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GERMINATION RESPONSE OF THE EPIPHYTIC CACTUS *RHIPSALIS BACCIFERA* (J. S. MILLER) STEARN TO DIFFERENT LIGHT CONDITIONS AND WATER AVAILABILITY

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In the forest canopy, seeds of epiphytic plants encounter heterogeneous environments created by a combination of factors such as solar radiation, humidity, and host characteristics. Germination requirements may explain the species distribution in the canopy; however, more knowledge is essential. Germination of *Rhipsalis baccifera*, a widespread tropical epiphytic cactus and representative of the humid montane forest in Mexico, was 80% or higher with far red, red, and white light and close to 0 in darkness. Germination was light saturated at very low photon flux density of only 13.5 μmol m^{-2} s^{-1}. Germination decreased gradually at low water potentials and with increased storage time. After storage for 1 yr, no seeds germinated. Seeds have the ability to germinate in both the internal and external positions of the tree crowns. The germinative requirements of *R. baccifera* indicate that it could colonize a wide range of light conditions in the canopy; however, substrate humidity and seed age could limit germination.

Keywords: cactaceae, epiphyte, germination, seed, humid montane forest.

Introduction

Epiphytes are plants that complete all or part of their life cycle on other plants, normally trees, and establish multiple relationships with the fauna of the canopy, providing shelter and food, and many animals pollinate the flowers and disperse the seeds (Benzing 1990; Zotz and Andrade 2002). Epiphytic plants are important elements in the ecosystem because they can constitute up to 50% of the tree leaf biomass and 45% of the nutrients present within the system, and 10% of all known vascular plant species are epiphytes (Nadkarni 1984; Kress 1989; Lüttge 1989). Spatial distribution of epiphytes depends on microclimatic conditions, age, and stability of the branches, among other factors (Freiberg 1996; Hietz 1997). In the epiphytic environment, plants encounter heterogeneous microenvironments that occur through a combination of factors such as solar radiation, humidity, and characteristics of the tree bark (Madison 1977; Benzing 1978, 1990). The different environmental requirements for germination of seeds and seedling growth could explain the preference of some epiphytes for growth in certain strata of the canopy. Epiphytes that grow on the treetops, or crown exteriors, receive greater quantities of solar radiation compared with those growing in the interior or lower parts of the tree and experience a reduction in water availability (Griffiths and Smith 1983; Lüttge 1989).

Although seed germination is a critical step in the life cycle of most plant species, germination physiology of epiphytes has been poorly studied except for orchids and some bromeliads and mistletoes (Benzing 1990; Baskin and Baskin 1998). As in other vascular plants, germination probably responds to specific combinations of light, temperature, and substrate humidity; however, age and seed viability can modify the germination performance (Baskin and Baskin 1998).

Epiphytes generally produce many seeds per fruit; 75% of the epiphytic genera have seeds that are smaller than 1 mm and only rarely exceed 2 mm in length (Madison 1977; Baskin and Baskin 1998); this size confers a greater chance of entry into bark microsites that allows the seed sufficient imbibition of water for germination. Imbibition in water can cause rapid germination of seeds in some epiphytes, and under controlled conditions, germination percentage is usually high for some bromeliad epiphytes (Benzing 1978; Baskin and Baskin 1998). However, in the plant canopy the germination is typically lower, and infrequent water availability in the field could be the explanation (Winkler et al. 2005; Bader et al. 2009). At increased levels of water stress in mannitol solutions, fewer strangler fig (*Ficus aurea*) seeds germinated (Swagel et al. 1997). Substrate with high humidity was the most important factor for *Ficus stupenda* germination in the rain forest canopy (Laman 1995). Water availability limited seeds germination of *Tillandsia eizii* to the same extent in the inner and middle parts of the plant canopy (Toledo-Aceves and Wolf 2008) The germination of two *Tillandsia* species was reduced by intermittent dry periods under controlled conditions (Bader et al. 2009). Epiphytes frequently experience a highly intermittent water supply, and they exhibit well-developed capacities to tolerate drought and avoid photo-injury (damage caused by excessive light; Benzing 1978, 2004). Seeds adapted to germinate at high soil humidity but not necessarily at the field water capacity of the substrate and with high speed of

