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Survival and early growth of two congeneric cacti that differ in their level of rarity

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ABSTRACT

In this paper we analyze the growth and early survival of two congeneric columnar cacti: the rare *Neobuxbaumia macrocephala* (with low population densities and a narrow distribution range), and the relatively common *Neobuxbaumia mezcalaensis* (with dense populations and a broader distribution range). Seeds of both species were germinated and seedlings were subjected to different radiation, nutrient and watering treatments in greenhouse conditions for six months. By the end of the experiment seedling average dry mass was similar in both species. Recently emerged seedlings of *N. macrocephala* were smaller than those of *N. mezcalaensis*; however, *N. macrocephala* showed higher relative growth rates (average RGR = 0.0138 mg/mg/day) than *N. mezcalaensis* (average RGR = 0.0126 mg/mg/day). For both species RGR decreased in the shade. Root:shoot ratio (*R/S*) and *K* were higher in *N. mezcalaensis* than in *N. macrocephala* and showed an increasing trend as water availability decreased. Seedling survival was followed in natural conditions for nine months. The survival of *N. mezcalaensis* was significantly higher compared to *N. macrocephala*. In both species a slightly higher seedling survival was observed under the shade of nurse plants. The two species displayed different growth and survival responses, which accounts to some extent for their contrasting level of rarity.

1. Introduction

The study of rarity as a biological phenomenon is at the core of ecological thinking, because it is unavoidably linked to our understanding of abundance and distribution patterns in nature. Additionally, understanding rarity is important also from the perspective of conservation ecology, as rare species have higher extinction probabilities than common ones and most endangered species show some degree of rarity (Gaston and Kunin, 1997).

The most widely used definition of rarity for plants has been based on three main components: abundance, distribution range and habitat specificity (Rabinowitz, 1981). Esparza-Olguín et al. (2005) proposed that different theoretical frameworks may be used when studying each of these rarity attributes: a) demographic analyses may aid in the study of population numbers; b) metapopulation theory may be useful in offering an understanding of a species' geographic distribution range; and c) habitat specificity may be understood by analyzing the species' ecophysiological traits, especially during the early life-cycle phases. Indeed, germination rates and seedling establishment success have been listed among the biological features that may determine the level of rarity of a species (Fiedler and Ahouse, 1992; Bevill and Louda, 1999). Clearly, given that no dispersal limitations exist, the reasons why a species is present or absent from a certain site are closely linked with the conditions under which seedlings establish most successfully and grow at a faster rate (Bowman and Panton, 1993; Cantin et al., 1997; Cleavitt, 2002; Shimono and Kudo, 2003); thus, analyzing the early survival and growth responses of seedlings to different environmental factors is a central issue in the understanding of rarity. In this paper we analyze the growth responses of two congeneric cacti with contrasting degrees of rarity to different environmental variables, and relate their growth responses to their early survival patterns in natural conditions.

Even though rarity is increasingly recognized as an idiosyncratic and multi-factor phenomenon, the search for general patterns among rare plants is still an important research field, as the documentation of recurrent differences between rare and common plants may allow us to deepen our understanding of rarity and partially compensate for the bias of the published literature toward studies of common taxa (Kunin and Gaston, 1993). In particular, the comparative analysis of closely related species with differing levels of rarity has been a fruitful approach in this field (Bevill and Louda, 1999 and references therein; Gaston and Kunin, 1997; Cleavitt, 2002; Esparza-Olguín et al., 2005; Murray et al., 2005; Ramírez-Padilla and Valverde, 2005; Rodríguez-Pérez, 2005). This approach is based on the premise that the differences between closely related species are not due to lineage effects because they are supposed to have originated relatively recently and have evolved in response to natural selection (Harvey and Pagel, 1991).

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It has been proposed that rarity is not evenly distributed among plant families (Gentry, 1986; Fiedler and Ahouse, 1992). While some authors have shown that ancient families tend to have more rare taxa than recent families, other authors have documented differing patterns on different floras (Edwards and Westoby, 2000). Although the Cactaceae is a family of relatively recent origin (ca. 30 million years ago – Hershkovitz and Zimmer, 1997), it certainly contains a high proportion of rare taxa. Yet, the study of rare-common pairs of related species has been an uncommon approach in the study of rarity among cacti; in fact, we know of only three published studies on this area (Esparza-Olguín et al., 2005; Ramírez-Padilla and Valverde, 2005; Ruedas et al., 2006).

Cacti share a number of features in relation to seedling survival and growth. In general, they show low individual growth rates (Steenbergh and Lowe, 1969; Ruedas et al., 2000; Godínez-Alvarez et al., 2003), which determines that seedlings remain vulnerable for long periods of time and makes them prone to high seedling mortality rates, especially as a result of desiccation and predation (Godínez-Alvarez et al., 2003). The stressful conditions that prevail in the arid and semi-arid regions where most cacti are distributed exert limitations to seedling recruitment and often restrict their establishment to microsites under the shade of nurse plants (Godínez-Alvarez et al., 2003; Valverde et al., 2004). Thus, drought is an important abiotic factor contributing to the high seedling mortality observed in many cactus species; in fact, it is thought that species-specific responses to drought are important determinants of their apparent preference for particular edaphic conditions (Ruedas et al., 2006). Although drought is buffered under the shade of nurse plants, the associated decrease in solar radiation (and the concomitant reduction in photosynthetic rate) represents an additional challenge for growth (Martínez-Berdeja and Valverde, 2008). A further strain that cacti seedlings must face is the low nutrient level characteristic of many desert soils. Although slow growing species are generally assumed to be rather indifferent to changing nutrient levels (Chapin et al., 1993), some cacti have shown to be highly responsive to them (Ruedas et al., 2000). Again, the strength of nutrient limitation may decrease under the shade of nurse plants (as the litter produced by them enriches the soil – Nobel, 1980), and also when water availability increases, thus enhancing nutrient availability. Clearly, the effect of the different environmental variables affecting cacti growth is factorial, as they vary simultaneously in time and space.

