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

Reference:
Quets Jan, El-Bana Magdy I., Al-Rowaily Saud L., Assaeed Abdulaziz M., Temmerman Stijn, Nijs Ivan.- Emergence, survival, and growth of recruits in a desert ecosystem with vegetation-induced dunes (nebkhas) : a spatiotemporal analysis
Journal of arid environments - ISSN 0140-1963 - 139(2017), p. 1-10
Full text (Publisher's DOI): https://doi.org/10.1016/J.JARIDENV.2016.11.013
To cite this reference: https://hdl.handle.net/10067/1384580151162165141

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

Jan J. Quets, Magdy I. El-Bana, Saud L. Al-Rowaily, Abdulaziz M. Assaeed, Stijn Temmerman, & Ivan Nijs

Quets, J. J. (Corresponding author, jquets@gmail.com)[1]

El-Bana, M. I. (mag_bana@yahoo.co.uk)[2]

Al-Rowaily, S. L. (srowaily@ksu.edu.sa)[3]

Assaeed, A. M. (assaeed@ksu.edu.sa)[3]

Temmerman, S. (stijn.temmerman@uantwerpen.be)[4]

Nijs, I. (ivan.nijs@uantwerpen.be)[1]

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

[2]Dept. of Botany, Faculty of Science, Port Said Univ., 42521 Port Said, Egypt;

[3]Dept. of Plant Production, College of Agriculture, King Saud Univ., PO Box 2460 Riyadh, Saudi Arabia;

[4]Ecosystem Management research group, Dept. of Biology, Univ. of Antwerp, Universiteitsplein 1, BE-2610 Wilrijk, Belgium

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.

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 & 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 & 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 & 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 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 & 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 & 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 & 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 & 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.

Methods

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 Figure 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 $CaCO_3$ 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.

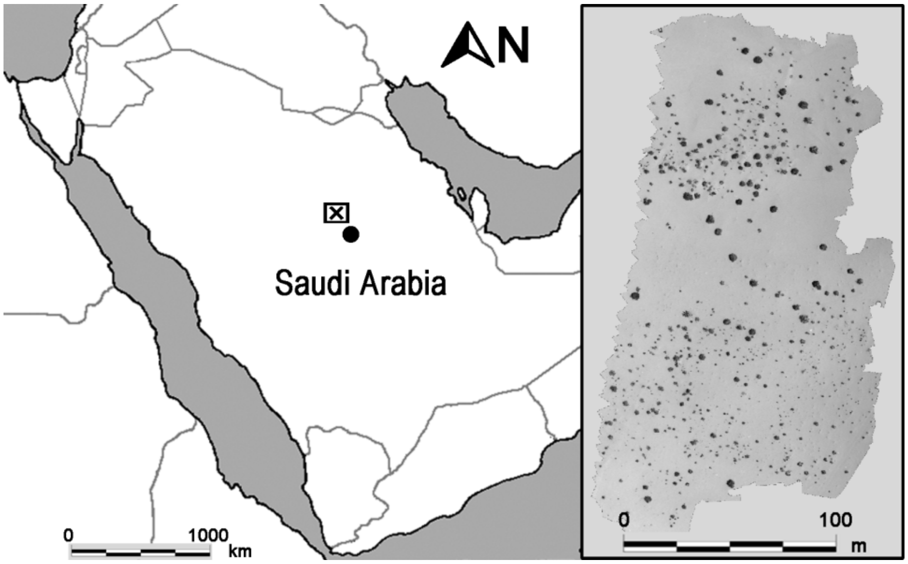


Figure 1 Study site. Left: The Arabian Peninsula. The dot in the middle represents Riyadh, the capital of Saudi Arabia; the crossed box indicates the study site. Right: detail of the study site (orthoimage at t_2), with nebkha host plants in black and bare soil in light grey.

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).

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 therefore better discernible from the soil on imagery. The specific dates of the field campaigns were December 2010 (t_1), March 2012 (t_2), April 2013 (t_3), and February 2014 (t_4). The time periods between the field campaigns over which emergence, survival and growth of recruits were measured were therefore about a year, never exactly 365 days. If this induced noise in the data set, then this noise did not preclude us from detecting relevant information. Indeed, the spatial patterns of rates of emergence, survival and growth were of much greater importance in our study than their temporal patterns as averaged over the entire landscape. Moreover, since the wet season is highly variable and unpredictable, few guarantees existed that environmental circumstances would be similar every 365 days.

The photography was performed using a tethered helikite (Allsopp Skyhook 3.3m^3) during t_1 and t_2 and a radio-controlled drone (MikroKopter Okto-XL) during t_3 and t_4. Both instruments yielded the same output quality of photo sets. However, the latter instrument could perform the same task in less time while demanding less effort and manpower, so we adopted the drone when it became available to us after the second field campaign.

With these unmanned aerial vehicles, sets of overlapping aerial pictures were shot, from which four orthoimages and a digital elevation model were created of the study site (technical details are explained in Supplementary Material, Appendix 2). The spatial resolutions of the resulting orthoimages and the digital elevation model were 100 and 20 pixels per m, respectively. The orthoimages were classified into Boolean maps depicting *R. stricta* vegetation using Adobe Photoshop CS5, while the digital elevation model was post-processed as to be classifiable into topographic depressions and (inter-nebkha) elevations.

R. stricta patch coordinates and sizes were measured on the aforementioned Boolean vegetation maps using the Image Processing Toolbox of MATLAB R2011a. The sizes were initially measured in areal units (m²), but were also expressed as diameter (Ø, in m) of the circle having the same area as the observed nebkha or nebkha recruit. To avoid confusion, we stress that the nebkha mounds (i.e. the mounds underneath the *R. stricta* canopies) were not considered topographic elevations in this study. Instead, elevations were defined as regions of locally raised topographic height of an extent larger than nebkhas, or in between nebkhas. In order to define these elevations, we replaced all digital elevation model values within *R. stricta* nebkhas with values linearly interpolated from the perimeters just outside these nebkhas (an algorithm called digital inpainting), thereby obtaining a nebkha-free digital elevation model. The digital inpainting was performed using the program *inpaint_nans* (D'Errico, J. 2004 in MATLAB Central File Exchange) in MATLAB R2011a. Based on field observations, most topographic elevations and depressions were estimated to have extents of about 10 m diameter. A smoothed version of the nebkha-free digital elevation model using a median filter with 10 m radius was therefore subtracted from the non-smoothed version, as to reveal a map of local topographic deviation (*LTD*), from which local topographic depressions and elevations could be classified (Head & Kreslavsky 2002).