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germination would have an advantage on germinating in the plant canopy. Germination is in general faster in water-delimited ecosystems than in those with high water availability, and some species are adapted to germinate under stressing water conditions and at water potentials lower than −0.8 MPa (Evans and Etherington 1990; Jurado and Westoby 1992; Flores and Briones 2001). Desert cacti species show higher percentages of germination in water potential close to 0 MPa (De la Barrera and Nobel 2003; Ramírez-Padilla and Valverde 2005; Cervera et al. 2006; Guillén et al. 2009); however, some columnar cacti show high (57%–70%) or maximum germination (94%) even when water potential is −0.4 MPa (Flores and Briones 2001; Ramírez-Padilla and Valverde 2005). Although *F. aurea* is sensitive to substrate water potential, its germination was high (>80%) when water potential was −0.5 MPa and was possible at substrate water potentials of below −1.0 MPa (Swagel et al. 1997). The seed germination time of five epiphytic bromeliads has been shown to be shorter in less exposed canopy sites, indicating that higher humidity could accelerate germination, although the probability of germination was not affected by the position within the crown (Winkler et al. 2005). It has been observed that *Rhipsalis baccifera* is mostly distributed on the bases of the relatively thick trunks and branches of trees located in the humid montane forest, where it may get greater access to moisture (Ruiz-Fernández 2006; E. De la Rosa, personal observation).

Canopy foliage reduces total irradiances and red/far red (RFR) ratio by absorbance of wavelengths of 600 nm (red light) relative to wider wavelengths (far red light) causing environmental heterogeneity at germination sites in the phorophyte (Parker 1995). This variation in the light environment can influence the germination process. Positive photoblastic seeds require light for germination although light sensitivity can be modulated by temperature conditions or degree of seed hydration (Vásquez-Yanes and Orozco-Segovia 1994; Baskin and Baskin 1998). Positive photoblastism plays an important role on the preservation of dormancy of buried seeds or of seed deposited on shaded sites (Vásquez-Yanes and Orozco-Segovia 1994). Small seeds have limited food reserves, and photoblastic species utilize light signals to select sites with conditions suitable for germination (Vásquez-Yanes and Orozco-Segovia 1994; Pearson et al. 2003).The light sensitivity is dependent on phytochrome action, and only extremely low photon flux density is necessary to promote the germination (Vásquez-Yanes and Orozco-Segovia 1994). The capability to germinate at low red/red far ratio can facilitate germination at microsites where humidity is available and predation is reduced (Benítez-Rodríguez et al. 2004). Light-stimulated germination has been demonstrated for 17 species of Bromeliaceae; however, six of these were capable of germination in darkness (Downs and Piringer 1958, quoted in Baskin and Baskin 1998). The hemiepipyhtic strangler figs *Ficus pertusa* and *Ficus tuerckheimii* need light for germination; however, the strangler fig *Ficus aurea* germinates in light or darkness (Titus et al. 1990; Swagel et al. 1997). The epiphytic cactus *Epiphyllum anguligerum* and *Hylocereus setaceus* require light for germination (Zimmer and Büttner 1982; Simão et al. 2007). The seeds of some Cactaceae species are indifferent to light, while most cactus species are light sensitive and increase germination when exposed to constant red or white light and decrease sharply when in darkness or under far red light (Fearn 1981; Rojas-Aréchiga and Vázquez-Yanes 2000; Flores et al. 2006). Cacti that require light for germination have small seeds (Flores et al. 2006). The epiphytic cacti *R. baccifera* has seeds 1.5 mm in length (Bravo 1987). Columnar cacti that can germinate equally well in the presence of light and in darkness include *Cephalocereus chrysacanthus*, *Neobuxbaumia tetetzo*, *Pachycereus hollianus*, *Pachycereus pringlei*, and *Pereskia aculeata* (Rojas-Aréchiga et al. 1997; Valiente-Banuet and Godínez-Álvarez 2002). Gibberellic acid may inhibit germination for some cactus species or substitute the light requirements for others (Zimmer and Büttner 1982; Rojas-Aréchiga and Vázquez-Yanes 2000). Under darkness, gibberellic acid at 1000 ppm promotes the germination of *E. anguligerum* (Zimmer 1998). Optimum germination of terrestrial cacti usually occurs between 20° and 30°C (Zimmer 1998; Rojas-Aréchiga and Vázquez-Yanes 2000). The optimum range for germination of two *Epiphyllum* and three *Rhipsalis* species is between 20° and 25°C; a temperature between 15° and 30°C decreases the rate of germination (Zimmer 1980).

