature, and temperatures between 15 and 25 °C induce their maximum germination percentage (Nobel 1988). For cacti seeds, a favorable temperature range occurs between 17 and 34 °C with optimal values frequently at 25 °C (Alcorn & Kurtz 1959; Dau & Labouriau 1974; Martínez-Holguín 1983; Cota Sánchez 1984; Del Castillo 1986). In some cacti species, germination is reduced by 50% when temperature is increased or decreased 9 °C from the optimal (Nobel 1988).

The capability of seeds to respond to alternating temperatures has been related to physiological adaptations that allow germination in the best site for establishment (i.e., in open areas vs the shade of plants or rocks) (Probert 1992). Many species that inhabit arid environments show high germination percentages at alternating temperatures (Hammouda & Bakr 1969; Mahmoud et al. 1983, 1984). Nevertheless, most investigations of the effect of temperature on cacti seeds have been performed only at constant temperatures. Fearn (1981) asserts that alternating temperatures induce germination in cacti species, but some other experiments showed that alternating temperatures did not significantly affect the germination of five cacti species (Baskin & Baskin 1977; Potter et al. 1984; Godínez-Alvarez 1991).

Cacti establishment from seed seems to be infrequent for some species because it must take place mainly during very favorable years with a long lasting growth season and only in safe sites like the shade of shrubs or rocks that provide the precise conditions required by a particular seed, such as enough moisture for germination and protection to seedlings from excessive sun irradiation (Valiente-Banuet & Ezcurra 1991). Nevertheless, establishment from seed is very important for the maintenance of the genetic diversity of natural populations (Harper 1977).

The main objective of this study was to investigate the effect of temperature on germination of two different cacti life forms and relate the response obtained to a presumably safe site for establishment. We selected three columnar and four barrel cacti species to determine the effect of seven constant and five fluctuating temperatures that may occur in a semiarid desert of México. We hypothesized that both types of cacti may have distinct temperature requirements for germination in agreement with their germination behavior at different light qualities (Rojas-Aréchiga et al. 1997).

Methods

Mature fruits of three columnar cacti species: *Pachycereus hollianus* (Weber) Buxb., *Cephalocereus chrysacanthus* (Weber) Britton & Rose and *Neobuxbaumia tetetzo* var. *tetetzo* (Coult.) Backeb., and of four barrel cacti species: *Echinocactus platyacanthus f. grandis* (Rose) Bravo, *Ferocactus flavovirens* (Scheidw.) Britton & Rose, *Ferocactus recurvus* var. *recurvus* (Mill.) Linds. and *Ferocactus robustus* (Link *ex* Otto) Britton & Rose, were collected from plants growing at the Zapotitlán Valley in Puebla, México (18 °20′N, 97 °28′W). For each species at least 10 plants were sampled during the years of 1989 and 1990 depending on its fruiting period (Table 1). These cacti species grow in the same area, and the collection area included a few square kilometers. Seeds were separated from the fruits and stored in paper bags at room temperature (20±2 °C). The following selected species are endemic to the state of Puebla: *Pachycereus hollianus*, *Ferocactus robustus* and *F. flavovirens* (Bravo-Hollis 1978; Bravo-Hollis & Sánchez-Mejorada 1991). *Echinocactus platyacanthus F. grandis*, *Cephalocereus chrysacanthus*, *Neobuxbaumia tetetzo* var. *tetetzo* and *Ferocactus recurvus* var. *recurvus* are endemic to the states of Puebla and Oaxaca (Bravo-Hollis 1978; Bravo-Hollis & Sánchez-Mejorada 1991).

Constant temperatures

Seven constant temperatures were chosen: 10 °C, 15 °C, 20 °C, 25 °C, 30 °C, 35 °C and 40 °C. Per species and per temperature, fifty seeds were sown inside each of four Petri dishes on the surface of 1% agar in distilled water. Dishes were incubated in growth chambers (Lab-Line Instruments, Inc., 844, Ill., USA) with a 12 h photoperiod. The experimental design consisted of a random 7 species × 7 temperatures factorial arrangement.

