Journal of Arid Environments 73 (2009) 414–420

Contents lists available at ScienceDirect

Journal of Arid Environments

journal homepage: www.elsevier.com/locate/jaridenv

Effect of environmental heterogeneity on field germination of *Opuntia tomentosa* (Cactaceae, Opuntioideae) seeds

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ARTICLE INFO

Article history:
Received 20 September 2007
Received in revised form
11 June 2008
Accepted 16 December 2008
Available online 21 January 2009

Keywords:
Lava field
Physiological dormancy
Plant shade effect
Safe sites
Seed burial

ABSTRACT

We studied in *Opuntia tomentosa* the effect of plant shade (orientation and distance), and the place where the seeds remained before germination. Seeds were collected in 1998 and a) sown immediately on soil (non-buried seeds), b) stored in the laboratory and sown on soil during the 1999 rainy season (control) or c) buried after collection (under the shade of a tree, a rock and in an open space), exhumed 7 months later and sown in 1999 (exhumed seeds). Seeds were sown under or outside the shade of several trees; or on the northern, eastern and western sides of a 14-m-tall tree. In 1999, germination was high in all samples, but the control seeds had delayed germination. After two rainy seasons, non-buried seeds had the lowest germination rate. Germination was not affected by the distance from the tree. Outside of the plant's shade, germination was low. Germination was affected more by the environmental heterogeneity than by the individual plant shade. Germination probabilities were the highest at 16–19 °C; field germination was zero at 20.6 °C. Seed polymorphism and microenvironmental heterogeneity spread germination across two rainy seasons creating a permanent seed bank.

1. Introduction

After dispersal, seeds are exposed to a changing and heterogeneous soil environment which, by interacting with their morphological and physiological traits, determines seed viability and modifies seed dormancy, germination, and seedling success (Chambers and MacMahon, 1994; Vázquez-Yanes and Orozco-Segovia, 1994; Allen and Meyer, 1998; Baskin and Baskin, 1998). In this sense, the regulation of germination through seed dormancy and mechanisms to detect environmental signals are essential to maximize seedling establishment, particularly in arid environments. Morphological and physiological diversities among individuals and populations are also greatly relevant to the plant's response to discontinuous and unpredictable environments (Gutterman, 1993; Spicer and Gaston, 1999).

In the field, safe sites for germination and establishment are rarely contiguous (Harper, 1977; Murray, 1986; Crist and Friese, 1993). Shade plants (nurse effect) create safe sites for seeds and seedlings (Steenbergh and Lowe, 1969; Franco and Nobel, 1989; Valiente-Banuet and Ezcurra, 1991; Valiente-Banuet et al., 1991). Several studies on seed germination and early establishment of cacti emphasize the protection that 'nurse' plants provide against high solar radiation and the consequent extreme variation in temperature and soil moisture (Méndez et al., 2004; Zúñiga et al., 2005; Suzán-Azpiri and Sosa, 2006).

Opuntia tomentosa Salm-Dyck (cactus pear) is a cactus distributed in the Central Plateau and south-western México (Guzmán et al., 2003). In the Valley of México, it is typical of the xerophilous vegetation that grows on lava fields, which are characterized by an irregular distribution of plants, exposed rocks, plains, pockets and crevasses with accumulated soil among the rocks. The vegetation has been defined as open deciduous shrubland with abundant grasses and isolated small trees (Rzedowski, 1994). Although climate in the area is not strictly typical of the arid zone, water is restricted because of excessive percolation caused by the rock's structure and the low water retentivity of the shallow soil. The microtopography, the seasonal climate, temperature and soil moisture, soil depth and vegetation structure and distribution make this area a heterogeneous, changing, and discontinuous habitat.

Seeds of *O. tomentosa* exhibit deep physiological dormancy (Orozco-Segovia et al., 2007); embryos are too weak to protrude

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0140-1963/$ – see front matter © 2008 Elsevier Ltd. All rights reserved.
doi:10.1016/j.jaridenv.2008.12.012

through the hard funicular envelope that surrounds the seed and, although those seed covers are permeable, funicular envelope hardiness also restricts water uptake. Formation of a germination valve in the funicular envelope is also required for germination (Orozco-Segovia et al., 2007). Additionally, the seeds are morphologically and physiologically heterogeneous, and so is their response to soil factors (Olvera-Carrillo et al., 2009), which suggests that *O. tomentosa* seeds may remain in the seed bank for a year or more or until conditions are adequate for germination, as has been suggested for other cacti species as well (Mandujano et al., 1998; De Viana, 1999; Bowers, 2000; Montiel and Montaña, 2003; Bowers, 2005).

This study was designed to test a) the effect of environmental heterogeneity (the layer of soil where seeds are deposited and potentially safe sites for germination) on seed germination through two successive rainy seasons after seed dispersal and b) the possibility of *O. tomentosa* forming a permanent seed bank. We hypothesized that germination and/or incorporation into the seed bank in *O. tomentosa* is determined by the environment the seeds experience before germination, the quality of sites safe for germination provided by any shade plant (governed by the orientation with respect to and distance from the shade plant), physiological and morphological polymorphism within seed population, and the interaction of all these.