The viability of epiphyte seeds can be extremely short lived, and they apparently do not form seed banks (Benzing 1990). Viviparity has been identified in various fleshy-fruited epiphytic cacti, including *R. baccifera* ssp. *horrida* and *Rhipsalis micrantha*, allowing seed germination within the fruit (Cota-Sánchez and Abreu 2007). During the first days following *R. baccifera* germination, succulent cotyledons develop which allow water storage and facilitate survival of intermittent drought and successful establishment (Madison 1977; Benzing 1990).

Rhipsalis baccifera (tribe Hylocereeae) is a widespread Neotropical species and is the only species of cactus that grows in the tropics of the Old World (Bravo 1987). The genera *Rhipsalis* contain 39% of the epiphytic species in the Cactaceae family (Kress 1989). Most cacti live in arid or semiarid environments; however, ~150 of the 1500 species are epiphytic plants that grow in tropical and subtropical regions (Kress 1989). *Rhipsalis baccifera* is a representative species of the Mexican cloud forest, where epiphytes form a very important group in terms of diversity, constituting 32% of species present (Rzedowski 1996). Considering the ecological importance of epiphytic cacti in the Neotropical forests and the scarcity of our current knowledge about the germination and establishment in this group of plants, a set of hypotheses was tested for the seeds of *R. baccifera*: (*a*) germination increases when exposed to red or white light and decreases in darkness or low RFR ratio; (*b*) germination is triggered at low photosynthetic photon flux; (*c*) germination requires substrates with high water availability and can be favored at sites near to the center of the tree crown if the branches are relatively humid; and (*d*) seed viability is less than a year.

Material and Methods

Species, Seed Collection and Study Area

Often grouped in large numbers, the 3–6-cm diameter cylindrical leafless stems up to 1 m long of *Rhipsalis baccifera* hang from the crevices, trunks, or branches of evergreen and decid-

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uous trees. Only the young parts of the stems have spines. The plants produce small flowers 4 mm in diameter and globose and fleshy fruits containing black seeds 1.5 mm in length that are embedded in a transparent and whitish pulp (Bravo 1987). From Florida in the United States and Mexico through Central America to South America, Africa, and Sri Lanka, *R. baccifera* occurs in evergreen rainforest, humid montane forest, and tropical deciduous forest (Bravo 1987). Ripe fruits were collected in more than 10 *R. baccifera* plants in humid montane forest fragments in central Veracruz, Mexico. Seeds were manually separated from the fruits and dried at room temperature in shredded paper within airtight amber bottles stored in the shade. Germination in situ within host trees was carried out in a humid montane forest fragment adjacent to the Institute of Ecology in Xalapa, Veracruz, Mexico (19°31′N, 69°57′W), at an altitude of 1350 m a.s.l. This site has an average annual temperature of 19°C and annual precipitation of 1500 mm. The forest structure has been described in Williams-Linera (1997) and the epiphytic community in Hietz and Hietz-Seifert (1995). In light quality, water availability, and storage time experiments, seeds were incubated at 25°C in germination chambers (Biotronette; Lab-Line Instruments) with photoperiods of 12L:12D. All experiments comprised 5 replicates of 25 seeds per petri dish. Germination was considered to have occurred on emergence of the radicle through the testa (Baskin and Baskin 1998).