Alternating temperatures

Five alternating temperature ranges were selected: 0/10 °C, 5/20 °C, 10/25 °C, 15/30 °C and 20/35 °C. Per species, per temperature, fifty seeds were sown inside each of four Petri dishes on the surface of 1% agar in distilled water. Dishes were incubated in growth chambers (Conviron, Winnipeg, Canada) with a 12 h photoperiod and a 14/10 h thermoperiod. The experimental design was a random 7 species × 5 temperatures factorial arrangement.

General procedures

White light inside each growth chamber was provided by fluorescent lamps (Sylvania, 20 W). Each Petri dish was examined every other day for a month or 45 days when germination was already completed, and a seed was considered germinated when the radicle appeared. The range of temperatures and the temperature fluctuations used for this study are registered in the study area at different periods throughout the year (Figure 1).

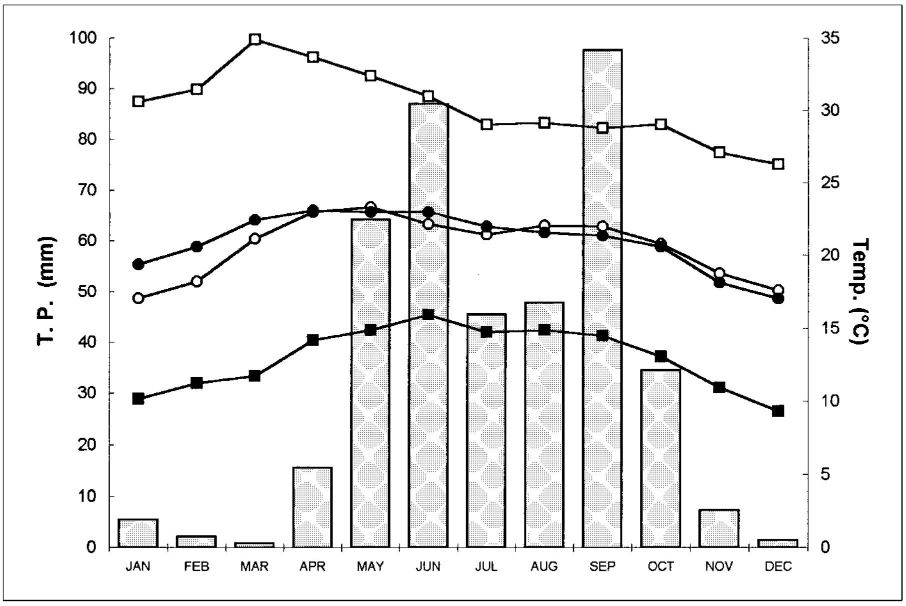
Germination data were normalized by an arcsine square-root transformation and were tested for statistical significance using a two-way analysis of variance (ANOVA)(Sokal & Rohlf 1981). Means were compared by the Least Significance Difference (LSD) test at $p < 0.05$ with the statistical program Statgraphics (v. 2.1).

Results

Seed germination were significantly different among cacti species ($F_{(6,335)} = 184.0$; $p < 0.0001$ and among the temperature treatments ($F_{(11,335)} = 248.2$, $p <$

Table 1. Fruiting periods of the species studied

Species	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.
E. platyacanthus	x	x	x	x		x	x				x	x
F. recurvus	x	x	x				x	x				x
F. robustus	x	x					x	x				x
F. flavovirens	x	x	x	x								x
C. chrysacanthus	x	x	x	x		x	x					x
N. tetetzo					x	x	x					
P. hollianus					x	x	x	x				



Mean T. (°C)	17	18.2	21.1	23	23.3	22.2	21.4	22	22	20.8	18.7	17.6	13 years
Mean T. (°C)	19.3	20.6	22.4	23.1	23	23	22	21.5	21.3	20.6	18.1	17	2 years (91-92)
Total P. (mm)	5.4	2.1	0.8	15.6	64.2	87	45.5	47.8	97.6	34.5	7.3	1.4	18 years

Figure 1. Annual distribution of mean temperature for 13 (○) and two years (●), minimum (■) and maximum (□) temperature for two years and precipitation bars for 18 years registered at the Climatological Station at Zapotitlán-Salinas, Puebla, México (Modified from Zavala-Hurtado, 1982).