Nebkha cover (*NC*) was measured inside contiguous grid cells laid over each Boolean vegetation map, as to acquire gridded maps of (local) *NC*. The size of these *NC* grid cells was chosen to represent 10 × 10 m plots in the field site. This grid cell size was deemed optimal since (i) it was sufficiently large to contain several large nebkhas; (ii) it was small enough to provide a statistically sufficient sample size covering a broad range of *NC* values; and (iii) most seeds of desert dune shrubs disperse locally (Danin 1996b), possibly yielding correlations between *NC* and recruit emergence as measured in these grid cells. The distance to the nearest adult was also calculated on the Boolean vegetation maps for each point in the study site. This resulted in maps of nearest adult distance (*NAD*).

Demographic trends in the nebkha population

In order to provide more context to the recruitment processes under study, we started with a demographic overview of the nebkha population in the study site. Hereto, we assumed that shrub size classes roughly represented shrub age classes and defined these as cohorts. Indeed, size and age are generally positively correlated in shrubs (Gadzia & Ludwig 1983), unless stunted growth occurs which we did not observe in the study site. We subdivided all mapped *R. stricta* individuals into five size classes. Unbranched individuals ($0 < Ø \leq 0.25$ m) were considered recruits (i.e. the youngest cohort) and the main focus of this study. Four additional size classes containing nebkhas represented older cohorts, and were divided as follows: $0.25 < Ø \leq 0.50$ m, $0.50 < Ø \leq 1.00$ m, $1.00 < Ø \leq 2.00$ m, and $Ø > 2.00$ m. The widths of these size classes increased exponentially as to compensate for the strong positive skew in frequency distribution of nebkha sizes (Quets et al. 2014). This way, each nebkha size class contained similar numbers of nebkhas, making the subdivision of classes more statistically sound. The demographic overview included the density of nebkhas and the vegetation cover from nebkhas (subdivided into cohorts), as measured from each field campaign. We also calculated the density and vegetation cover of recruits and nebkhas which emerged and died in between subsequent field campaigns.

Drivers behind spatial patterns of recruitment

USED DATA SETS

The datasets for emergence, survival, and growth rates of recruits were strategically chosen. The emergence rate (ha^{-1} yr^{-1}) was measured between t_1 and t_2 (i.e. during t_{1-2}) because high numbers of recruits emerged only during this time period without increased human disturbance, the latter of which we deem the first growth stage especially vulnerable to. The overall survival rate of recruits, as averaged over the years, was very high (i.e. 92% yr^{-1}), which indicates a low variance in survival rate. To better detect differences in survival rate (under low survival variance) between recruits present in locations with different properties (e.g. depressions versus topographic elevations), we therefore preferred data with high sample sizes. Because the number of recruits was clearly the highest in t_1, mean recruit survival rate (% yr^{-1}) was computed during t_{1-2}. Mean annual growth rate

(m^2 yr^{-1}) was measured during t_{1-2}, t_{1-3} and t_{1-4} on recruits present in t_1 that stayed alive and did not merge with other recruits or nebkhas, at least until t_4.

DATA ANALYSES

This section describes how we quantified the effects of seed dispersal, competition, facilitation, and topographic-induced spatial redistribution of runoff water on the spatial patterns of emergence, survival and growth of *R. stricta* recruits. Because it was very challenging to measure the above-mentioned potential drivers of nebkha recruitment during several years across the entire study site directly, we used proxies for these drivers, which were measurable on remotely sensed two- and three-dimensional data (i.e. *LTD*, *NC*, and *NAD*). In this respect, *LTD* served as a proxy for topographic-induced spatial redistribution of runoff water and water dispersed seeds: runoff water would be diverged from positive *LTD*-values, and converged to negative ones. *NC* was considered as a proxy for local seed availability, protection from wind, and enhanced sedimentation. Finally, *NAD* was assumed to relate with seed density, competition or facilitation: lower *NAD*-values (i.e. shorter distance to the nearest adult) would correspond with higher seed densities and stronger competitive or facilitative forces on recruits.

Each observed recruitment process (i.e. emergence, survival and growth rate of *R. stricta* recruits) was then measured on a gradient of each observed driver proxy (i.e. *LTD*, *NC*, and *NAD*). We then compared these observations with simulations of Monte Carlo null models, which assume that the emergence, survival and growth of recruits is independent from driver proxy gradients. In this way, the effects of driver proxies on recruitment processes could be assessed in a statistical manner using *p*-values (see section 'null models and Monte Carlo simulations' for details; see Figure 2 for an illustration).

To detect for possible relationships between recruitment processes and driver proxies, we subdivided the range of driver proxy values into classes (see section 'subdivision of driver proxies' for classification details). In each class of a driver proxy (for example *NC*) we then measured the observed recruitment parameters (for instance emergence rate) and tested how they deviated from the recruitment parameters simulated by the null model (see section 'null models and Monte Carlo simulations' for details). Subdividing the driver proxies into more classes would enhance the resolution of the relations between recruitment process and driver proxy, but would also decrease the sample size inside each class, thereby lowering the statistical power to compare observations with null models. A trade-of between these two motifs led to a choice of four classes for each driver proxy.

SUBDIVISION OF DRIVER PROXIES

The *LTD* classes were chosen as to divide the area of the study site into parts of similar size.

This led to a *LTD* subdivision as follows: (i) parts of depressions deeper than 0.10 m, (ii) parts of depressions between 0.05 and 0.10 m deep, (iii) parts of elevations between 0.05 and 0.10 m high, and (iv) parts of elevations higher than 0.10 m.

Since the frequency distribution of *NC,* as measured in 10 × 10 m grid cells, was positively skewed, the widths of *NC* classes were chosen to enlarge with increasing *NC*. Classifying in this way led to an equally distributed surface area among *NC* classes. The *NC* classes were defined as follows: either (i) less than 2.5%, (ii), between 2.5 and 5%, (iii) between 5% and 10%, or (iv) more than 10%.

Seed density often decreases with distance from the parent plant. In order to equalize the number of observed recruits among *NAD* classes, the widths of *NAD* classes were therefore chosen to be wider for higher *NAD* values. In addition, effects of nebkhas on survival and growth of nearby recruits were assumed better detectable in this way since competition or facilitation imposed by nebkhas on recruits is often restricted to a limited action radius. The *NAD* classes were thus defined as specific distance ranges from adults, being either (i) less than 2 m, (ii) between 2 and 5 m, (iii) between 5 and 10 m, and (iv) beyond 10 m.