Light Quality and Quantity

Petri dishes with *R. baccifera* seeds were placed inside transparent acrylic boxes (30 cm × 25 cm × 10.5 cm; Rojas-Aréchiga et al. 1997). The boxes were placed in germination chambers, which were equipped with a fluorescent lamp (GE cool white, 20 W) for the red light treatment and two incandescent lights (25 W) for far red. Red acrylic boxes (series 2424, Rohm and Haas) were used to achieve the red light treatment, while in the far-red light treatment, the boxes were made from red and blue acrylic (series 2423). Petri dishes in the red light treatment had a RFR ratio of 1.92, and the photosynthetic photon flux density (PPFD) was 3.63×10^0 μmol m^{-2} s^{-1}, and the far-red light treatment had an RFR ratio of 0.48 and a PPFD of 1.48×10^1 μmol m^{-2} s^{-1}. Treatment with white light was carried out using a fluorescent lamp, which gave an RFR ratio of 2.22 and a PPFD of 2.92×10^1 μmol m^{-2} s^{-1}. For the germination-in-darkness treatment, the petri dishes were covered with a double layer of aluminum foil. Spectral composition and quantity of light were measured with a portable spectroradiometer (LI-1800; LI–COR). The spectra of red and far red light were delimited from 654 to 666 and 724 to 736 nm, respectively (Rojas-Aréchiga et al. 1997). Germination was recorded daily until day 7 and then once again on day 30. In the darkness treatment, to avoid any light effect during the incubation period, germination was not checked until the end of the treatment at day 30. To test the light quantity effect on germination, seeds were exposed to 13 light treatments: 0, 1.1×10^{-5}, 8.3×10^{-5}, 6.1×10^{-4}, 4.5×10^{-3}, 3.3×10^{-2}, 2.4×10^{-1}, 1.83×10^0, 1.35×10^1, 6.68×10^1, 7.94×10^1, 9.62×10^1, and 1.32×10^2 μmol m^{-2} s^{-1}. Light was provided by four fluorescent lamps (LG, 20 W). The first light treatment (0) was achieved by covering the petri dishes with double layers of aluminum foil; the rest of the treatments were achieved by covering the dishes with various layers of white and gray plastic films.

Water Availability and Storage Time

Rhipsalis baccifera seeds were placed in concentrations of polyethylene glycol (PEG 8000, Sigma) equivalent to water potentials of −0.99 to 0.0 MPa (Michel and Radcliffe 1985; De la Barrera and Nobel 2003; Ramírez-Padilla and Valverde 2005; Cervera et al. 2006). The water potential of each solution was measured with an osmometer (Vapro 5520El, Wescor). Filter paper within each petri dish was kept saturated with the appropriate aqueous solution of PEG throughout the experiment. To keep the concentration of PEG constant, each petri dish was firmly wrapped with adherent plastic foil. Germination was recorded daily until the seventh day and thereafter every third day until day 30.

The effect of seed storage time on germination of *R. baccifera* was evaluated using seeds that had been stored within amber bottles for periods ranging from 9 to 365 d. We used a fluorescent lamp (GE, cool white 20 W, PPFD = 2.92×10^1 μmol m^{-2} s^{-1}), and germination was recorded every third day until day 30.

Germination within Host Trees

To evaluate the effect of position within the tree crown on germination of *R. baccifera* seeds, three individuals of *Quercus germana* (Fagaceae) were selected in the humid montane forest adjacent to the Institute of Ecology. Four similar branches were chosen in each tree, and two positions were selected: close to the trunk and 2 m from the trunk on each branch. A small log of the same oak species, 3.2 cm in diameter on average (±0.83 SD) and 20 cm long and free of mosses and lichens, was placed at each of the two selected positions of *Q. germana*. On each of these logs, 90 *R. baccifera* seeds were glued in place with Resistol 850. Preliminary laboratory tests showed that this glue had no effect on the germination of *R. baccifera*. Likewise, Benzing (1990) and Toledo-Aceves and Wolf (2008) found no effect of glue on the germination of epiphytic bromeliads. In addition, at one end of each log, a lidless petri dish containing 90 seeds in agar was secured in order to identify the potential differences caused by substrate type (agar and log). We recorded the height, slope of branch, and canopy cover in all internal and external canopy positions. The canopy cover was calculated as the mean of four measurements, taken at the four cardinal points using a convex Spherical Crown densiometer, model A. These values were obtained while the leaves of *Q. germana* were present on the tree. In both internal and external positions within the canopy, temperature, and relative humidity were recorded every hour during October 6–9, 2007, using sensors 1000/16 (LI–COR) and HMP45A/D (Vaisala) connected to a LI–1000 data logger (LI–COR). The number of germinated seeds was recorded every 15 d from October to December, 2007, which included both the end of the wet season and part of the relatively dry and cold season of the year.

