NOTES

EFFECT OF GIBBERELLIC ACID ON GERMINATION OF SEEDS OF FIVE SPECIES OF CACTI FROM THE CHIHUAHUAN DESERT, NORTHERN MEXICO

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ABSTRACT—We determined the effect of three concentrations of gibberellic acid on germination and photoblastic behavior of five species of Opuntioideae from the Mapimi Biosphere Reserve, southern Chihuahuan Desert, Durango, Mexico. For *Cylindropuntia imbricata*, addition of high concentrations (1,500 ppm) of gibberellic acid gave a 30% germination similar to the control; for *Opuntia rastrera*, medium concentrations (1,000 ppm) gave <40% germination; and for *O. microdasys*, low concentrations (500 ppm) gave 35% germination. High concentrations restricted germination. *Opuntia macrocentra* and *Cylindropuntia leptocaulis* did not differ significantly from the control. *Opuntia macrocentra* required light for germination; addition of gibberellic acid did not substitute for light. For all species, light increased germination and the effect of gibberellic acid is species dependent, rarely better than the control. Species we studied did not seem to have physical dormancy and may have had physiological dormancy that was unaffected by gibberellic acid.

RESUMEN—Determinamos la respuesta fotoblástica y el efecto de tres concentraciones de ácido giberélico en la germinación de cinco especies de Opuntioideae de la Reserva de la Biósfera de Mapimí en el desierto Chihuahuense, México. Para *Cylindropuntia imbricata* con la adición de una concentración alta (1,500 ppm) se obtuvo una germinación de 30% similar al control; para *Opuntia rastrera*, con una concentración media (1,000 ppm) se obtuvo una germinación <40%; y para *O. microdasys*, con una concentración baja (500 ppm) se obtuvo una germinación de 35% y una concentración media inhibió la germinación. *Opuntia macrocentra* y *Cylindropuntia leptocaulis* no difirieron significativamente del control. *Opuntia macrocentra* requirió luz para su germinación y la adición de ácido giberélico no sustituyó el requerimiento de luz. Para todas las especies estudiadas, la luz incrementó la germinación y el efecto del ácido giberélico es dependiente de la especie, y en pocas ocasiones mejor que el control. Las especies estudiadas no parecieron presentar latencia física y posiblemente tuvieron latencia fisiológica que no fue afectada por el ácido giberélico.

In some Cactaceae, recruitment is particularly difficult, either because of low germination (Rojas-Aréchiga and Vázquez-Yanes, 2000) or inadequate establishment of seedlings (Steenbergh and Lowe, 1969; Nobel, 1984; Godínez-Alvarez and Valiente-Banuet, 1998). Therefore, detecting mechanisms that promote germination have important implications; especially, with regard to propagation of species for conservation and management.

Physiological dormancy in seeds of some plants depends on the ratio of levels of growth inhibitor (abscisic acid) and growth promoter (gibberellic acid). This has been tested in species such as *Albizia grandibracteata*, where three concentrations of gibberellic acid promoted germination with respect to the control (Tigabú and Odén, 2001). In seeds of *Arbutus andrachne*, a treatment with 250 or 500 mg/L of gibberellic acid resulted in >80% germination (Karam and

Al-Salem, 2001). For plants inhabiting arid environments, some research has been done to promote germination with gibberellic acid (Ismail, 1990; Maiti et al., 1996). Plants in arid environments tend to have mechanisms that defer germination as an adaptive response to unpredictable environmental conditions (Jurado and Moles, 2003).

Results from studies of effects of gibberellic acid on seeds of Cactaceae are scarce and diverse. The first studies with gibberellic acid in Cactaceae were by Alcorn and Kurtz (1959) and McDonough (1964) who demonstrated that concentrations of 500 and 1,000 ppm increased germination of seeds of *Carnegiea gigantea* and *Stenocereus thurberi* under light and dark treatments in a temperature range close to optimum. Since then, experiments with other species of Cactaceae have had contrasting results (Table 1). Particularly for species of *Opuntia*, the difficulty of germinating seeds has been recognized since the 1960s, so several pretreatments have been used to increase germination (Pilcher, 1970; Potter et al., 1984; Trujillo-Argueta and González-Espinosa, 1991; Mandujano et al., 1997, 2005; Pendley, 2001). Results are varied, but even acid and mechanical scarification treatments have not promoted better germination for species such as *Opuntia rastrera* (Mandujano et al., 2005), which probably is associated with lack of physical dormancy that has been seen in other species of *Opuntia* (Orozco-Segovia et al., 2007). It also has been suggested that the best way to achieve better germination is by means of an afterripening period, which suggests presence of non-deep, physiological dormancy (Baskin and Baskin, 1998; Mandujano et al., 1997). This dormancy can be overcome during dry storage (Orozco-Segovia et al., 2007). The diminished capacity in production of amylase in the aleurone from seeds apparently is due to a decrease in expression of the α-amylase genes. This reduction is associated with a decrease in the response to gibberellic acid (Bernal-Lugo et al., 1999). Deno (1994) suggested that species of *Opuntia* need gibberellic acid to germinate, although available data do not seem to support this idea (Table 1).