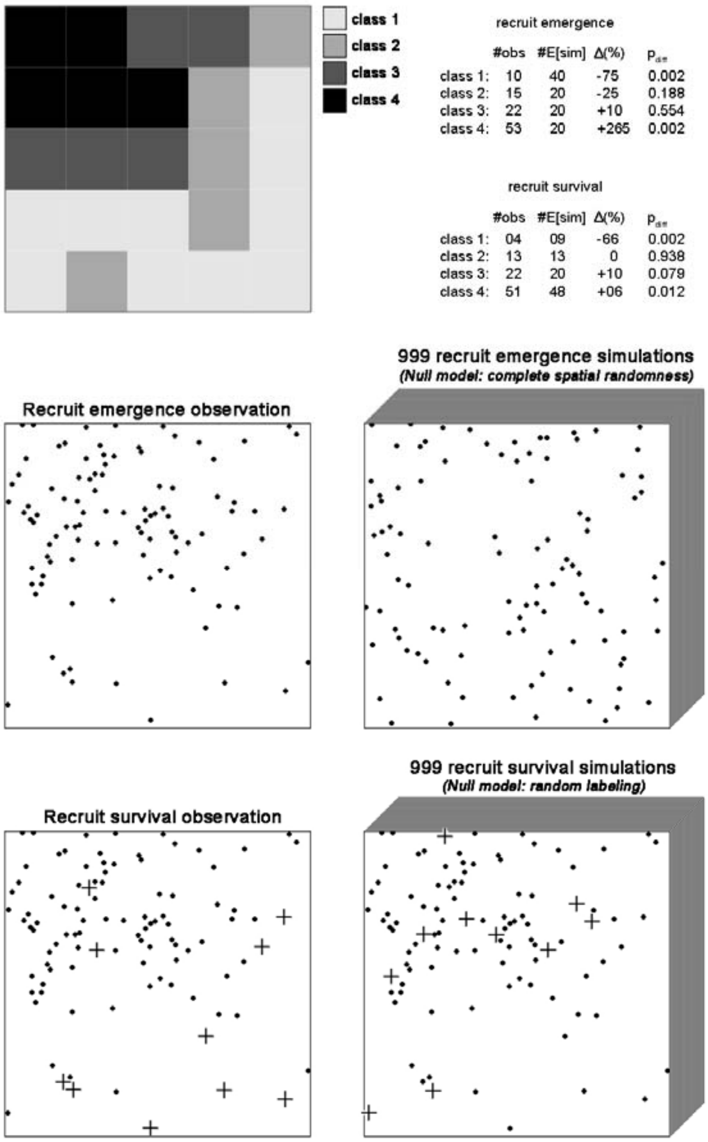
NULL MODELS AND MONTE CARLO SIMULATIONS

Three null models were built, each one associated with either emergence rate, survival rate, or growth rate of recruits. These null models assume that emergence, survival and growth rates of recruits are not dependent on the driver proxies studied in this paper. Monte Carlo simulations of these null models thus produce spatial patterns of emergence, survival and growth of recruits, which are spatially homogeneous. These simulated patterns were then compared with observed ones in order to detect and quantify influences of driver proxies on spatial patterns of emergence, survival, and growth of recruits (see Figure 2 for an illustrative example).

The null model associated with recruit emergence assumed that recruit emergence was equally likely in all locations in the study site, and therefore simulated complete spatial random patterns of recruit emergence. Monte Carlo simulations of this null model repositioned in a random fashion the observed spatial coordinates of nebkha recruits, as emerged during t_{1-2}.

The null models concerning survival and growth assumed that rates of survival and growth of recruits were independent from spatial location. The Monte Carlo simulations of these null models were therefore based on the random labeling hypothesis (Wiegand & Moloney 2004), which involved the exchange of observed survival (i.e. dead or aliveness) and growth rate (expressed in $m^2\ yr^{-1}$) labels among the *R. stricta* recruits present in t_1, while keeping their spatial coordinates fixed.

The null models involving growth and survival in *NAD* classes were built and run in Microsoft Excel 2010, all other null models were built and run in R 3.0.2 using the spatstat package (Baddeley & Turner 2005). The deviations between observed and simulated recruitment processes within all driver proxy classes were systematically assessed by two-tailed significance tests as we aimed to make unexpected relations detectable too, on four different significance levels (i.e. $\alpha = 0.1$, 0.05, 0.01, and 0.002). Hereto, for each above-mentioned deviation between observation and Monte Carlo null model simulation, a p-value was computed using the minimum of $2p_L$ and $2p_U$, where p_L and p_U were the fractions of the 1000 values, composed of 999 simulated Monte Carlo null model values and one observation, which were as small or smaller (p_L), or as large or larger (p_U) than the observed recruitment processes under study (Manly 1997). Vegetation cover encroachment, or the absolute increase of vegetation cover arising from recruits, was estimated too, after 1, 2, and 3 years. This calculation was performed by multiplying above-mentioned observations of emergence density, survival rate and growth rate of recruits, in each driver class. Figure 2 shows a simplified fictive example, which illustrates and summarizes the methodology discussed in this section.



recruit emergence

	#obs	#E[sim]	Δ(%)	p_{diff}
class 1:	10	40	-75	0.002
class 2:	15	20	-25	0.188
class 3:	22	20	+10	0.554
class 4:	53	20	+265	0.002

recruit survival

	#obs	#E[sim]	Δ(%)	p_{diff}
class 1:	04	09	-66	0.002
class 2:	13	13	0	0.938
class 3:	22	20	+10	0.079
class 4:	51	48	+06	0.012

Figure 2 Fictive simplified example to illustrate the used methodology for the spatial analysis conducted in our study. The upper left plot displays a subdivision of a fictive study site into four classes of a driver proxy of choice. In this example we choose *NC* as the driver proxy, but the space could analogously be divided into classes of the other driver proxies, *LTD* and *NAD*. The mid left plot depicts the spatial pattern of 100 observed recruits. The mid right plot shows one of 999 null model simulations in which the emerged recruits are completely spatially randomized across the study site. The lower left plot shows which of the emerged recruits were observed to survive after one year (the 10 recruits that not survived are shown by crosses). The lower right plot visualizes one of 999 null model simulations in which the labels of survival were randomized among the spatial pattern of observed emerged recruits. Note that

the random labeling hypotheses could analogously be performed on recruit growth, by randomizing growth labels among the spatial pattern of observed emerged recruits. The tables in the upper right summarize the number of counts of emerged and survived recruits in each driver proxy class, both for the observation (#obs) and for the mean value of 999 simulations (#E[sim]). The relative difference between observed counts and the mean value of simulated counts is depicted as well (Δ(%)), together with the associated p-value (p_{diff}), which quantifies the significance of the difference between observed and simulated counts, in this fictive example.

Results

Demographic trends in the nebkha population

The density of *R. stricta* individuals fluctuated around 450 ha^{-1} at t_1, t_2, and t_3, and decreased to 367 ha^{-1} at t_4 (Figure 3). In all time steps, the cohort of recruits was the most abundant, and the cohort with the largest plants the least. However, the size class proportions were not highly stable. For instance, the density of recruits almost halved, and the density of individuals in the cohort with the second smallest nebkhas more than tripled during t_{1-2}, though they stayed relatively stable afterwards (upper left chart of Figure 3). With respect to recruitment, many more nebkha recruits emerged during t_{1-2} (61 ha^{-1}) and t_{3-4} (44 ha^{-1}) as compared to t_{2-3} (only 7 ha^{-1}), as seen in the upper middle chart of Figure 3.