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Data Analysis

Because germination was measured as a ratio, it was appropriate to use generalized linear models (GLMs) that follow a binomial distribution (Crawley 2007). The number of seeds (25) in each petri dish was used as the denominator. To test whether the factors of light quality (4 levels), PPFD (13 levels), water potential (7 levels), and storage time (7 levels) affected the germination of *R. baccifera*, we used GLMs with one factor, analyzing the deviance in a manner similar to ANOVA. To reduce data overdispersion, GLMs were adjusted using a quasibinomial link. Differences between treatments were assessed using Tukey HSD multiple comparisons. Binomial logistic regression GLMs were fitted to describe the functional relationship between the proportion of germination and both water potential and storage time. The relationship between germination percentage and the amount of light could not be linearized by any transformation of data, so a nonlinear regression model was fitted to describe the functional relationship between both variables. To test the effect of the quality of light, water potential, and storage time on the speed of germination, parametric ANOVA models were applied. The germination speed was calculated according to Kotowski's coefficient of velocity: $\mathrm{KCV} = [\Sigma n_i / \Sigma(n_i t_i)] \times 100$, where n_i is the number of seeds germinated on day i and t_i is the number of days after sowing. KCV values range from 0 to 100, and a high value of KCV represents a high velocity of germination (González-Zertuche and Orozco-Segovia 1996).The germination speed data from the water potential and storage time treatments were adjusted for normality following the removal of data where no seeds germinated (−0.99 MPa and 365 d of storage, respectively). Differences in germination speed between treatments were assessed by Tukey HSD multiple comparisons (Zar 1999). The analysis of deviance of the ANOVA-type GLMs and Tukey HSD multiple comparisons of logistic regression and nonlinear regression were performed with the program R, version 2.6.1 (R Development Core Team 2007). ANOVA models and Tukey HSD multiple comparisons were performed using the program JMP, version 5.0.1a (SAS Institute). The threshold of significance in all cases was $P = 0.05$.

Results

Laboratory Germination

Rhipsalis baccifera seeds incubated in darkness germinated at a percentage close to 0, while germination was approximately 80% in the far red, red, and white light treatments; the differences in the proportion of seeds germinated in these light treatments were not significant (Tukey HSD multiple comparisons after analysis of deviance, $P < 0.001$; table 1; fig. 1*A*). The same effect was observed in germination speed, which was relatively high and showed no significant difference between far red, red, and white light treatments but was much lower in the darkness treatment (Tukey HSD multiple comparisons following ANOVA, $F_{3,16} = 11.19$, $P = 0.0003$; table 2*A*).

Germination was significantly affected by the PPFD (Tukey HSD multiple comparisons following analysis of deviance, $P < 0.001$; table 1; fig. 1*B*). The proportion of germinated seeds increased significantly, from 8% at 0 μmol m^{-2} s^{-1} to 78% at 1.35×10^1 μmol m^{-2} s^{-1}. Subsequent increases in PPFD did not significantly increase the proportion of seeds germinated.

Water potential significantly affected the proportion of germinated seeds (Tukey HSD multiple comparisons following analysis of deviance, $P < 0.001$; table 1; fig. 2*A*). The highest values of germination were found at high water potentials (88% and 74% in the 0 and −0.16 MPa treatments, respectively), decreasing gradually to 0 at a water potential of −0.99 MPa. Germination speed was relatively high at 0 MPa and also progressively decreased to 0 as water potential became more negative. (Tukey HSD multiple comparisons following ANOVA, $F_{5,21} = 14.02$, $P < 0.001$; table 2*B*).

Storage time significantly decreased the percentage of seed germination (Tukey HSD multiple comparisons following analysis of deviance, $P < 0.001$; table 1; fig. 2*B*). After up to 1 mo of storage, the germination of seeds was approximately 90%. This rate fluctuated around 70% after 3–6 mo storage, while seeds stored for a year did not germinate. Germination speed decreased gradually with increased storage time (Tukey HSD multiple comparisons following ANOVA, $F_{5,21} = 44.62$, $P < 0.001$; table 2*C*).

Germination in Host Trees

The dimensions and characteristics of the branches in the two canopy positions were similar ($P > 0.05$): diameter 0.50 m (SD = 0.129), inclination 36° (SD = 13.5), and height 6.39 m (SD = 1.62). However, weak but significant differences ($P < 0.05$) were registered in the canopy cover and vapor pressure deficit (VPD). The canopy cover was a little higher (91.98%, SE = 0.63) and the VPD was slightly lower (0.00021 MPa, SE = 0.00002) in the interior of the tree crown in comparison with the exterior position (canopy cover = 87.72%, SE = 1.04; VPD = 0.00024 MPa, SE = 0.00002). *Rhipsalis baccifera* had the ability to germinate in both the internal and external positions of the branches. It was observed that 39 seeds germinated on the exterior and 202 seeds germinated in the interior of the branch when seeded in agar, while 4 and 30 seeds germinated in the external and internal positions, respectively, when planted directly on the logs. However, a very high number of seeds (>81%) placed in the branches were lost due to the occurrence of heavy rains in the forest during the experiment; in consequence, it was not possible to estimate the differences between the numbers of germinated seeds in each position of the branch.