0.0001) and interaction between them was significant too ($F_{(66,335)} = 15.04$; $p < 0.0001$). The multiple range analysis clearly separated the barrel cacti from the columnar cacti. Due to these results both groups were analyzed separately. Also, for all studied species, germination results at any fluctuating temperature were not significantly higher than seed response to the most favorable constant temperature ($F_{(1,187)} = 1.98$, $p = 0.16$ for barrel cacti, and $F_{(1,143)} = 3.16$; $p = 0.1$ for columnar cacti).

Constant temperatures

The two-way ANOVA showed that there were significant differences in seed germination response to constant temperatures of the seven studied species ($F_{(6,195)} = 55.15$; $p < 0.0001$), there were significant differences among the studied species ($F_{(6,195)} = 242.46$; $p < 0.0001$) and the interaction between both factors was significant, too ($F_{(36,147)} = 10.22$; $p < 0.0001$). The multiple range analysis also indicated significant differences in seed response to temperature within each species.

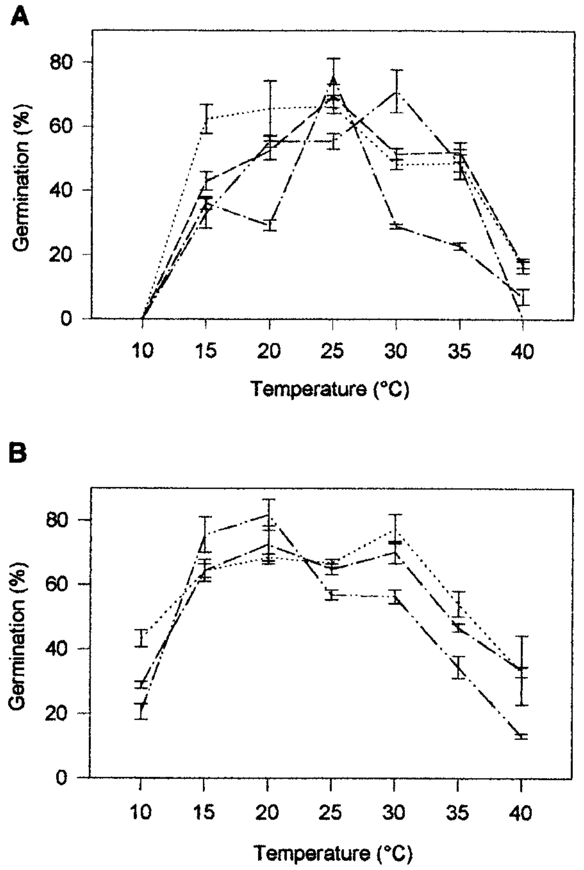


Figure 2. Germination percentage of cacti species at each one of the constant temperatures. A) Barrel cacti species: (· · ·) *Ferocactus flavovirens*, (-· · -) *F. robustus*, (-··-) *F. recurvus*, (- - -) *Echinocactus platyacanthus*. B) Columnar species: (· · ·) Cephalocereus chrysacanthus, (-·-) *Neobuxbaumia tetetzo*, (-··-) *Pachycereus* hollianus. Bars indicate standard errors.

Barrel cacti

Barrel cacti did not show germination at 10 °C; however, at 15 °C, all the species showed a germination percentage above 30% and at the highest temperature (40 °C), three species only reached a germination percentage below 17%, and *F. robustus* did not germinate (Figure 2A).

E. platyacanthus did not show significant differences in germination at 20, 30 and 35 °C, and showed maximum germination percentage at 25 °C. *F. flavovirens* did not show significant differences among the 15–25 °C range where it had the maximum significant germination percentage. There were no significant differences between 30 and 35 °C, too. *F. recurvus* showed low germination (around 25%) at 15, 20, 30 and 35 °C with no significant differences among them (Figure 2A). This species germinated above 50% only at 25 °C. *F. robustus* did not show significant differences in germination among 20, 25 and 35 °C, and also between 10 and 40 °C, and had its maximum germination percentage at 30 °C (Figure 2A).