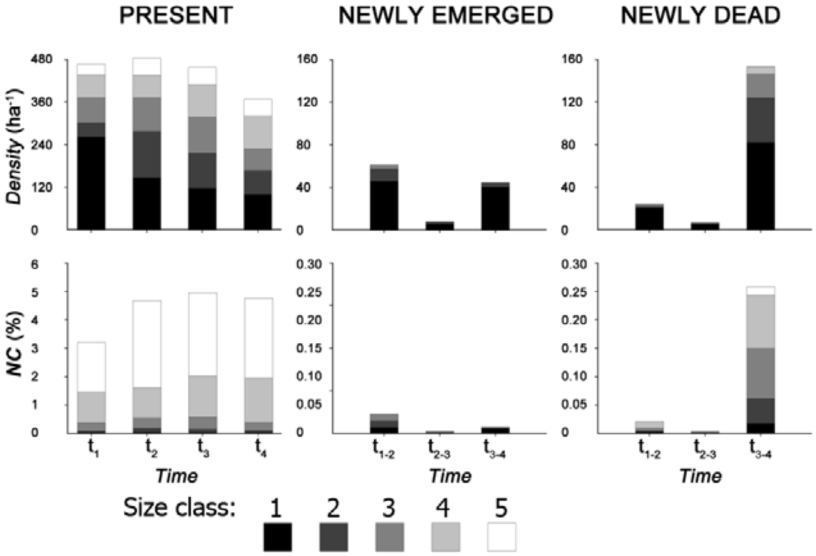


Figure 3 Demographic trends of *R. stricta* nebkhas and recruits. The size classes, considered as proxies for age cohorts, are size class 1 or recruits (Ø ≤ 0.25 m), size class 2 (0.25 m < Ø ≤ 0.50 m), size class 3 (0.50 m <

Ø ≤ 1.00 m), size class 4 (1.00 m < Ø ≤ 2.00 m) and size class 5 (Ø > 2.00 m). The density and nebkha cover (*NC*), as measured over the entire study site, together with the contribution of each size class to this density and nebkha cover (*NC*) is depicted on the two most left plots, for each of the four campaigns t_1, t_2, t_3 and t_4. The two middle plots illustrate the density and *NC* of recruits emerged between $t_{1\text{-}2}$, $t_{2\text{-}3}$, and $t_{3\text{-}4}$ in the study site, as measured on t_2, t_3, and t_4 respectively, and how the different size classes contributed to the newly appeared density and *NC*. The two most right plots depict the density and *NC* of *R. stricta* which died off between $t_{1\text{-}2}$, $t_{2\text{-}3}$, and $t_{3\text{-}4}$, as measured on t_2, t_3, and t_4 respectively, and how the different size classes contributed to these vegetation die-offs.

The total *NC* of all nebkhas and recruits together fluctuated from around 3% in t_1 to around 5% in t_2, t_3, and t_4 (lower left chart of Figure 3). The contribution of new recruits to *NC* was always minor, and usually much less than 1% of the total *NC* (compare lower left with lower middle chart in Figure 3). New recruitment mostly surpassed mortality, both in numbers and in *NC*, except for the last inter-census period (compare middle with right charts in Figure 3), where death numbers were more than six times and *NC* loss rate more than twelve times higher than before (right charts of Figure 3). The mean recruit survival percentage was very high (92.3%) and mortality further declined with increasing nebkha size during $t_{1\text{-}2}$ (Figure 3).

Drivers behind spatial patterns of recruitment

This section describes the relations between emergence density, survival rate, and growth rate of *R. stricta* recruits on the one hand, and *LTD*, *NC*, and *NAD* (as potential drivers) on the other hand. The deviations from the null models per driver proxy class and for emergence density, survival rate, and mean growth rate are summarized in Figure 4, and the estimated vegetation encroachment (i.e. the absolute increase in vegetation cover) arising from recruits is shown in Figure 5.

Emergence density and mean growth rate of recruits were significantly greater than average in depressions (negative *LTD*), and significantly lower than average on elevations (positive *LTD*), as illustrated by Figure 4. Moreover, recruit emergence and growth (Figure 4), as well as encroachment from recruits (Figure 5), exhibited a clear gradually decreasing trend over the *LTD* classes ordered as follows: depression parts deeper than 0.10 m, depression parts between 0.05 and 0.10 m deep, dune parts between 0.05 and 0.10 m high, dune parts higher than 0.10 m. These trends were quite strong: computed over a three-year period, emergence density and growth rate were respectively about six and fifteen times higher in deep depressions as compared to elevations above 0.10 m.

Survival rate, however, showed no clear trend with *LTD* (Figure 4). The simultaneous decrease of emergence and growth of recruits on elevations (and vice versa in depressions) resulted after three years in a total areal vegetation encroachment from recruits on elevations that was about 20 times lower than mean-field values, and about 50 times lower with respect to encroachment in depressions (Figure 5).

Emergence density and survival rate were significantly positively related with *NC*, the nebkha cover (Figure 4). Emergence density was lower than average in the lowest *NC* class and higher than average in all three other *NC* classes, with about a threefold difference between classes. Recruit survival rate was significantly higher than mean-field values but only in areas with more than 10% *NC*. Conversely, mean growth rate was very strongly and very significantly negatively related with *NC* in spite of an expected positive relation: the recruits grew about eight times slower in highly vegetated as opposed to poorly vegetated areas (Figure 4). Interestingly, in low *NC* areas, the increased mean growth rate dominated over the decreased emergence density. This led to greater encroachment rates in these bare areas (Figure 5), so recruitment dynamics in *R. stricta* nebkha fields would tend to equalize the spatial *NC* distribution.

