Acta Oecologica 71 (2016) 52–60

Contents lists available at ScienceDirect

Acta Oecologica

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

Original article

Pulse seedling recruitment on the population dynamics of a columnar cactus: Effect of an extreme rainfall event

Gabriel Arroyo-Cosultchi [a, c], Jordan Golubov [a, *], María C. Mandujano [b]

[a] Departamento El Hombre y su Ambiente, Laboratorio de Ecología, Sistemática y Fisiología Vegetal, Universidad Autónoma Metropolitana Xochimilco, Calzada del Hueso 1100, Col Villa Quietud, 04960, México DF, Mexico
[b] Instituto de Ecología, Universidad Nacional Autónoma de México (UNAM), Departamento de Ecología de la Biodiversidad, Laboratorio de Genética y Ecología, Apartado Postal 70-275, Ciudad Universitaria UNAM, 04510 México DF, Mexico
[c] Doctorado en Ciencias Biológicas y de la Salud, Universidad Autónoma Metropolitana, Mexico

ARTICLE INFO

Article history:
Received 1 October 2015
Received in revised form
11 January 2016
Accepted 14 January 2016
Available online 28 January 2016

Keywords:
Elasticity
Establishment
Matrix population models
Seed-seedling limitation

ABSTRACT

Demographic studies on the Cactaceae have highlighted several threats which are clearly human induced (e.g., disturbance) or intrinsic to their biology (e.g., infrequent recruitment). Most demographic studies suggest that early life stages of germination and seedling recruitment are crucial and often a limitation for population growth. The population dynamics of *Neobuxbaumia polylopha* (DC) Backeb. was modeled for a three-year period to assess the contribution of the early life cycle stages on population growth rate (λ). Two annual size-classified matrix population models were constructed for standard analysis, applied a life table response experiment (LTRE) analysis to explore the contributions of demographic processes, plant size, and temporal variability (years) to λ, and changes in the matrix elements were simulated including a seed bank, and seed-to-seedling transition using observed and experimental data. The population growth rates for 2012–2013 and 2013–2014 were 0.9916 (0.9906–0.9929) and 1.0216 (1.011–1.0280) respectively, suggesting two opposite growth rates for the studied period. The increase in λ in 2013–2014 was driven primarily by the increased growth and seedling recruitment and survival of small individuals. The rate of recruitment was higher in 2013–2014 with a left-skewed stable size distribution. Elasticity values were high for matrix entries corresponding to individuals remaining in the same category (stasis), followed by growth, retrogression and fecundity. The simulations show that the seed bank has a minor effect in comparison with the seed-seedling transition which became the population bottleneck under the assumption that seeds are not limited, so programs designed to preserve *N. polylopha* populations must focus on seedling establishment.

1. Introduction

Arid environments pose limiting conditions for species because of the extreme temperatures and unpredictable precipitation. As a consequence of the high variation in environmental conditions, plant life cycles are determined by pulse or interpulse years of rainfall that have directs effect on population growth rates (Huxman et al., 2004; Reynolds et al., 2004; Bullock et al., 2005; Holmgren et al., 2006). Unpredictable environmental conditions usually lead to an increase in dormant stages of the life cycle, reduction in individual growth, recruitment pulses, and substantial fluctuations in demographic traits such as population size, size structure, stage of reproductive maturation, contribution of sexual or clonal reproduction, generation time and population growth rate (Mandujano et al., 1997; Godínez-Álvarez et al., 2003; Méndez et al., 2004; Ferrer-Cervantes et al., 2012; Salguero-Gómez et al., 2012; Pierson et al., 2013).

The population dynamics of many cactus inhabiting semi-arid environments are often dominated by the survival of adults, vulnerable early stages of development and, in particular, the recruitment of seedlings as a relatively infrequent event (Jordan and Nobel, 1979; Esparza-Olguín et al., 2002; Godínez-Álvarez et al., 2003; Pierson et al., 2013). The presence of seedlings in semiarid environments is often attributed to favorable climatic and microclimatic conditions (Pierson and Turner, 1998; Coles et al., 2012; Pierson et al., 2013). These often occur with intense rains caused by hurricanes, tropical cyclones, *El Niño/La Niña* cycles or

* Corresponding author.
E-mail addresses: gcosultchi@gmail.com (G. Arroyo-Cosultchi), gfjordan@correo.xoc.uam.mx (J. Golubov), mcmandu@ecologia.unam.mx (M.C. Mandujano).

http://dx.doi.org/10.1016/j.actao.2016.01.006
1146-609X/

floods that generate sufficient soil moisture and at sufficient depth to generate a significant biological response such as recruitment and seedling survival (Bowers, 1997; Reynolds et al., 2004; Holmgren et al., 2006). In addition to seedling survival, the excess moisture benefits other stages of the life cycle by increasing reproduction, growth and survival (Mandujano et al., 2001; Cruz and Pavón, 2013) but may also be harmful by increasing root rot and toppling from excessive water-logged tissue or might not have a significant effect (Drezner, 2004; Drezner and Lazarus, 2008).

Demographic projection matrix models have been used to explore the potential fate of a population under different scenarios, as well as the evaluation of the relative contributions of the demographic processes occurring in different life cycle stages (de Kroon et al., 1986; Silvertown et al., 1993; Caswell, 2001). Published demographic studies on the Cactaceae using these models have increased drastically in the last decade (review in Godínez-Álvarez et al., 2003), although quantitative demographic trends, particularly among endangered cactus species are still lacking. Of the ca. 60 cacti species listed in CITES appendix 1 (35 which are found in Mexico), a handful (7%) have had formal demographic studies (Martínez-Ávalos, 2007; Mandujano et al., 2007a; Valverde and Zavala-Hurtado, 2006; Portilla-Alonso and Martorell, 2011; Coles et al., 2012). For columnar cactus, of the ca. 70 species, only 10 have been studied, and of these, seedling recruitment has consistently been estimated through laboratory or field experiments as all studies have consistently failed to find evidence of seedling recruitment in natural conditions. Scarce seedling recruitment is usually ascribed to either seed and/or seedling limitation and the lack of suitable environmental conditions for these phases of the life cycle. Other key life stages such as seed longevity and the presence of transient of persistent seed banks have only barely been studied even though they represent a buffering mechanism to environmental variability (Valverde and Zavala-Hurtado, 2006).