Gibberellic acid is widely used to promote germination by photoblastic seeds in the dark (Lewak and Khan, 1977). Its effect has been shown for many species that belong to several families of plants (Baskin and Baskin, 1998). Again, results for Cactaceae are as diverse as the number of species used in trials (Brencher et al., 1978; Zimmer and Buttner, 1982; Arias and Lemus, 1984; Trejo Hernandez and Garza Castillo, 1993; Zimmer, 1998; Rojas-Aréchiga et al., 2001; Ortega-Baes and Rojas-Aréchiga, 2007; Rojas-Aréchiga, 2008).

We determined the effect of giberellic acid on germination with seeds undergoing an ageing process in five species of Opuntioideae that occur sympatrically in the southern Chihuahuan Desert. We also studied photoblastic behavior in all species to determine the effect of addition of gibberellic acid at three concentrations under light and dark conditions. Species studied were *Cylindropuntia leptocaulis*, *C. imbricata*, *Opuntia rastrera*, *O. macrocentra*, and *O. microdasys*. In 1996, we collected seeds from ripe fruits of these five species in the Mapimi Biosphere Reserve in the Chihuahuan Desert of Durango, Mexico (26°29–52′N, 103°32–58′W; mean annual precipitation, 227 mm; mean annual temperature, 21°C; Montaña and Breimer, 1988). Seeds were extracted from fruits and pulp residues were removed from seeds, which were then air dried at room temperature and stored in paper bags at room temperature until onset of the experiment (9 years after harvest). This period corresponds to prior experiments with *O. rastrera*, demonstrating that seeds do not germinate unless they undergo an after-ripening period of $\geq$1 year. Percentages of germination remain high (>45% in 12L:12D photoperiod and a constant 25°C temperature) even after 12 years in storage (Aguilar-Morales, 2005); thus, seeds remain viable for a long time. Seeds were sown in Petri dishes with 1% agar and we added three concentrations of gibberellic acid (500, 1,000, and 1,500 ppm) and a control (no addition of gibberellic acid). We used four replicates of 25 seeds/Petri dish/treatment. Four replicates each containing 25 seeds/Petri dish were used to test for photoblastism, each Petri dish was wrapped within two layers of aluminum foil and kept in total darkness until the end of the experiment. Experimental units were placed in a germination chamber (Conviron CMP3000; Controlled Environments Limited, Winnipeg, Manitoba, Canada) at 25°C and a 12L:12D photoperiod. The experiment was followed daily for 4 months and we considered a seed to be germinated once the radicle appeared.

Results were analyzed adjusting a generalized-linear model on the number of germinated seeds

Table 1—Studies of Cactaceae in which germination has been assessed using different treatments with gibberellic acid.