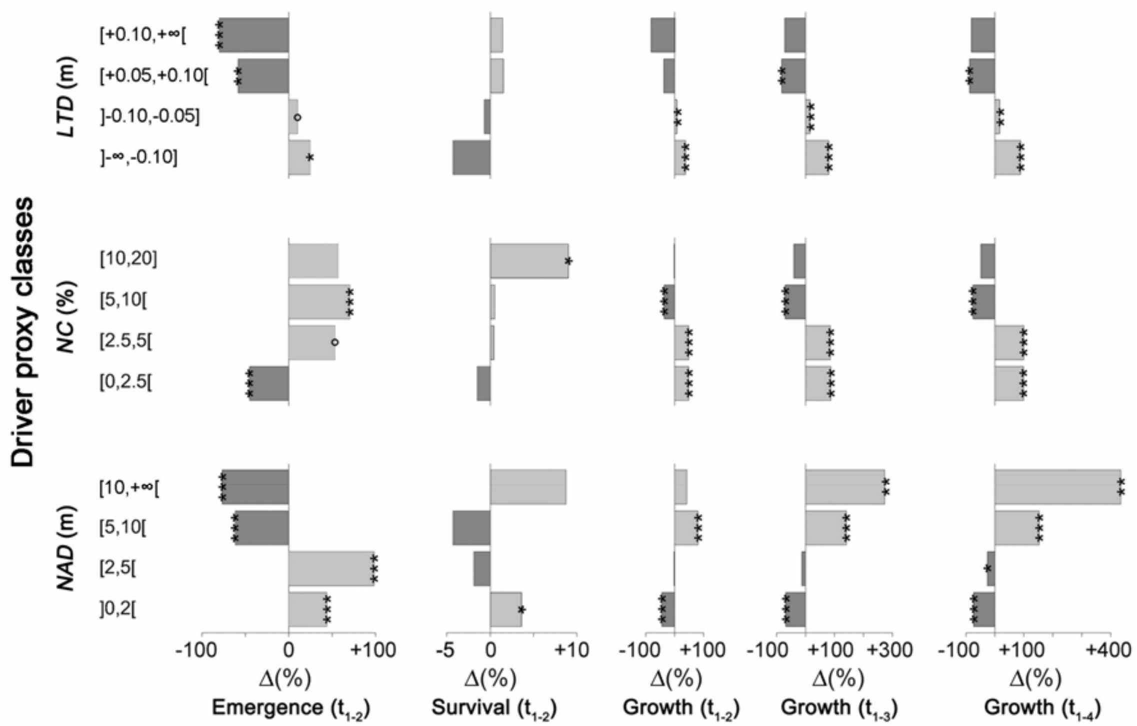


Figure 4 Percent deviations (Δ) from mean-field values of emergence, survival and growth of *R. stricta* recruits within classes of local topographic deviation (*LTD*), nebkha cover (*NC*), and nearest adult distance (*NAD*). The significances of these deviations are examined using Monte Carlo simulations of null models representing randomness (complete spatial randomness for emergence, and random labeling for survival

and growth). Emergence density was observed during t_{1-2} (mean value: 61 ha^{-1}); survival rate during t_{1-2} (mean value: 92.3%); and growth during t_{1-2} (mean value: 0.13 m^2), t_{1-3} (mean value: 0.42 m^2) and t_{1-4} (mean value: 0.57 m^2). Significance level codes are: ° $p < 0.10$; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.002$.

Analogous to *NC*, emergence density and survival rate followed hypothesized relations with *NAD*, the distance from the nearest *R. stricta* adult (Figure 4). We found a clear negative relation between *R. stricta* recruit emergence and *NAD* over all *NAD* classes. Emergence density was higher than average closer than 5 m from adults, and lower than average beyond this distance. Of all studied classes, emergence density was highest between 2 and 5 m from adults, where it was almost the double of the average field value, and about eight times higher compared to regions beyond 10 m from adults. Recruit growth rate showed a strong but unpredicted positive relation with *NAD*: the mean growth rate computed over 3 years was about 20 times higher in areas more distant than 10 m, as compared to regions within 2 m from adults. Similar to *NC*, the increased growth rate dominated the lower emergence density with increasing *NAD*, so that encroachment from recruits after 3 years was above average beyond 2 m and below average within 2 m from nebkha edges (Figure 5), even in isolated vegetation-free areas.

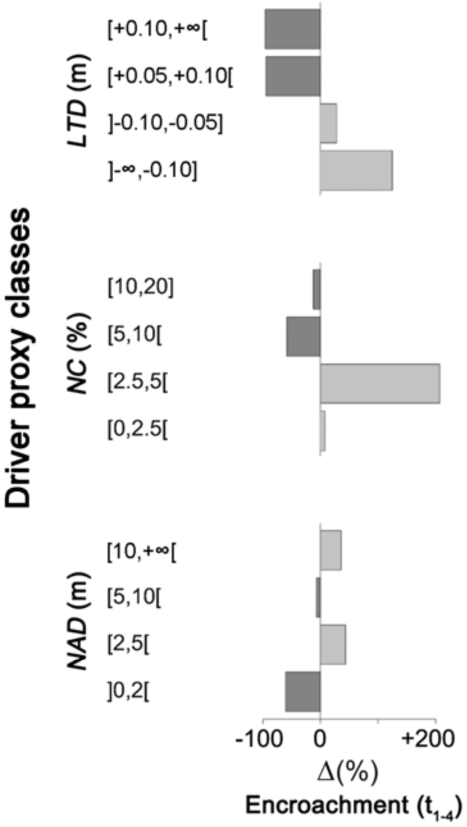


Figure 5 Percent deviations (*Δ*) from mean-field values of vegetation encroachment (i.e. the absolute increase of vegetation cover arising from recruits) within classes of local topographic deviation (*LTD*), nebkha cover (*NC*), and nearest adult distance (*NAD*). The vegetation encroachment was predicted from observed values of emergence, survival and growth of *R. stricta* recruits as arising from recruits during $t_{1\text{-}4}$ (mean value: 0.78%).

Discussion

Demographic trends in the nebkha population

The nebkha ecosystem in our study site was dynamic. The density decline of *R. stricta* individuals during $t_{3\text{-}4}$ was probably a consequence of a camel farm which was settled nearby the study site during the last three months of $t_{3\text{-}4}$. Indeed, although *R. stricta* is toxic, it probably suffered from trampling by camels and off-road vehicle use during $t_{3\text{-}4}$. Water competition seems unlikely the cause for this density decline as more recruits emerged during $t_{3\text{-}4}$ as compared to $t_{2\text{-}3}$. The increased death rate which led to a density decline during $t_{3\text{-}4}$ did not lead to a strong decline in *NC*. This indicates that small plants are more prone to mortality than large ones, as the former contributed the least to the total *NC*. Since the mean recruit survival percentage was very high, established recruits that survive their first summer will likely reach old age when not exposed to increased human disturbance. *NC* increased notably during $t_{1\text{-}2}$, probably owing to higher-than-average overall growth rates during that period since substantially more nebkhas belonged to larger size classes in t_2 than t_1 (upper left chart of Figure 3). Although t_1 was a few months after the regular start of the wet season, no rain had fallen yet. To cope with the resulting increased drought stress, *R. stricta* canopies (unlike their roots) may have been shrinking during the long dry period preceding t_1 (Goldberg & Turner 1986), which would explain the sudden *NC* recovery during $t_{1\text{-}2}$ (Salguero-Gomez & Casper 2011).