Columnar cacti

The three columnar species showed significant differences in seed germination response to temperature ($F_{(6,83)} = 75.08, p < 0.05$); also there were significant differences among the three studied species ($F_{(2,83)} = 11.45$; $p < 0.05$) and the interaction between both factors was significant too ($F_{(12,83)} = 4.74$; $p < 0.05$).

The three columnar cacti germinated more than 50% in a wide temperature range (15–30 °C) (Figure 2B). At the lowest temperature used (10 °C), *C. chrysacanthus* germinated over 40%, *N. tetetzo* above 25% and *P. hollianus* slightly above 20%. At the highest temperature used (40 °C), only two species, *C. chrysacanthus* and *N. tetetzo* germinated above 30%. *C. chrysacanthus* did not show significant differences in the range 15–25 °C, and maximum germination percentage was obtained at 30 °C. *N. tetetzo* did not show significant differences from 15 to 30 °C (where it got its maximum germination percentage) and between extreme temperatures (10 and 40 °C), too. Also, there were no differences between 35 and 40 °C, probably because at 40 °C, seed germination showed a wide variation. On the other hand, *P. hollianus* showed a narrow range of maximal germination at 15–20 °C. Lower germination, but without significant differences, was found at 10 and 40 °C and also at 25 and 30 °C.

Alternating temperatures

The two-way ANOVA showed that there were significant differences in seed germination response to alternating temperatures of the seven studied species ($F_{(4,139)} = 233.45$; $p < 0.05$), there were significant differences among the studied species ($F_{(6,139)} = 154.14$; $p < 0.05$); also the interaction between both factors was significant ($F_{(24,139)} = 20.86$; $p < 0.05$). The multiple range analysis also indicated significant differences in seed response to temperature within each species.

0/10 °C treatment

Germination for all barrel cacti was strongly inhibited by the 0/10 °C treatment, and only *F. robustus* showed slight germination (5.5%). The three columnar species germinated at this temperature *C. chrysacanthus* and *N. tetetzo* had germination percentages above 40% and *P. hollianus* below 13% (Figure 3A).

5/20 °C treatment

Two barrel cacti, *E. platyacanthus* and *F. flavovirens* had a germination percentage above 25%, while germination of the other two barrel cacti was practically null. The three columnar species showed germination above 60% (Figure 3B).

10/25 °C treatment

All barrel cacti increased their germination percentage at this alternating temperature. The most tolerant to low temperatures were *E. platyacanthus* and *F. flavovirens*, which germinated above 50%. *F. robustus* and *F. recurvus*, which did not tolerate low temperatures, increased their germination percentage. The first species increased germination from 5.5% at 5/20 °C to 38.3% and *F. recurvus* which did not germinate at 5/20 °C, reached 20% germination (Figure 3C).

15/30 °C treatment

E. platyacanthus, F. flavovirens and *F. robustus* had a 15/30 °C treatment germination above 40% at this alternating treatment. *F. recurvus* had a germination above 30%. At this alternating temperature, *F. recurvus* expressed its maximum germination percentage, although it was much lower than that one obtained at the constant temperature of 25 °C (Figure 2A). *E. platyacanthus* germinated as in the 10/25 °C treatment. *N. tetetzo* and *C. chrysacanthus* increased their germination percentage, but *P. hollianus* reduced it (Figure 3D).

20/35 °C treatment

E. platyacanthus and *F. flavovirens*, which were more tolerant to high temperature, increased their germination percentage. *F. robustus* behaved similarly to the 15/30 °C treatment, and to *F. recurvus*. Two of the columnar species, *N. tetetzo* and *C. chrysacanthus* which are more tolerant of low temperatures, showed a significant germination reduction. The exception was *P. hollianus* which germinated similar to the 15/30 °C treatment (Figure 3E).