The population dynamics of *Neobuxbaumia polylopha* (DC) Backeb was analyzed for one of the nine species in the genus (Guzmán-Cruz et al., 2003) over a three year period to: 1) estimate population growth rate (deterministic and stochastic) under two contrasting rainfall regimes (abnormally dry and wet), using population projection matrix models, 2) contrast the demographic implications of natural and experimental seed-seedling transitions on the intrinsic population growth rate (λ) and 3) assess the relative contribution of the early stages of the life cycle using prospective and retrospective analyses and matrix simulations.

2. Methods

2.1. Species and study site

N. polylopha (DC) Backeb is listed as Vulnerable by the World Conservation Union (IUCN, 2014), monopodial columnar cactus, juveniles are unbranched, whereas some adults (approx. 15%) can develop lateral branching and may reach 13 m in height. Flowers are dark-red and emerge along the stem beginning wet season from May to July, 4–6 cm long, with nocturnal anthesis and remain open until midday (Anderson, 2001; Arroyo-Cosultchi et al., 2010). The fruit is 2.4–4 cm long, reddish and dehiscent that matures 2–3 months after pollination (Anderson, 2001). *N. polylopha* is a rare cactus that grows in canyons on calcareous soils in deciduous forests and occurs in six isolated populations (extent of occurrence of approx. 6000 km^2, IUCN, 2014). Commercially, individuals are valued in the horticultural industry and biogeographically it is one the northernmost representatives of the genus *Neobuxbaumia* (Anderson, 2001; Guzmán-Cruz et al., 2003). The study was carried out in central Mexico (between 20°43′32.8″N and 98°54′56.9″W, 967 m a.s.l). Within the Barranca of Metztitlan Biosphere Reserve, an intertropical semiarid environment which is biologically important because it its high degree of endemism and functions as a corridor between the northern Neartic and southern Neotropical vegetation (Challenger, 1998). The study site has a semiarid and warm climate with a mean annual rainfall ($n = 61$ years) of 388.40 mm (range 92–799 mm) and mean temperature of 20.7 °C (14.1–27.3 °C). Over 85% of the rainfall is concentrated in the summer and autumn (CONAGUA, San Cristobal, Metztitlán Weather Station 20°38′29.04″N; 98° 49′42.96″W, at 1300 m a.s.l, on the web http://smn.cna.gob.mx/climatologia/Diarios/13087.txt, accessed on November 28, 2014) located 12 km from the study area. The vegetation is classified as deciduous forests and microphyllous scrub, dominated by the columnar cactus *Cephalocereus senilis* (Haw.) Pfeiff., Allg and *Isolatocereus dumortieri* (Scheidw.) Backeb. (Cruz and Pávon, 2013) as well as shrubby legumes such as *Mimosa leucaenoides* Benth. (Herce et al., 2013).

2.2. Data collection

All individuals of *N. polylopha* ($n = 723$) were tagged in April 2012 and censused during three annual periods (two transitions). Average annual rainfall was drastically different during the study period. Precipitation from June 2012 to May 2013 was the lowest in recorded history for this weather station (120.4 mm) and it represented an abnormally "dry year", due to an El Niño-Southern Oscillation (ENSO) event (on the web http://ggweather.com/enso/oni.htm, accessed on November 27, 2014). On the contrary, June 2013 to May 2014 was characterized by a "rainy year" in which 447.2 mm of rainfall was recorded. During the 2013–2014, the month of September 2013 had a unique rainfall event (189 mm) in the last 15 years and an unusual event mainly caused by two simultaneous hurricane systems: hurricanes "Manuel" from the Pacific Coast and "Ingrid" from the Gulf of México (on the web http://smn.cna.gob.mx/climatologia/analisis/reporte/Anual2013.pdf, accessed on November 27, 2014). Only considering the seasonal rainfall when seedling establishment of *N. polylopha* occurs (June–October period), the chances of having a rainfall equivalent to that found during each year was 16.4% (2012–13) and 71% (2013–14).

All individuals within the plots were mapped, tagged and total height (cm) were measured. When adult individuals were multi-branched, the length of each branch was measured from the tip to the point of attachment to the main stem and then added to the length of the highest stem to provide a measure of the total stem length. Each year we recorded for each individual: apical growth (cm) and number of reproductive structures (floral buds, flowers or fruits) from April to August; and, the mortality and newly recruited individuals were registered in the population. The stem growth of each plant was measured with a caliper, or with a level staff (for plants taller than 200 cm. The main stem of each individual was marked at a fixed length from the apex, such that subsequent censuses (2013 and 2014) would quantify the relative increments in stem height (Esparza-Olguín et al., 2005). Individuals could lose size (retrogression) by branch or apical death similar to other branched and monopodial cactus (Bashan et al., 1995; Zavala-Hurtado and Díaz-Solís, 1995).

2.3. Density and spatial distribution

The number of individuals within each plot was recorded and a mean density per m^2 was obtained as the average across plots (Krebs, 1999). An index of spatial distribution was applied to determine spatial arrangement of individuals and how these responded to the variation found at the study site (Krebs, 1999). Briefly, this index R ranges in value from 0 for a distribution with maximum aggregation to 2.1491 for a distribution which is as