Drivers behind spatial patterns of recruitment

We showed that emergence and growth of *R. stricta* recruits were favored in topographic depressions and suppressed on elevations in our study site. Surface runoff water would explain this as it diverges from elevations towards depressions during and after heavy showers, thereby improving soil moisture and concentrating seed availability in depressions (Maliva & Missimer 2012). In contrast, rapid desiccation of mobile sand on elevations may prevent the roots of newly germinated *R. stricta* individuals from reaching the deeper, wetter soil before post-rain drought. Further causes for slower growth on elevations might be higher root to shoot ratios (Xu et al. 2014) and severe burial (Zhao et al. 2007). In contrast to emergence and growth, *LTD* did not affect recruit survival. This might be related to a short lifespan of topographically induced spatial soil moisture heterogeneity, which might only be pronounced days to weeks after heavy rains. During summer, when most recruit mortality is expected to occur in hyper-arid drylands, soil moisture may be spatially homogenized again due to the pervasiveness of extreme soil desiccation. The observed effects of *LTD* on recruit emergence and growth were consistent with our literature-based expectations, as depicted in Table 1. This suggests that an increased presence of mobile dunes, for instance due to enhanced sand supply mediated by the onset of land degradation in adjacent upwind areas, might suppress recruitment (both in density and growth rate of recruits).

Likewise as hypothesized *a priori* (Table 1), *R. stricta* emergence density associated positively with the *NC* composed of adult shrubs, and negatively with *NAD*. The former suggests that seed production is tied to *NC*, while the latter indicates that most produced seeds were probably not dispersed beyond inter-adult distances (Nathan & Muller-Landau 2000). Indeed, if most seeds would be dispersed more remotely, patches of seeds originating from distinct parent plants would considerably overlap, diluting the observed relation between recruit emergence and *NAD*. Emergence density of *R. stricta* recruits was above the mean-field value for *NAD*s smaller than 5 m, and below beyond 5 m. However, this density did not peak closest to the seed source as expected from seed shadows (Nathan & Muller-Landau 2000), but peaked between 2 to 5 m from adults. This might be caused by competition from adults at distances shorter than 2 m, for instance via lateral water extraction by roots and allelopathy (Friedman 1971), or by rodents living in nebkhas predating on seeds close to their holes (Campos et al. 2007). Survival of *R. stricta* recruits was slightly, but significantly, higher both in the highest *NC* class ($NC \geq 10\%$) and within 2 m from adult nebkhas (Figure 4). This suggests biogeomorphologically-induced stress reduction acting on recruit survival, for example, as a result of less sand abrasion due to weaker winds near nebkhas, and biotic facilitation, for instance, because of fertile islands around shrubs, cooling by nebkha shadows, or connections with mycorrhizal networks.

Table 1 Matrix of possible positive (plus sign) and negative (minus sign) relations between emergence, survival and growth of *R. stricta* recruits, and local topographic deviation (*LTD*), nebkha cover (*NC*), and nearest adult distance (*NAD*). *LTD*, *NC*, and *NAD* are proxies of mechanisms driving the relations. These mechanisms are mentioned in the table, where applicable. Proven relations are depicted in black, together with their assumed underlying mechanism, if any. Unproven relations are greyed out.

	Emergence	Survival	Growth
LTD	+	+	+
	– Runoff water flows from inter-nebkha dune (*LTD*>0) to depression (*LTD*<0), thereby causing redistribution of soil water and seeds floating on runoff water	– Runoff water flows from inter-nebkha dune (*LTD*>0) to depression (*LTD*<0), thereby causing redistribution of soil water and seeds floating on runoff water	– Runoff water flows from inter-nebkha dune (*LTD*>0) to depression (*LTD*<0), thereby causing redistribution of soil water
NC	+ Greater nebkha cover promotes seed availability, seed burial, and impedes sand abrasion	+ Greater nebkha cover impedes sand abrasion	+ Greater nebkha cover promotes seedling burial, and impedes sand abrasion
	–	–	–
NAD	+ Competition	+ Competition	+ Competition
	– Facilitation and/or seed availability	– Facilitation	– Facilitation

Conversely to emergence and survival, Recruit growth was affected by *NC* and *NAD* in the opposite of the *a priori* hypothesized direction (see Table 1 and Figure 4). Indeed, growth rates were significantly reduced within 5 m from nebkhas and in high *NC* regions (*NC* > 5%; Figure 4; Table 1). This trend of *R. stricta* recruits growing better with increasing isolation from nearby vegetation was even amplified over longer time periods (Figure 4), indicating that the underlying processes remain active for several years. The explanation may lie in the fact that isolated unvegetated areas are often sources of aeolian sediment as wind speeds and thus the capacity to carry sediment are typically higher (Field et al. 2012), whereas highly vegetated areas are usually sinks. The unexpected greater recruit growth rates in bare areas might arise from this locally increased capacity to deposit sand on and around obstacles where the wind is reduced (such as recruits), as recruits can increase their above ground growth rate after burial (Zheng et al. 2012).

The paradox that *R. stricta* recruits near adult vegetation were positively influenced for survival but negatively for growth, has also been observed in other systems, where it is sometimes explained by stating that competition and facilitation may change with life stage of plants (Miriti 2006). The reason for such a shift is not entirely clear, but could ensue from the smallest recruits having roots that search for nutrients and water in shallower soil layers than the roots of nearby adults. Recruits might therefore initially only be subjected to the benefits of adult closeness (cooling by shadows, increased nutrients), while growing recruits could gradually become competitors of nearby adults as their roots might share resources in identical soil layers. In addition, benefits experienced by recruits as mediated by mycorrhizal networks connecting them with adults could decrease or turn direction when recruits grow into a different life stage (van der Heijden & Horton 2009).

The results in this investigation were based on one case study, and hence we cannot exclude that other nebkha landscapes may behave differently. For instance, the texture of the soil in our study site is sandy clay loam (USDA texture triangle), and therefore highly capable to produce runoff water (Rawls et al. 1982). This might not be the case in all nebkha fields, where soils with a higher infiltration capacity are present and where topographic induced runoff water redistribution may consequently be less prominent, which would make the emergence, survival and growth of recruits less impacted by *LTD*. In addition, competitive forces might be reduced in nebkha fields with host species that have less developed root systems near the surface, and more pronounced ones in deeper grounds. Seed limitation may also differ between various nebkha fields, depending on the nebkha host plant species and seed predators involved. More case studies in future research might help to assess the generality of the results found in this study to nebkha landscapes on other places around the world.