While these common features may account for similarities in the population dynamics of cactus species, differences in the responses of rare and relatively more common species to their environment may explain variation in their abundance, extent of distribution range, or habitat specificity. In this study we analyze the early survival and growth of two *Neobuxbaumia* species, a rare and a relatively common one, to contribute to our understanding of the factors that determine their differing level of rarity. We conducted a greenhouse experiment to evaluate seedling growth in response to different levels of radiation, watering frequency and nutrient availability, using a factorial design. The latter is an important feature of our experimental approach, as it opens the possibility of evaluating the effect of each factor in isolation, and of the interaction among factors. Additionally, we established an experiment in the field to compare seedling survival in microsites with different levels of shade and evaluate the degree of seedling dependence on the presence of nurse plants. In the field, the two species studied show association with a variety of nurse plants (Ruedas et al., 2006).

2. Materials and methods

2.1. The species studied

a) *Neobuxbaumia macrocephala* (Weber) Dawson is a branched columnar cactus that reaches between 3 and 15 m in height in its adult stage. Between March and July, it produces red–purple flowers on the tip of branches; reproductive branch tips produce a reddish cephalium from which flowers emerge. Flowers are bat pollinated, and seeds (ca. 2.5 mm in diameter and weighting ca. 0.9 mg) are dispersed by bats and birds between April and August Valiente-Banuet et al. (1997). *N. macrocephala* grows in xerophytic shrublands on calcareous soils at altitudes between 1600 and 2300 m and is endemic to the Tehuacán Valley in the state of Puebla. Population densities vary between 130 and 200 individuals per hectare (Ruedas et al., 2006). Here, this species is considered the rarest of the two.
b) *Neobuxbaumia mezcalaensis* (Bravo) Backeberg is an unbranched columnar cactus that may reach between 3 and 14 m in height. Its flowers emerge along the stem between March and May and are white (occasionally green-red) with nocturnal anthesis; they are pollinated by bats. Seeds (ca. 2.5–3 mm in diameter, and weighting 6.0 mg) are dispersed by bats and birds between May and June Valiente-Banuet et al. (1997). This cactus species grows in thorny forests, xerophytic shrublands and tropical dry forests on calcareous soils. It is commonly found at altitudes between 800 and 2000 m, with a geographic distribution range that covers the whole of the Tehuacán-Cuicatlán region (Mexican states of Puebla and Oaxaca), as well as the river Balsas basin (on the southwest of Mexico). Populations are dense, with 1000–17,000 individuals per hectare (Ruedas et al., 2006); thus this species is considered as common.

2.2. The study site

The study consisted of two parts: the first one was carried out in a greenhouse in Mexico City, whereas the second one was a field experiment conducted in the valley of Tehuacán, near Zapotitlán Salinas (18° 20′ North, 97° 28′ West), in the Mexican state of Puebla. This is a semi-arid region covered by a highly diverse xerophytic shrubland. For a detailed description of the area see Valiente-Banuet and Ezcurra (1991), Esparza-Olguín et al. (2002, 2005) and Ruedas et al. (2006).

2.3. Seedling growth analysis in the greenhouse

Seeds of *N. mezcalaensis* and *N. macrocephala* were collected from nine adult individuals per species in June, 2002. After removing them from fruit tissues, seeds were stored in darkness and at room temperature in sterilized glass bottles. In January 2003 (six months after collection) 300 seeds of each species were sown in a tray filled with a 1:1 mixture of tepojal (volcanic sand) and vermiculite. Trays were maintained in a growth chamber with a constant temperature of 25 °C and a photoperiod of 16:8 h (light-dark).

Seed germination took place during the first five days after sowing. Twenty days after germination, 120 seedlings per species were transplanted to 7 × 7 × 6 cm plastic pots (one seedling per pot) filled with the same soil mix described above (the same amount of soil was placed in each pot). Additionally, 15 seedlings per species were harvested, oven dried (at 80 °C for 48 h), and weighted (root and shoot separately) to obtain their dry mass values; these were considered the initial harvest (W_1). The rest of the seedlings (120 per species) were taken to a greenhouse (in Ciudad Universitaria, UNAM, Mexico City) where the growth experiment was conducted.

Immediately after transplanting the seedlings, 55 ml of Peter's nutrient solution (9% N, 45% P and 15% K) were added to each pot. After a 15-day period of acclimatization in the greenhouse, 15 seedlings per species were allocated randomly to each of eight experimental treatments composed from the combination of three