Discussion

The very low amount of light required for germination and the favorable germination rates demonstrated in red, far red, and white light, suggest that *Rhipsalis baccifera* has the potential for successful establishment on branches with varying degrees of shade. The capability to germinate at a low RFR ratio can facilitate germination at sites where humidity is available and predation is reduced (Benítez-Rodríguez et al. 2004). The positive photoblastism of *R. baccifera* supports the proposal of Flores et al. (2006), that cacti with small seeds (<1 mg) require light in order to germinate. However,

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Table 1

Analyses of Deviance for the Effects of Light Quality, Water Potential, Storage Time, and Photosynthetic Photo Flux Treatments on Seed Germination in *Rhipsalis baccifera*

Source	df	Deviance	*F*	*P* (>*F*)
Null	19	355.43		
Light quality	3	324.29	65.694	3.259^{-9}
Residual	16	31.14		
Null	34	622.95		
Water potential	6	523.63	26.963	2.067^{-10}
Residual	28	99.32		
Null	34	451.87		
Storage time	6	415.06		
Residual	28	36.802	49.636	1.217^{-13}
Null	64	898.54	P (>χ^2)	
PPFD	12	858.37	4.972^{-176}	
Residual	52	40.17		

Note. An *F*-like test instead of a χ^2 test was used for light quality, water potential, and storage time because the data showed overdispersion and a quasibinomial error was employed. PPFD = photosynthetic photon flux density.

small seeds of epiphytes from other families are not photoblastic: *Tillandsia brachycaulus*, *Tillandsia calcifanii*, and *Tillandsia elongata* (Bromeliaceae) have the ability to germinate both in light and in darkness (Graham and Andrade 2004; García-Suárez et al. 2006). On the other hand, positive photoblastism of *R. baccifera* may be linked to their phylogenetic origin as the light effect on inducing seed germination has been found for a good number of cactus species including various terrestrial globose, barrel-shaped, and columnar cacti species (Fearn 1981; Rojas-Aréchiga and Vázquez-Yanes 2000; Benítez-Rodríguez et al. 2004).

In common with the hemiepiphyte *Ficus aurea*, for which germination occurs on the trunks of trees (Swagel et al. 1997), *R. baccifera* showed a high germination rate (>74%) in substrates with water potentials of between 0 and −0.16 MPa, but the rate decreased to 0 at a water potential of −0.99 MPa. In the plant canopy, the germination of *R. baccifera* was between 4% and 18%, although many seeds were lost due to heavy rains. Epiphyte germination may decrease sharply as a result of factors that cause a lack of moisture in the tree crowns, such as exposure of the branches and the water absorption capacity of the tree bark (Benzing 1978; Hietz and Hietz 1995; Winkler et al. 2005). In the same study site in which this work was carried out, seeds of *Tillandsia deppeana*, *Tillandsia juncea*, *Tillandsia multicaulis*, and *Tillandsia punctulata*, exposed near the exterior of the tree crowns, took longer to germinate compared with seeds placed in the canopy interior (Winkler et al. 2005). Benzing (1978, 1981) found 35% germination of *Tillandsia circinnata* after 14 wk in a greenhouse but less than 4% in the field. Similarly, 92% germination has been reported in the laboratory for *Tillandsia eizii*, but there was only ~5% germination after 3 mo in the tree crowns (Toledo-Aceves and Wolf 2008). At low water potentials of close to 0 MPa, the germination speed of *R. baccifera* was similar to those reported for other terrestrial cacti of arid environments, such as *Neobuxbaumia macrocephala, Neobuxbaumia mezcalensis*, and *Neobuxbaumia tetezo* (Ramírez-Padilla and Valverde 2005). These three cacti species and *Mammillaria gaumeri*, *Stenocereus queretaroensis*, and *Stenocereus pruinosus* show higher percentages of germination in substrate water potential close to 0 MPa (De la Barrera and Nobel 2003; Ramírez-Padilla and Valverde 2005; Cervera et al. 2006; Guillén et al. 2009). However, the columnar cacti *Neobuxbaumia tetezo* and *Pachycereus hollianus* practically did not germinate at soil water potential of 0 MPa,