Taxon	Treatment	Effect of gibberellic acid	Source
Astrophytum capricorne, Leuchtenbergia principis, Echinocactus grusonii	Scarification plus gibberellic acid at 0.1%	Positive response	De la Rosa-Ibarra Garcia and García (1994)
Opuntia joconostle	Imbibition during 30 min in a 40-ppm solution of gibberellic acid	Positive response	Sánchez-Venegas (1977)
Sclerocactus mariposensis	Scarification plus imbibition for 18 h plus gibberellic acid at 0.5%	Positive response	Moreno et al. (1992)
Myrtillocactus geometrizans, Mammillaria ritteriana	500 and 2,000 ppm of gibberellic acid	Positive response	Zimmer and Buttner (1982)
Arequipa erectocylindrica, Eulychnia longispina, Eulychnia castanea	500 and 1,000 ppm of gibberellic acid	Positive response	Zimmer and Buttner (1982)
Cereus	Soaking seeds for 30 min in 100–200 ppm of gibberellic acid	Positive response	Krulik (1981)
Cereus griseus	0.001M gibberellic acid	Negative response	Williams and Arias (1978)
Rebutia minuscula, Pachycereus hollianus	500, 1,000, and 1,500 ppm of gibberellic acid	Negative response	Brencher et al. (1978)
Oreocereus maximus, Oreocereus celsianus, Notocactus leninghausii, Epiphyllum anguliger	500, 1,000, and 2,000 ppm of gibberellic acid	Negative response	Zimmer and Buttner (1982)
Opuntia tomentosa	1,000 ppm of gibberellic acid	No response	Olvera-Carrillo (2001)
Notocactus submammulosus	10–100 mg/L of gibberellic acid	No response	Shimomura et al. (2000)
Trichocereus terscheckii	500 and 1,000 ppm of gibberellic acid	No response	Ortega-Baes and Rojas-Aréchiga (2007)
Opuntia rastrera, Opuntia microdasys, Opuntia macrocentra	200 ppm of gibberellic acid	No response	Mandujano et al. (2007*b*)
Mammillaria haageana, Mammillaria mystax, Mammillaria supertexta, Mammillaria carnea	500 and 1,000 ppm of gibberellic acid	No response	Rojas-Aréchiga (2008)

with JMP version 6.0, assuming a binomial error distribution (Crawley, 2002). Total percentages of germination were contrasted among species. In addition, separate analyses for each species were fitted as we detected great variation in germination between species in response to addition of gibberellic acid.

Mean proportions of seeds that germinated differed among species ($\chi^2 = 70.64$, $df = 4$, $P < 0.001$; Fig. 1a). The greatest proportions of germinated seeds were for *O. rastrera* and the lowest for *O. macrocentra*. The only difference was the low proportion of germination by seeds of *O. macrocentra*; all other species did not differ in germination ($P > 0.05$). In the photoblastic experiment, we detected consistent significant effects of light ($\chi^2 = 174.37$, $df = 4$, $P < 0.001$; Fig. 1b) for all species implying that they germinate at higher proportions under light conditions. The significant species-light interaction ($\chi^2 = 20.87$, $df = 4$, $P < 0.001$) only suggests high variation among species that require light. We detected neither a significant effect of concentration of gibberellic acid ($\chi^2 < 0.01$, $df = 3$, $P > 0.999$) nor a light-gibberellic acid concentration ($\chi^2 = 0.04$, $df = 3$, $P > 0.998$),

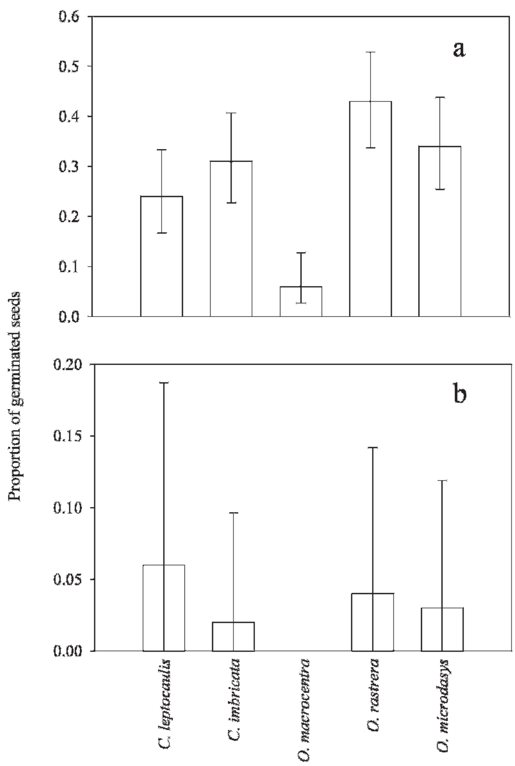

FIG. 1—Proportion (mean ± 95% CI) of germinated seeds under a) light and b) dark conditions for five species of Opuntioideae (*Cylindropuntia imbricata*, *C. leptocaulis*, *Opuntia microdasys*, *O. rastrera*, and *O. macrocentra*) that are sympatric in the Mapimi Biosphere Reserve, southern Chihuahuan Desert, Durango, Mexico.

meaning that under both light conditions germination of seeds behaved similarly. There was, however, a significant effect of gibberellic acid by species ($\chi^2 = 55.48$, $df = 12$, $P < 0.001$) suggesting different responses of species to concentrations of gibberellic acid (Figs. 2 and 3). *Opuntia macrocentra* exhibited no germination under dark conditions suggesting strict photoblastic behavior for seeds of this species.