Discussion

Similar to many tropical arid land species (Hammouda & Bakr 1969), most of the species studied reached full germination in a 20–30 °C range. Germination at the highest temperature incorporates them into the species considered as thermophilous (Hendricks & Taylorson 1976; Boeken & Gutterman 1990). Columnar species germinated above 10% at the most extreme temperatures (10 and 40 °C). Among them, *C. chrysacanthus* had the widest response to temperature, germinating above 30% in both extreme temperatures, whereas barrel cacti did not germinate at the lowest temperature and, at the highest, only two species germinated but below 20%. Only the barrel cactus *F. recurvus* showed an unusual seed response to a range of temperatures among the perennial desert plants; it only achieved maximal germination over 50% at 25 °C. This germinative response could limit its germination and establishment to certain periods of the year or exclusively to shaded microhabitats which could moderate temperature extremes (Valiente-Banuet & Ezcurra 1991).

At the high temperatures of 35 or 40 °C we found rotted seeds that did not germinate. Probably this is due to leakage of amino acids, endogenous sugars and other substances that may occur at temperatures above 30–35 °C upon imbibition (Hendricks and Taylorson 1976; Berry & Raison 1981).

Considering the 50% germination criterion, Nobel (1988) concluded that extreme temperatures (maximum and minimum) for cacti are above 30 °C and below 12 °C. This assumption coincides for the highest temperature with the results obtained for some of the species studied which reach high germination percentages even at 35 °C. On the other hand, in the temperature below 12 °C (10 °C) none of the species germinated 50%. Because the species studied are geographically restricted to tropical deserts, they seem to be less tolerant to low temperatures than the species studied and reviewed by Nobel (1988) from subtropical deserts.

Alternating temperatures favor the germination process of diverse plant families growing in arid zones (Hammouda & Bakr 1969; Mahmoud et al. 1983, 1984) among them, species of cacti (Fearn 1974, 1981). However, alternating temperatures in the species considered here did not significantly favor ger-

