



Emergence, survival, and growth of recruits in a desert ecosystem with vegetation-induced dunes (nebkhas): A spatiotemporal analysis



Jan J. Quets^{a, *}, Magdy I. El-Bana^b, Saud L. Al-Rowaily^c, Abdulaziz M. Assaeed^c, Stijn Temmerman^d, Ivan Nijs^a

^a Center of Excellence PLECO (Plant and Vegetation Ecology), Dept. of Biology, Univ. of Antwerp, Universiteitsplein 1, BE-2610 Wilrijk, Belgium

^b Dept. of Botany, Faculty of Science, Port Said Univ., 42521 Port Said, Egypt

^c Dept. of Plant Production, College of Agriculture, King Saud Univ., PO Box 2460 Riyadh, Saudi Arabia

^d Ecosystem Management Research Group, Dept. of Biology, Univ. of Antwerp, Universiteitsplein 1, BE-2610 Wilrijk, Belgium

ARTICLE INFO

Article history:

Received 24 June 2016

Accepted 29 November 2016

Available online 21 December 2016

Keywords:

Spatial pattern

Null model

Recruitment

Saudi Arabia

Rhazya stricta

ABSTRACT

We studied how emergence, survival, and growth of nebkha recruits are spatially affected by prevailing biotic and abiotic ecological drivers in a landscape with vegetation-induced dunes (nebkhas) in Saudi Arabia. Hereto Monte Carlo-based spatiotemporal analyses were performed on four remotely sensed study site maps, including adult nebkhas, recruits and elevation data, acquired over a three-year period. The emergence of new nebkha recruits was found substantially higher in topographic depressions and around adults, which we interpret as being a result of runoff water convergence to depressions and distance-limited seed dispersal from adults. The survival of recruits was also higher nearby nebkhas. However, the growth of already present recruits was suppressed near adult vegetation indicating competition, but unexpectedly increased far away from nebkhas which could be induced by augmented sand burial in these open areas, stimulating the nebkha development and its host plant. Combining the three demographic processes emergence, survival, and growth revealed systematically greater encroachment from nebkha recruits in zones with low vegetation cover, which creates a buffer against local disturbances in nebkha fields.

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1. Introduction

Nebkhas are vegetated dunes which arise from aeolian sediment deposition on burial-tolerant shrubs in arid regions (Danin, 1996a). At the landscape scale, these nebkhas occur as patchy spatial vegetation patterns surrounded by bare soil (Quets et al., 2013). Such nebkha landscapes are highly prevalent in most deserts worldwide (Du et al., 2010), and are considered as useful as buffers against desertification (Dougill and Thomas, 2002) and for land restoration (El-Bana et al., 2003) as nebkhas can reduce wind erosion, encourage aeolian sediment deposition, and hold water and nutrients (Schlesinger et al., 1990; El-Bana et al., 2002; Field et al., 2012). Nebkha landscapes are dynamic, as the density and vegetation cover of nebkhas often change, for instance due to

population dynamics, meteorological variability, increased grazing pressure and climate change (Bendali et al., 1990; Goslee et al., 2003; Baas and Nield, 2007). Recruitment, which occurs in the bare areas, is an important aspect in these dynamics as it co-determines the properties of the future nebkha landscape, such as vegetation cover and the biodiversity of associated species [e.g. annuals (El-Bana et al., 2007), rodents, lizards and snakes (Le Houérou and Gillet, 1986)]. Indeed, without recruitment of nebkha host plants, nebkha dunes would finally disappear, and their associated species would be co-threatened (Colwell et al., 2012). In this study, we focus on three aspects of recruitment, namely on emergence density, and on rates of survival and growth of recruits. More specifically, we quantify the spatial patterns of these three parameters with respect to gradients of environmental factors explained below. To our knowledge, such study has never been conducted before. In the next paragraphs, we review existing knowledge and hypotheses on the factors which potentially affect the emergence, survival and growth of recruits in desert ecosystems.

Topography may affect recruits of nebkha host plants and thus

* Corresponding author.

E-mail addresses: jquets@gmail.com (J.J. Quets), mag_bana@yahoo.co.uk (M.I. El-Bana), srowaily@ksu.edu.sa (S.L. Al-Rowaily), assaeed@ksu.edu.sa (A.M. Assaeed), stijn.temmerman@uantwerpen.be (S. Temmerman), ivan.nijs@uantwerpen.be (I. Nijs).

the spatial patterns of recruitment in nebkha landscapes. Indeed, water, the main limiting factor for plants in deserts, can runoff, possibly together with floating seeds, and converge toward topographic lows, thereby improving recruit emergence, survival and growth in depressions (McGrath et al., 2012). Vegetation cover controls recruitment as well, either directly or indirectly. Vegetation cover correlates well with seed production (Nathan and Muller-Landau, 2000), and controls sedimentation and erosion processes (Field et al., 2012), which in turn affect recruitment processes. Indeed, most seeds will only germinate if they are not buried deeper than 2 cm under the surface (Ren et al., 2002), survival commonly declines under both erosion and burial (Zhao et al., 2007), while growth usually suffers from erosion (Li et al., 2010), but can increase under limited burial (Zheng et al., 2012). Another factor which probably determines spatial patterns of recruitment, is the distance from adjacent adult nebkha plants. It is expected that the proximity of seed producing adult nebkhas and seed dispersal patterns will affect spatial patterns of recruitment, as seed density commonly decreases with distance from the parent plant (Nathan and Muller-Landau, 2000). However, nebkhas may affect recruitment not only by producing and dispersing seeds. For example, enrichment of nutrients near nebkhas, driven by nutrient concentration mechanisms in nebkha landscapes (Schlesinger et al., 1990), could ameliorate the emergence, survival, and growth of adjacent recruits (Flores and Jurado, 2003). On the other hand, adult nebkha host plants may compete for water and nutrients with their neighboring recruits (Friedman, 1971) or produce autoallelopathic chemicals which could restrain nearby recruitment processes (Assaeed, 1997). However, it remains elusive what role above-mentioned processes play in the recruitment dynamics of nebkhas. The aim of this study is therefore to quantify the spatial patterns of emergence, survival, and growth of recruits of *Rhazya stricta* Decne., a nebkha species in Saudi Arabia, and based on these spatial patterns to deduce the factors shaping emergence, survival, and growth of recruits.