The concentration of gibberellic acid seems to have species-specific responses (Figs. 2 and 3) and was significant for only two species (*C. imbricata*: $\chi^2 = 18.47$, $df = 3$, $P < 0.01$; *O. microdasys*: $\chi^2 = 34.65$, $df = 3$, $P < 0.01$) under light conditions and for three species under dark conditions (*O. imbricata*: $\chi^2 = 7.88$, $df = 3$, $P = 0.048$; *O. rastrera*: $\chi^2 = 12.23$, $df = 3$, $P = 0.066$; *O. microdasys*: $\chi^2 = 29.42$, $df = 3$, $P < 0.001$). A similar pattern for both light treatments was detected for *C. imbricata* and *O. microdasys* (Figs. 2 and 3). For these two species, low and high concentrations increased germination with respect to the control, and for *O. microdasys*, concentrations of gibberellic acid of 1,000 ppm inhibited a proportion of seeds germinating in dark conditions. However, low concentrations of gibberellic acid significantly promoted higher germination in *O. microdasys* ($\chi^2 = 14.07$, $df = 1$, $P < 0.01$) for both light treatments. The highest concentration significantly increased germination in *C. imbricata* ($\chi^2 = 8.33$, $df = 1$, $P < 0.01$) under light conditions, as compared to the control. The addition of gibberellic acid in *C. leptocaulis*, *O. rastrera*, and *O. macrocentra* had no apparent effect on germination with respect to the control ($P > 0.05$ for the three cases; Fig. 2), except for *O. rastrera* under dark conditions (Fig. 3). Even under control conditions, *O. macrocentra* had low overall germination. The proportion of germination for the five species was low (<0.5), which is consistent with other species of O*puntia* (Pilcher, 1970; Trujillo-Argueta and González-Espinosa, 1991; Pendley, 2001). In particular, the low proportion of seeds of *O. macrocentra* that germinated also was detected for 1-year-old seeds (Mandujano et al., 2007*b*), so viability can be discarded partially as a factor responsible for the low rate of germination. Although viability of seeds was not quantified in our study and may be confounding our results, and the interpretation of our results cannot be entirely ascribed to our treatments, standard assays for testing viability of seeds (e.g., tetrazolium) may not be reliable in seeds that have deep dormancy because of low levels of respiration. In addition, seeds of *Opuntia* have high viability (Gimeno and Vilá, 2002; Orozco-Segovia et al., 2007), so we assume that much of the differences we observed may be due to our treatments. *Opuntia macrocentra* probably is facing a more serious problem than other species of Opuntioideae, as recruitment is mainly through seeds that have low percentages of germination, and germination does not seem to be enhanced by gibberellic acid. The first factor partially could explain the absence of seedlings in long-term demographic studies (Mandujano et al., 2007*a*). Our results are also the first reports of germination of seeds within *Cylindropuntia*; these two species seem to behave like *Opuntia.* The addition of gibberellic acid in the Opuntioideae we studied had contrasting results. Only a high

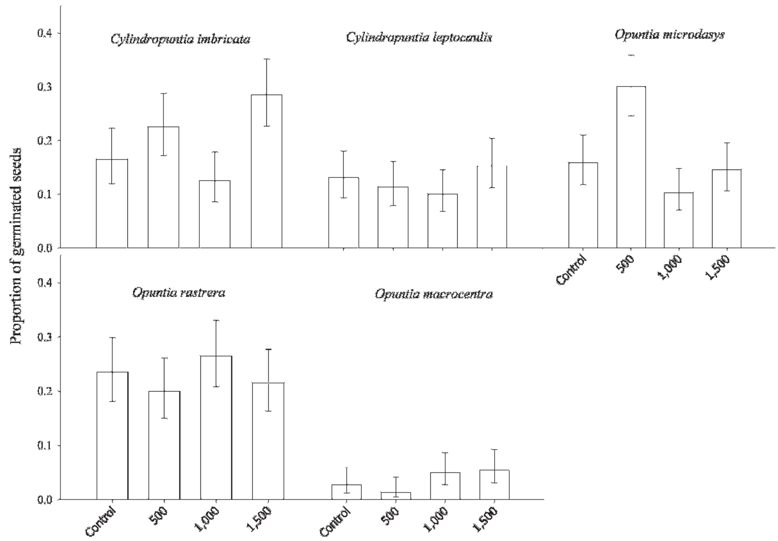

FIG. 2—Proportion of germinated seeds of five species of Opuntioideae that are sympatric in the Mapimi Biosphere Reserve, southern Chihuahuan Desert, Durango, Mexico, assessed using a control (no addition of gibberellic acid) and three treatments of gibberellic acid (500, 1,000 and 1,500 ppm) in light conditions.

