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Research article

Environmentally dependent expression of heritable variation on early recruitment traits induced by light conditions and provenance in the columnar cactus *Pilosocereus leucocephalus*

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ABSTRACT

Response to selection depends on heritable genetic variation, which is affected by environmental conditions. The present study experimentally assessed whether the effect of light-related stress and the attenuating effect of shade as a facilitator of seedling germination, survival and growth affect the expression of heritable variation and the potential for a response to selection in the columnar cactus *Pilosocereus leucocephalus*. A reciprocal transplant experiment combined with the artificial manipulation of light/shade conditions within greenhouses was performed using seeds from controlled crosses of two natural populations (demes PN and SI). Additive genetic variance (V_A), heritability (h^2) and the coefficient of variation of additive variance (CV_A) were estimated for per cent of germination, per cent of seedling survival and growth (biomass) under each treatment combination. Although all three recruitment traits showed evidence of different from zero heritability, this result was highly dependent upon the particular transplant site, deme and light treatment combination. The deme that is still not locally adapted (SI) showed significant heritability for all traits and much more potential for a response selection as indicated by a higher CV_A than the locally adapted deme PN. The effect of light conditions on the expression of V_A, h^2 and CV_A depended on whether the deme was grown in its native or an alien site, but this interaction was only detected for the less adapted deme of SI. Shade conditions promoted by facilitation reduced the evolutionary potential for germination of both demes through an attenuation of genetic differences among genotypes.

Introduction

Evolutionary changes (**R**) driven by natural selection rely on both the intensity of selection (β) and the amount of heritable variation (h^2) in the target trait ($\mathbf{R} = \beta \times h^2$) (Lande, 1979). Both components of the response to selection equation are also sensitive to environmental conditions (Hoffmann and Parsons, 1991; Bennington and McGraw, 1996; Falconer and Mackay, 1996; Fornoni et al., 2003; Strauss et al., 2005), although these effects depend on the particular environmental agent of selection and target trait (Stinchcombe and Rausher, 2001; Carmona and Fornoni, 2013; Charmantier et al., 2014). However, several laboratory studies concluded that environmental stressors increase heritability (h^2) in quantitative characters (Hoffmann and Merilä, 1999; Bubliy et al., 2003; Swindell and Bouzat, 2006). Thus, any physical or biotic environmental factor that reduces the intensity of the stress experienced by a population would affect its evolutionary potential. This hypothesis is consistent with the observation that adaptive novelties usually arise after environmental changes when organisms experience low to moderate levels of stress (Badyaev, 2005).

Positive interactions among plants, like facilitation, are more prevalent under stressful conditions (He et al., 2013) due to the benefit of attenuating the impact of physical and biotic stressors (Bronstein, 2009; Maestre et al., 2009; Ariza and Tielbörger, 2011; García-Cervigón et al., 2013). If heritability increases under

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stressful environmental conditions, nurse plants would reduce this effect on the species benefited by facilitation by constraining their evolutionary response to selection. Despite recent discussions on the evolutionary consequences of facilitation, its direct effect on the adaptation process to stressful environments is still poorly understood (Liancourt et al., 2005; Espeland and Rice, 2007, 2012; Ariza and Tielbörger, 2011; Miranda-Jácome et al., 2013).

The hypothesis that stress increases heritability considers that stressful conditions represent a novel environment for populations; hence, the time and intensity of exposure to the stressor will also determine the magnitude of its effect on heritable variation (Hoffmann and Merilä, 1999; Espeland and Rice, 2007). The extent of local adaptation of populations (either to favourable or unfavourable conditions) also account for the amount of heritable variation, as selection is expected to remove alleles with low fitness. Locally adapted populations will have eroded genetic variation for fitness-related traits, reducing the chances that what was initially a novel (stressful) condition will have a higher genetic variation than more benign environmental conditions (e.g. Espeland and Rice, 2007). Hence, whereas natural selection is expected to reduce the amount of genetic variation, stressful conditions are expected to increase the expression of genetic differences among genotypes. Although rarely controlled, limiting stressful conditions are not always equivalent to novel environments. To date, there have been few if any attempts that took into account whether populations are locally adapted or not to understand how stress affects the expression of heritable variation and the consequences for a response to selection (see Swindell and Bouzat, 2006).