An effective way to unravel the mechanisms affecting recruitment, is to firstly generate a scientifically-grounded hypothesis of the recruitment spatial patterns expected to arise from these mechanisms, and then to compare the observed recruitment spatial patterns with the expected ones: agreement (or disagreement) between the observed and expected recruitment patterns would then confirm (or reject) the hypothesized mechanisms of recruitment (McIntire and Fajardo, 2009). Here, we applied this approach to find out how the previously-mentioned biotic and abiotic ecological drivers affect the emergence, survival and growth of *Rhazya stricta* Decne. recruits in a desert. We hypothesize that spatial variations in emergence density, survival rate and growth rate of *R. stricta* recruits are related to (1) local topographic variation, (2) cover of nebkhas and (3) nearest adult distance. The underlying rationale is the following: (1) Local topographic depressions are considered to attract runoff water, and with it floating seeds, thereby increasing soil moisture and seed density. Therefore, we hypothesize a positive relation between local topographic depressions and *R. stricta* emergence, survival and growth. (2) We predict a positive relation between cover of nebkhas and the emergence, survival and growth of *R. stricta* recruits, as adult canopy area typically correlates well with local seed availability, weakened wind speeds (less stress on recruits), and consequently sedimentation (burying seeds and promoting recruit emergence). (3) Finally, we expect a decreasing recruit emergence density with increasing distance from the nearest adult, as seed densities typically decline with the distance from parent plants. The relation between recruit growth and survival rate, on the one hand, and nearest adult distance, on the other hand, could be positive or negative, respectively indicating competition and facilitation.

The objective of this study is to analyze the observed spatial and temporal patterns of recruitment of *R. stricta*, based on a time series of aerial pictures from a plot in Saudi Arabia. Hereto, we compared observed recruitment patterns with simulated ones, which are expected to arise from the hypothesized mechanisms of recruitment, as outlined above.

2. Methods

2.1. Site description and focal species

We performed a case study in a 2.56 ha study site (25.510°N, 46.002°E), which lies about 120 km northwest of Riyadh, Saudi Arabia, at 631 m above mean sea level. It approximates a rectangle of 125 × 250 m roughly aligned SSW-NNE (see Fig. 1) and is part of an extensive *R. stricta* nebkha field controlled by the Saudi Ministry of Agriculture. The local climate is hyper-arid, with long-term average annual precipitation and pan evaporation amounting to 83 and 2816 mm, respectively. The study area is subjected to multi-directional winds (Vincent, 2008). Only two seasons exist here: a wet season with infrequent, unpredictable, but mostly high-intense rains extending from the start of October to the end of June (Jones et al., 1981), and a hot rainless dry season during July to September. Long-term mean daily temperatures range from 14.2 °C in January to 33.7 °C in July (Vincent, 2008). The soil at the study site consists of a cemented CaCO₃ hardpan – in which the focal species of this study, *R. stricta*, was able to root – covered with a top layer of loose sediment ranging from a few millimeters to almost 1 m in thickness.

Most of the original native plant species of the Arabian Peninsula are livestock-palatable. However, since decades this region has been overstocked by camels (Al-Rowaily, 1999). As a consequence, both vegetation cover and biodiversity have been drastically decreased. Unpalatable species usually flourish in drylands during regimes of overgrazing due to lack of competition from palatable species (Al-Rowaily et al., 2012). This is also the case for *R. stricta* (Apocynaceae), an autoallelopathic, and nebkha-forming shrub which has been dominating vast areas in Saudi Arabia since overstocking initiated, including the study site.

The study site was highly limited in *R. stricta* seeds, both in locations with low and high densities of *R. stricta* recruits (for experimental evidence, see Supplementary Material, Appendix 1). Once emerged, recruits of *R. stricta* begin to branch at about 0.25 m canopy diameter (observation by the authors); at that time they start capturing wind-blown sediment, thereby forming nebkhas. *R. stricta* shrubs typically stay infertile (i.e. juvenile) until their canopies reach 0.5 m diameter, whereas larger ones mostly are fertile (i.e. adult). The largest adults found at the study site exceeded 4 m diameter. Occasionally, canopies of closely neighboring nebkhas or nebkha recruits merge into one vegetation patch upon further growth. However, this is much more the exception rather than the rule, and one of the merging individuals may die in the process. The nebkhas did not have sediment tails, indicating the lack of dominant wind directions (Danin, 1996b).

2.2. Data collection and preprocessing

Spread over a three-year period, four low-altitude aerial photography field campaigns were annually conducted in the study site, which enabled us to map in time the spatial coordinates and canopy sizes of *R. stricta* individuals, as well as the topographic variation in the inter-nebkha area. Canopy sizes were considered good proxies of nebkha sizes.

These campaigns all took place during the wet season as we assumed the vegetation was then the most healthy and green, and

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