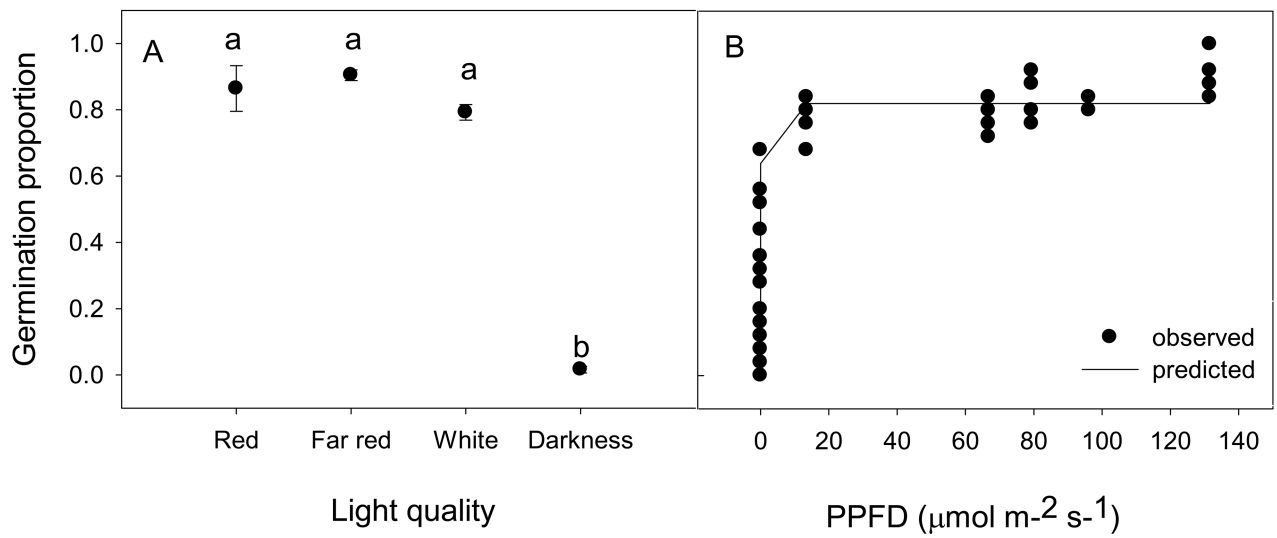

Fig. 1 Effects of light on germination of *Rhipsalis baccifera*. *A*, Germination under different conditions of light quality after 30 d. Data are means ± 1 SE; $n = 5$; different letters indicate significant differences between treatments. *B*, Relationship between PPFD and germination proportion. Data were significantly adjusted to a nonlinear regression model $(0.82106 + 0.7165\exp[-0.75194 \times \text{PPFD}(\mu\text{mol m}^{-2}\text{s}^{-1})])$, $P < 0.0001$; $n = 65$. PPFD = photosynthetic photon flux density.

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Table 2

Effect of Light Quality, Water Potential, and Storage Time on Speed of Germination of *Rhipsalis baccifera*

	Germination speed (%)
A. Light quality:	
Red	18.65 ± 2.71^{A}
Far red	20.10 ± 2.44^{A}
White	18.05 ± 3.73^{A}
Darkness	$1.33 \pm .81^{B}$
B. Water potential (MPa):	
0	21.02 ± 1.18^{A}
−.06	19.75 ± 1.69^{A}
−.16	13.89 ± 1.32^{AB}
−.37	15.27 ± 5.46^{AB}
−.58	15.87 ± 8.75^{BC}
−.77	3.66 ± 2.26^{C}
−.99	0^{D}
C. Storage time (d):	
9	24.44 ± 2.92^{A}
30	$13.64 \pm .49^{AB}$
90	8.16 ± 1.22^{C}
120	11.38 ± 1.08^{BC}
150	$9.69 \pm .86^{C}$
180	$8.95 \pm .36^{C}$
365	0^{D}

Note. Data are means ± 1 SE. Different letters indicate significant differences between treatments. $n = 5$.

while the maximum germination (47%–78%) was registered from −0.2 to −0.66 MPa for the first species and 94% at −0.41 MPa for the second (Flores and Briones 2001).