In this study, we tested the hypothesis that shade conditions promoted by facilitation reduce the potential evolutionary response to selection of populations (under stressful environments, diminishing genetic differences among plant genotypes. The hypothesis was tested controlling for the extent of local adaptation of populations following a reciprocal transplant experiment in which a specific stressor (light availability) was manipulated. The columnar cactus *Pilosocereus leucocephalus* (Polselg.) Byles & G.D. Rowley was used as the studied system because it grows throughout the dry forests of Eastern Mexico across a gradient of light exposure during recruitment. In this species, reduction in sunlight incidence provided by nurse plants has a positive effect on recruitment (Miranda-Jácome et al., 2013). A recent study in this species experimentally demonstrated different levels of local adaptation between two demes due to light conditions induced by the presence/absence of facilitation (Miranda-Jácome et al., 2013). This study performed a reciprocal transplant experiment combined with the artificial manipulation of light conditions simulating the presence/absence of one component mediating facilitation during recruitment (Miranda-Jácome et al., 2013). In the present study, we extended previous analyses to include the effect of a paternal half-sib family source of variation to describe the pattern of the environmentally dependent expression of heritable genetic variation. The specific goal of the study was to estimate and compare the additive genetic variance, heritability and the coefficient of variation of additive variance on per cent of germination, per cent of early survival and early seedling growth (biomass) between two demes of the columnar cactus *P. leucocephalus* grown under contrasting light conditions (full sunlight and shade) and transplant sites. When heritability differs significantly from zero, the coefficient of variation of additive variance represents a standardised estimate for comparison among populations of the opportunity for selection (Houle, 1992; Espeland and Rice, 2012).

Materials and methods

Species and study site

P. leucocephalus (Cactaceae) is a bat-pollinated, hermaphroditic, self-incompatible columnar cactus (Munguía-Rosas et al., 2010) distributed from Nicaragua to northeast Mexico (Guzmán et al., 2003). Within the study site in the state of Veracruz (Mexico), this species is distributed along dry forests from 50 to 1200 m a.s.l. (Bravo-Hollis, 1937). Plant material for the experiment was gathered from two geographically isolated sites represented by the populations (hereafter deme) of San Ignacio (SI) (19° 35′ 26″N, 96° 58′ 38″W) and Puente Nacional (PN) (19° 20′ 37″N; 96° 28′ 05″W). The SI deme is located 70 km away from the other site, at 1150 m a.s.l., over a rocky substrate of lava flows deposited during the Holocene, around 10,000 years ago (Negendank et al., 1985). At this site, the mean annual temperature is 20.4 °C (means of the hottest and coldest months, May and January, are 29.2 °C and 11.5 °C, respectively), and annual precipitation is 1300.0 mm, with 79.1% of the rain concentrated between May and October (Fernández-Eguiarte et al., 2012; period 1903–2010). A detailed description of both plant communities can be found elsewhere (Miranda-Jácome et al., 2013). The PN deme is located within a dry forest at 87 m a.s.l., with a mean annual temperature of 25.91 °C (means of the hottest and coldest months, May and January, are 34.6 °C and 16.3 °C, respectively), and annual precipitation is 1144 mm (92.1% of rainfall is between May and October) (Fernández-Eguiarte et al., 2012; period 1903–2010). At this site, vegetation covers 93.8 ± 5% of the soil surface (Miranda-Jácome et al., 2013).

Genetic material

In December 2008, a sample of 27 parental plants (branches of less than 1.5 m long) were harvested from each studied site and transplanted to a common garden within the locality of Puente Nacional. Plants were watered every three days to ensure survival. When flowering started (April 2009), each of the nine parental plants were randomly selected to function as pollen donors (sire) and manually cross-fertilised with two other plants (dams) within each population following a North Carolina I breeding design (Lawrence, 1984). Each maternal plant was crossed with only one of the nine pollen donors. This crossing design was repeated for two sets of nine pollen donors each corresponding to the selected populations for this study. In May and June 2009, fruits were harvested and seeds were used in a reciprocal transplant experiment.

Reciprocal transplant experiment

The seeds were washed to eliminate mucilage and then air-dried and stored in paper bags at 25 °C. The experiment involved two demes (SI and PN), two sites (SI and PN) and two treatments (full sunlight and shade conditions) (hereafter light treatment). For this experiment, seeds from each deme were grown in both sites and under both treatments under greenhouse conditions specifically constructed to simulate full sunlight and shade conditions. Within each greenhouse and light treatment, pots were randomly located. Because the plants were grown in pots filled with soil from mixed soil samples collected at both transplant sites, we controlled for possible soil effects in our results. Following this design, we were not able to test for local adaptation to edaphic conditions. Also, because herbivory was eliminated within the greenhouses through the application of insecticide, this source of variation was also controlled. Given that our study sites correspond to areas of natural vegetation, we reduced possible disturbances caused