concentration of gibberellic acid affected seeds of *C. imbricata*. Within *Opuntia*, only one of the species responded to addition of gibberellic acid. *Opuntia rastrera* and *O. macrocentra* did not respond to addition of gibberellic acid under light conditions and only *O. rastrera* showed a positive effect of gibberellic acid under dark conditions. Positive responses were detected for *O. microdasys* at low concentrations. Lack of effects of gibberellic acid in some concentrations,

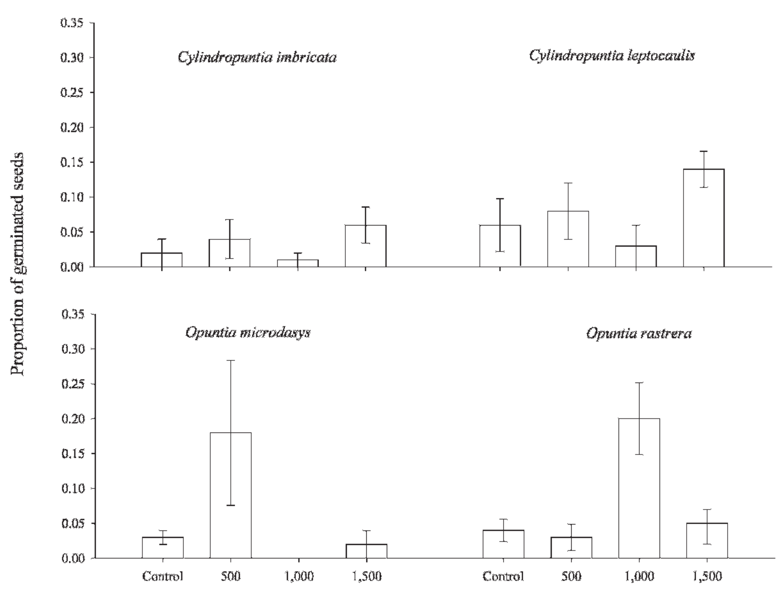

FIG. 3—Proportion of germinated seeds of four species of Opuntioideae that are sympatric in the Mapimi Biosphere Reserve, southern Chihuahuan Desert, Durango, Mexico, assessed by a control (no addition of gibberellic acid) and three treatments of gibberellic acid (500, 1,000 and 1,500 ppm) in dark conditions. *Opuntia macrocentra* did not show germination in dark conditions.

especially in *O. macrocentra,* compared to the control are consistent with results of other species of *Opuntia* (Williams and Arias, 1978; Olvera-Carrillo, 2001), but contrast with results for *O. joconostle* (Sánchez-Venegas, 1997). This may be due to *O. joconostle* (and other species of Cactaceae where gibberellic acid enhanced germination) previously being imbibed in distilled water, which could be confounding the effect of gibberellic acid. In general, results of other studies suggest that the increase in percentage of germination with gibberellic acid may be promoted by the previous treatment of the seeds (i.e., scarification or imbibition), rather than the effect of gibberellic acid. Our results led us to conclude that there is no clear pattern of the effect of gibberellic acid on germination of seeds within Cactaceae. In a previous study with seeds of *O. rastrera*, the only mechanism that overcame dormancy was an afterripening period, neither mechanical scarification nor acid scarification gave better results than ageing (Mandujano et al., 2005), which is consistent with what Orozco-Segovia et al. (2007) have suggested about the lack of physical dormancy in the *Opuntia*. Results obtained here and in other studies of *Opuntia* (Mandujano et al., 1995; Orozco-Segovia et al., 2007) suggest that these species do not have physical dormancy, although the trait would be favored in arid environments. The best way to promote germination could be an afterripening period (for some species), which would be consistent with seeds of Opuntioideae being able to form persistent seed banks (Mandujano et al., 1997; Montiel and Montaña, 2003).

The common belief that gibberellic acid is a promoter of germination may not hold for Cactaceae. Instead, treatments that trigger germination may be more related to environmental cues than to biological attributes.

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