Implications and perspectives

The *R. stricta* recruit growth rates observed in isolated areas were so high that the total areal vegetation encroachment in those places (arising from recruits after three years) exceeded mean-field values, in spite of the low recruit emergence on poorly vegetated land. The total volume of sand captured by these recruits will be even higher than their areal encroachment, as nebkha volume should be a power function of horizontally projected canopy area. The compensating effect of increased encroachment from nebkha recruits in zones with low nebkha cover is hopeful, as it would create a buffer against local disturbances in nebkha fields. However, upon more severe degrees of land degradation, for example, due to climate change or intensified human disturbance, boosted mobile sand flux and subsequent dune formation may ultimately hamper recruitment encroachment, possibly provoking a catastrophic shift leading to a less vegetated alternative stable state which may not be easily reversed (Scheffer 2009). Determining the possible tipping point will be a challenge for further research.

As demonstrated by the germination experiment (see Supplementary Material, Appendix A), the field site was highly seed limited, yet *R. stricta* is known as very seed productive (Assaeed & Al-Doss 2002). Possibly, seed production is high only in mast years, and we may not have collected soil samples in such a year. Alternatively, *R. stricta* seeds decay rapidly or disappear through predation. Although no literature was found on whether *R. stricta* masts, *R. stricta* seed setting seems to be abundant every year (personal communication, Abdulaziz Assaeed). Moreover, the species' recruits quickly decay and disappear when put in meshed bags in soil (personal communication, Abdulaziz Assaeed), indicating the second mechanism of seed limitation. The observation of strong seed limitation in our study site opens the perspective to increase nebkha field *NC*, and thus its capacity to capture sand and reduce mobile sand dunes, by adding *R. stricta* seeds. For restoration efforts to have a chance, added seeds should be released under favorable conditions or so-called windows of opportunity (Balke et al. 2014). For instance, the natural release of seeds during May 2010 co-occurred with a strong precipitation peak during that month (70 mm), which may explain the higher than average recruit density observed in t_1 (Figure 3). Seed addition subsequent to heavy rain events and in the depressions of zones devoid of vegetation, could thus be an avenue to explore as a potential measure to restore vegetation and hence combat desertification. The latter might be performed by unmanned aerial vehicles, but would require also the production of the seeds.

Another concept to reverse land-degradation in bare lands might be the artificial creation of nebkha fields, for instance by planting cuttings. If such cuttings behave similar to recruits, our results suggest that individual growth and the collective capacity to trap sand from fields of planted cuttings will depend on the spatial configuration of these cuttings. Dense configurations may produce high *NC* rapidly, but negatively feedback on individual growth. In contrast, less dense configurations of cuttings may bring an equal *NC* within the same time frame with less effort (fewer planted cuttings) since the individual cuttings may grow faster due to increased nearest nebkha distances. Temporary irrigation of the cuttings would be required, however, unless planting after rain events would suffice. Improving basic knowledge of plant demography and biogeomorphic interactions in deserts may thus offer prospects for combating desertification.

Acknowledgements

We thank Dmitry Semenov and Alexey Pasumansky from Agisoft, for their excellent customer service on Agisoft software. We are grateful to B.A. Dar, who was of tremendous help in most aspects of the fieldwork. This project was supported by NSTIP strategic technologies programs, number 11-ENV1471-02 in the Kingdom of Saudi Arabia.

References

Al-Rowaily, S.L., El-Bana, M.I. & Al-Dujain, F.A.R. 2012. Changes in vegetation composition and diversity in relation to morphometry, soil and grazing on a hyper-arid watershed in the central Saudi Arabia. *Catena* 97: 41-49.

Al-Rowaily, S.L.R. 1999. Rangeland of Saudi Arabia and the Tragedy of Commons. *Rangelands* 21: 27-29.

Assaeed, A.M. 1997. Allelopathic effects of *Rhazya stricta* on seed germination of some range plant species. *Annals of Agricultural Sciences* 42: 159-167.

Assaeed, A.M. & Al-Doss, A.A. 2002. Soil seed bank of a desert range site infested with *Rhazya stricta* in Raudhat al-Khafs, Saudi Arabia. *Arid Land Research and Management* 16: 83-95.

Baas, A.C.W. & Nield, J.M. 2007. Modelling vegetated dune landscapes. *Geophysical Research Letters* 34.

Baddeley, A. & Turner, R. 2005. spatstat: An R package for analyzing spatial point patterns. *Journal of Statistical Software* 12: 1-42.

Balke, T., Herman, P.M.J. & Bouma, T.J. 2014. Critical transitions in disturbance-driven ecosystems: identifying windows of opportunity for recovery. *Journal of Ecology* 102: 700-708.

Bendali, F., Floret, C., Le Floch, E. & Pontanier, R. 1990. The dynamics of vegetation and sand mobility in arid regions of Tunisia. *Journal of Arid Environments* 18: 21-32.

Campos, C.M., Giannoni, S.M., Taraborelli, P. & Borghi, C.E. 2007. Removal of Mesquite seeds by small rodents in the Monte Desert, Argentina. *Journal of Arid Environments* 69: 228-236.

Colwell, R.K., Dunn, R.R. & Harris, N.C. 2012. Coextinction and Persistance of Dependent Species in a Changing World. *Annual Review of Ecology, Evolution, and Systematics* 43: 183-203.

Danin, A. 1996a. Adaptations of *Stipagrostis* species to desert dunes. *Journal of Arid Environments* 34: 297-311.

Danin, A. 1996b. *Plants of desert dunes*. Springer.

Dougill, A.J. & Thomas, A.D. 2002. Nebkha dunes in the Molopo Basin, South Africa and Botswana: formation controls and their validity as indicators of soil degradation. *Journal of Arid Environments* 50: 413-428.

Du, J., Yan, P. & Dong, Y. 2010. The progress and prospects of nebkhas in arid areas. *Journal of Geographical Sciences* 20: 712-728.

El-Bana, M.I., Li, Z.Q. & Nijs, I. 2007. Role of host identity in effects of phytogenic mounds on plant assemblages and species richness on coastal arid dunes. *Journal of Vegetation Science* 18: 635-644.

El-Bana, M.I., Nijs, I. & Khedr, A.H.A. 2003. The importance of phytogenic mounds (nebkhas) for restoration of arid degraded rangelands in northern Sinai. *Restoration Ecology* 11: 317-324.

El-Bana, M.I., Nijs, I. & Kockelbergh, F. 2002. Microenvironmental and vegetational heterogeneity induced by phytogenic nebkhas in an arid coastal ecosystem. *Plant and Soil* 247: 283-293.

Field, J.P., Breshears, D.D., Whicker, J.J. & Zou, C.B. 2012. Sediment capture by vegetation patches: implications for desertification and increased resource redistribution. *Journal of Geophysical Research-Biogeosciences* 117.

Flores, J. & Jurado, E. 2003. Are nurse-protégé interactions more common among plants from arid environments? *Journal of Vegetation Science* 14: 911-916.