In *R. baccifera*, germination was greater in seeds which had undergone shorter lengths of storage time, and no germination was recorded in seeds after 365 d of storage. In the epiphyte *Tillandsia recurvata*, maximum germination has been measured at the opening of the capsules and for the subsequent 4 or 5 mo (Fernández et al. 1989). This is consistent with the proposal of Benzing (1990), who states that the viability of epiphyte seeds is extremely short and that they do not form seed banks. A number of cacti including globose and columnar terrestrial species seem not have the capacity to form seed banks in the soil because their germination rate is higher in fresh seeds than in old seeds (Fearn 1977; Flores et al. 2005, 2008). On the other hand, other cactus species remain viable for years and can form a soil seed bank because the seed germination is lower in fresh seeds than in old seeds or the germination is equal between fresh seeds and old seeds (Fearn 1977; Rojas-Aréchiga and Vázquez-Yanes 2000; Flores et al. 2005; Olvera-Carrillo et al. 2009). The response of the germination capacity of the seeds with the time is widely variable in the Cactaceae familiy (Fearn 1977; Rojas-Aréchiga and Vázquez-Yanes 2000; Flores et al. 2005). Maturity, seed coat characteristics, temperature and moisture fluctuations, fungi, bacteria, and insect infestation affect the longevity of seeds (Fearn 1981).

In conclusion, seeds of *R. baccifera* are photoblastic-positive, able to germinate at very low PPFD; they have no special requirements in terms of light quality, and they have the ability to germinate in both the internal and external positions of the tree crown. The germinative requirements of *R. baccifera* indicate that it could colonize in a wide range of light conditions in the plant canopy; however, substrate humidity and seed age could limit germination of *R. baccifera* within the humid montane forest.

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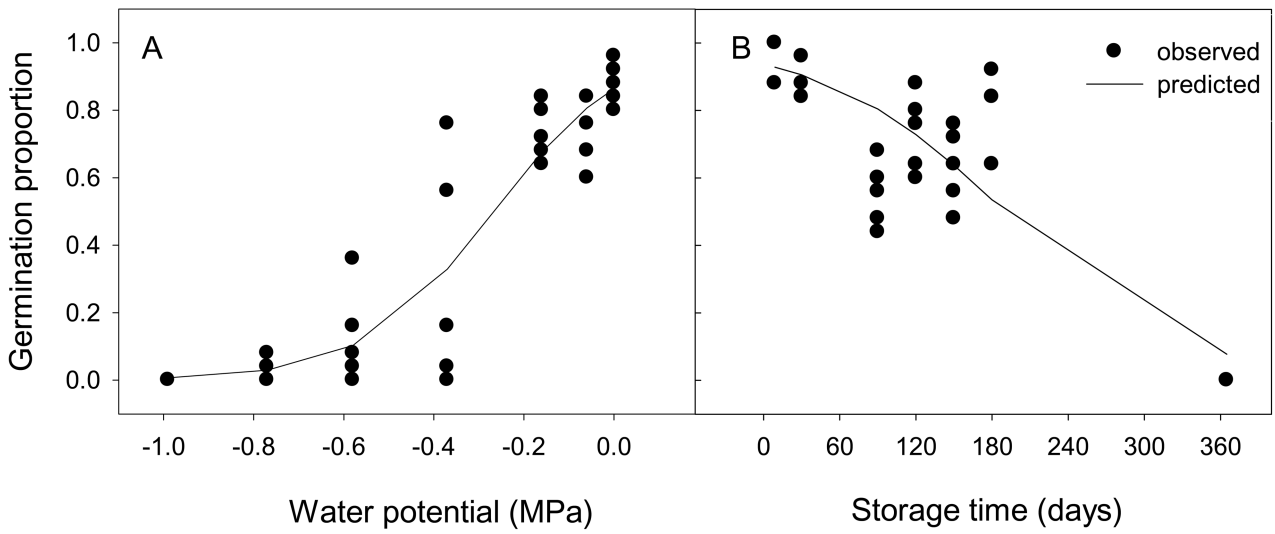

Fig. 2 Effects of water potential and storage time on germination of *Rhipsalis baccifera*. *A*, Relationship between water potential and germination proportion. Data were significantly adjusted to a binomial regression model ($1.846 + 6.92 \times$ water potential(MPa)), $R^2 = 0.82$, $P = 3.12^{-10}$; $n = 35$. *B*, Relationship between storage time and germination proportion. Data were significantly adjusted to a binomial regression model ($2.682–0.014$ time $\times (d)$), $R^2 = 0.67$, $P = 3.08^{-7}$, $n = 35$.

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