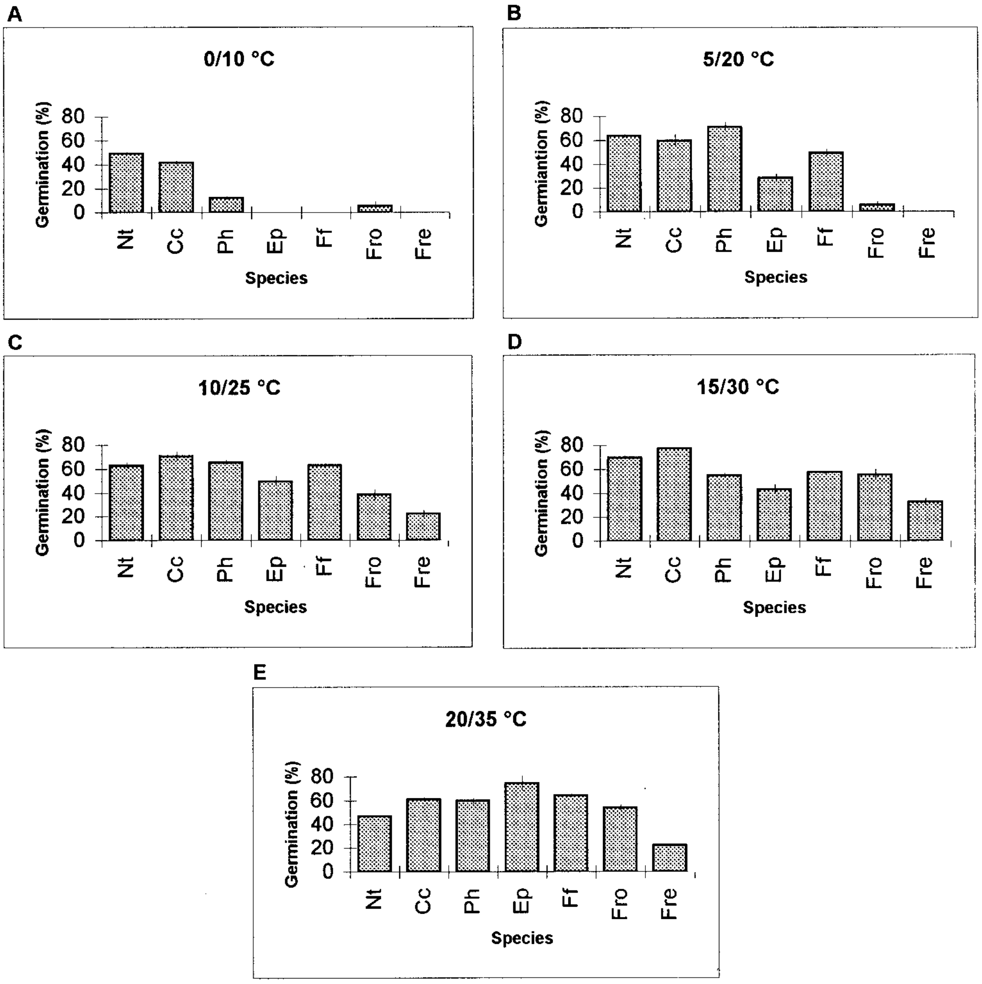


Figure 3. Germination percentage of cacti species for each one of the alternating temperature treatment indicated. Columnar species: Nt= *Neobuxbaumia tetetzo,* Cc= *Cephalocereus chrysacanthus,* Ph= *Pachycereus hollianus.* Barrel cacti species: Ep= *Echinocactus platyacanthus,* Ff= *Ferocactus flavovirens,* Fr= *Ferocactus robustus* and Fre= *Ferocactus recurvus.* Bars indicate standard errors.

mination compared with the results obtained at constant temperatures. On the other hand, some of the fluctuating temperature treatments reduced seed germination when too low or too high temperatures were involved. Seed response to fluctuating temperatures for these species could be inferred from seed response to constant temperatures, because the species were very sensitive to the extreme temperatures used. Similarly, some species of *Opuntia* were not favored by alternating temperatures (Baskin & Baskin 1977; Potter et al. 1984).

The requirement of alternating temperatures could be expected as a response to the daily temperature oscillations (14–15 °C) registered during the wet season (Zavala-Hurtado 1982). Nevertheless, germination of the species studied here did not show significant differences compared to results obtained at constant temperatures.

The species studied did not show endogenous dormancy, they germinated at high percentages without any pretreatment (scarification or washing) as it has been noticed in other cacti species (Williams & Arias 1978; Arias & Lemus 1984; Potter et al. 1984; Rabenda 1990). In the study area, minimum and maximum temperatures agree to the range of temperature fluctuations most favorable for germination of the species (Figure 1). Cacti species studied fructificate in certain periods of the year (Table 1). Then, the lack of this dormancy mechanism in these species could be an advantage, because it means that seeds could avoid predation if they germinate immediately after dispersal, during summer and autumn rainfalls.

Barrel cacti studied here in relation to columnar cacti are less tolerant to low temperatures than columnar cacti species. This agrees with the light requirements of these species at constant and alternating temperatures. Barrel cacti require light to germinate while columnar cacti are indifferent to light (Rojas-Aréchiga et al. 1997). Barrel cacti can germinate at the soil surface where light and high temperatures are present while columnar cacti can germinate underground where temperatures are not so high and light could be absent. Similar to light requirements for germination, barrel and columnar cacti temperature requirements could be associated with vertical distribution of environmental temperatures during seed development (Rojas-Aréchiga et al. 1997). Plants growing in open desert areas can be subjected to extremely high temperatures near the soil surface and to high wind speed, which may have a great influence on maximum plant temperature (Nobel 1978; Nobel et al. 1986). Then, small spherical cacti are more exposed to high temperatures than columnar cacti. At the end of July at the Zapotitlán Valley, barrel cacti may be exposed to temperatures between 16 and 44 °C, while temperatures at the top of *N. tetetzo*, oscillate only from 13 to 30 °C (Valiente-Banuet, pers. comm.).

Temperature effects during seed maturation on seed germination response to temperature have been widely demonstrated (Gutterman 1980/81; Roach & Wulff 1987; Wulff 1995). High constant temperatures or the extreme high one of a temperature fluctuation during seed maturation increases tolerance to high temperature during germination or induces conditional dormancy at low temperatures (Koller 1962; Junttila 1973). Tolerance to low temperatures of columnar cacti could be related to relatively less extreme temperatures during seed development than in barrel cacti. Nevertheless, it is necessary to perform more experiments including more barrel and columnar cacti species to confirm this interpretation.

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