2. Materials and methods

2.1. Study site and plant material

Fieldwork was carried out at the "Pedregal de San Ángel Ecological Reserve" (19°19′N, 99°11′W) in the southern region of México City, 2240 m above sea level. Mean annual precipitation is 803 mm and mean annual temperature is 15.5 °C (Rzedowski, 1994). In spite of this precipitation, the vegetation in the area is an open xerophilous shrubland characterized by *Muhlembergia robusta* in the herbaceous stratum, *Senecio praecox*, *Verbesina virgata*, *Eupatorium* spp. and others, in the shrubby stratum; there are also isolated trees of *Buddleia cordata*, *Wigandia urens*, *Dodonaea viscosa* and several legumes which can also be found as shrubs (Cano-Santana and Meave, 1996, Castillo-Argüero et al., 2004). *O. tomentosa* is established mainly in the shallowest soil, where >50 °C can be registered during winter on the soil surface (Olvera-Carrillo, 2001). Daily temperature fluctuation and precipitation, and mean, minimum, and maximum temperatures during the study are shown in Fig. 1a and b.

Three hundred ripe fruits were collected in September and October 1998 (end of rainy season) from 12 adult plants of *O. tomentosa*. A typical ripe fruit contains on average 80 ± 9 (SD) seeds, each of which weighs 16 ± 1 mg (Olvera-Carrillo et al., 2003). The seeds were removed from the fruit, washed with tap water, mixed, dried, and stored for one week in paper bags in the laboratory (23–25 °C, 20–50% relative humidity). Chronological events from seed collection to seed germination are shown in Table 1.

2.2. Seed burial and treatments

In November 1998, the seeds were buried 10 cm deep in the soil (to avoid seed predation), placed inside double-layered nylon bags (25 × 25 cm) within a plastic mesh bag (30 × 30 cm), at three contrasting and representative locations at the Pedregal Ecological Reserve: 1) under the canopy of a *B. cordata* H.B.K. tree (T), 2) in open space covered with herbaceous vegetation (O), and 3) under the shade of a 2-m-tall rock (R). All seeds were retrieved 7 months later (June 1999) and air-dried in dark, at 23–25 °C, 20–50% relative humidity, for three days.

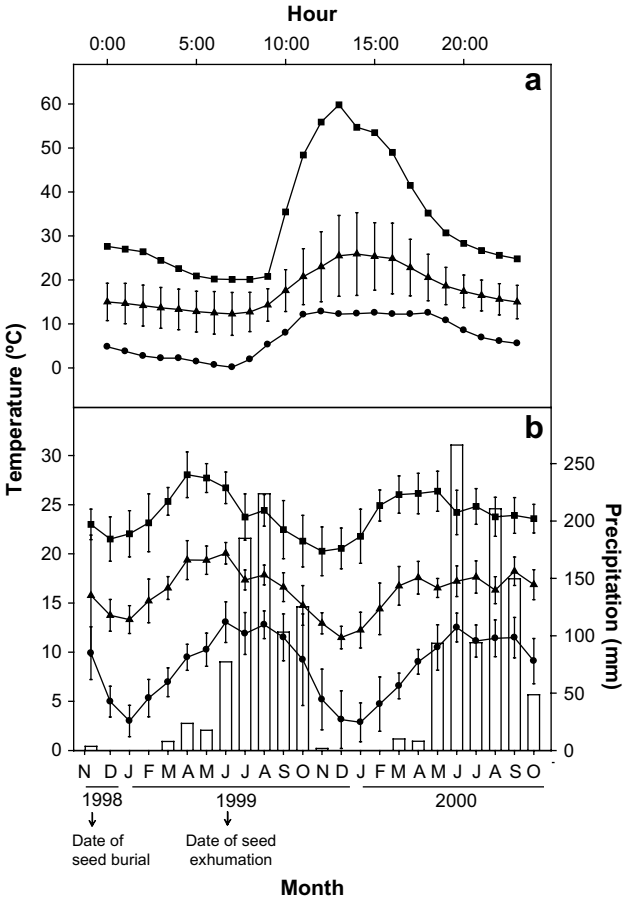

Fig. 1. (a) Daily and (b) monthly mean (▲), maximum (■) and minimum (●) temperatures and precipitation during the study years at the El Pedregal de San Ángel reserve. Standard deviations are indicated.

Treated seeds were sown as follows: 1) in November 1998, at the beginning of the dry season, seeds were sown in the field on the soil surface (non-buried seeds); 2) in June 1999, seeds stored for 8 months in the laboratory (from collection to the beginning of the following rainy season) were sown in the field (control seeds); and 3) seeds buried for 7 months in three burial locations were dug up and sown in June 1999 (exhumed seeds T, O, and R). The seeds were sown in pots (9 cm in diameter and 5 cm tall) containing 3 cm of sterilized soil from the Pedregal de San Ángel. Each pot was made of cloth and the seeds were placed in a cage to protect them against predation (cage: 25 cm × 25 cm × 10 cm, with 0.2 cm^2 opening). In the sites described below, the bottom of the pots was buried 3 cm deep in the soil. Each treatment (non-buried seeds sown in 1998 or 1999, T, O, and R) comprised 21 pots – a total of 105 pots – containing 30 seeds each. The emergence of the hypocotyl was regarded as successful germination, recorded every other day during the rainy seasons of 1999 and 2000.

2.3. Germination sites

Trees and shrubs growing at the study site were randomly chosen as possible shade providers (safe sites). Because of the heterogeneity in the substrate and vegetation structure, the criteria used to select shade-providing plants were adequate plants' size and substrate's microtopography to place the pots - without a doubt - in the positions indicated below. The shade-providing plants were: a) *B. cordata* (6 m tall) and *S. praecox* D.C. (4 m),