Friedman, J. 1971. Effect of competition by adult *Zygophyllum dumosum* Boiss. on seedlings of *Artemisia herba-alba* Asso in the Negev Desert of Israel. *Journal of Ecology* 59: 775-782.

Gadzia, J.S.G. & Ludwig, J.A. 1983. Mesquite age and size in relation to dunes and artifacts. *Southwestern Naturalist* 28: 89-94.

Goldberg, D.E. & Turner, R.M. 1986. Vegetation change and plant demography in permanent plots in the Sonoran Desert. *Ecology* 67: 695-712.

Goslee, S.C., Havstad, K.M., Peters, D.P.C., Rango, A. & Schlesinger, W.H. 2003. High-resolution images reveal rate and pattern of shrub encroachment over six decades in New Mexico, USA. *Journal of Arid Environments* 54: 755-767.

Head, J.W. & Kreslavsky, M.A. 2002. Northern lowlands of Mars: evidence for widespread volcanic flooding and tectonic deformation in the Hesperian Period. *Journal of Geophysical Research-Planets* 107.

Jones, K.R., Berney, O., Carr, D.P. & Barrett, E.C. 1981. *Arid zone hydrology for agricultural development*. FAO.

Le Houérou, H.N. & Gillet, H. 1986. Conservation versus desertization in African arid lands. In: Soulé, M.E. (ed.) *The Science of Diversity and Scarcity*. Sinauer Associates, Sunderland.

Li, S.-L., Zuidema, P.A., Yu, F.-H., Werger, M.J.A. & Dong, M. 2010. Effects of denudation and burial on growth and reproduction of *Artemisia ordosica* in Mu Us sandland. *Ecological Research* 25: 655-661.

Maliva, R. & Missimer, T. 2012. *Arid lands water evaluation and management*. Springer, Berlin.

Manly, B.F.J. 1997. *Randomization, bootstrap and Monte Carlo methods in biology*.second ed. Chapman & Hall, London.

McGrath, G.S., Paik, K. & Hinz, C. 2012. Microtopography alters self-organized vegetation patterns in water-limited ecosystems. *Journal of Geophysical Research-Biogeosciences* 117.

McIntire, E.J.B. & Fajardo, A. 2009. Beyond description: the active and effective way to infer processes from spatial patterns. *Ecology* 90: 46-56.

Miriti, M.N. 2006. Ontogenetic shift from facilitation to competition in a desert shrub. *Journal of Ecology* 94: 973-979.

Nathan, R. & Muller-Landau, H.C. 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology & Evolution* 15: 278-285.

Quets, J.J., Temmerman, S., El-Bana, M.I., Al-Rowaily, S.L., Assaeed, A.M. & Nijs, I. 2013. Unraveling landscapes with phytogenic mounds (nebkhas): an exploration of spatial pattern. *Acta Oecologica-International Journal of Ecology* 49: 53-63.

Quets, J.J., Temmerman, S., El-Bana, M.I., Al-Rowaily, S.L., Assaeed, A.M. & Nijs, I. 2014. Use of spatial analysis to test hypotheses on plant recruitment in a hyper-arid ecosystem. *PLOS ONE* 9: 11.

Rawls, W.J., Brakensiek, D.L. & Saxtonn, K.E. 1982. Estimation of soil water properties. *Transactions of the American Society of Agricultural Engineers* 25: 1316-1320.

Ren, J., Tao, L. & Liu, X.M. 2002. Effect of sand burial depth on seed germination and seedling emergence of *Calligonum* L. species. *Journal of Arid Environments* 51: 603-611.

Salguero-Gomez, R. & Casper, B.B. 2011. A hydraulic explanation for size-specific plant shrinkage: developmental hydraulic sectoriality. *New Phytologist* 189: 229-240.

Scheffer, M. 2009. *Critical Transitions in Nature and Society*. Princeton, Princeton.

Schlesinger, W.H., Reynolds, J.F., Cunningham, G.L., Huenneke, L.F., Jarrell, W.M., Virginia, R.A. & Whitford, W.G. 1990. Biological feedbacks in global desertification. *Science* 247: 1043-1048.

van der Heijden, M.G.A. & Horton, T.R. 2009. Socialism in soil? The importance of mycorrhizal fungal networks for facilitation in natural ecosystems. *Journal of Ecology* 97: 1139-1150.

Vincent, P. 2008. *Saudi Arabia and environmental overview*. Taylor & Francis/Balkema, London.

Wiegand, T. & Moloney, K.A. 2004. Rings, circles, and null-models for point pattern analysis in ecology. *Oikos* 104: 209-229.

Xu, G.Q., Yu, D.D., Xie, J.B., Tang, L.S. & Li, Y. 2014. What makes *Haloxylon persicum* grow on sand dunes while *H. ammodendron* grows on interdune lowlands: a proof from reciprocal transplant experiments. *Journal of Arid Land* 6: 581-591.

Zhao, W.Z., Li, Q.Y. & Fang, H.Y. 2007. Effects of sand burial disturbance on seedling growth of *Nitraria sphaerocarpa*. *Plant and Soil* 295: 95-102.

Zheng, M., Lai, L., Jiang, L., An, P., Yu, Y., Zheng, Y., Shimizu, H., Baskin, J.M. & Baskin, C.C. 2012. Moderate water supply and partial sand burial increase relative growth rate of two *Artemisia* species in an inland sandy land. *Journal of Arid Environments* 85: 105-113.

Supplementary Material

Appendix A: Germination experiment

To assess the overall *R. stricta* seed limitation in the study site, and to experimentally determine whether its spatial distribution can explain the observed recruit distribution, we performed an experiment using soil gathered from either vegetation-free regions or locations with high recruit densities across the study site. The gathered soil was put into plastic trays (0.7 × 0.5 × 0.07 m), which were split in two parts using cardboard and subsequently placed outdoors under a nethouse to avoid seed predation by birds and rodents. One part of each tray did not receive additional seeds, while the other part was saturated with one hundred *R. stricta* seeds. After seed planting, water limitation was removed by manual irrigation in both parts of all trays to promote recruit emergence. Emerged recruits were subsequently censused every three to four days until recruit numbers stabilized or declined in every tray.

We compared the maximum numbers of recruits emerged from tray parts saturated with seeds with those emerged from tray parts without seed addition, for both location types (i.e. for soil sampled in vegetation-free locations and in locations with high recruit density). The greater the difference in emerged recruit number between the two parts, the stronger the inferred local seed limitation, for each location type. We also compared the maximum number of emerged recruits between soil location types. In case significantly less recruits arise from trays filled with soil from vegetation-free locations compared to trays filled with soil from locations with high recruit density, we infer that spatial seed distribution significantly contributes to the spatial distribution of recruits (especially for the tray parts without seed addition as the difference in seed number will be potentially diluted in tray parts with seed addition).

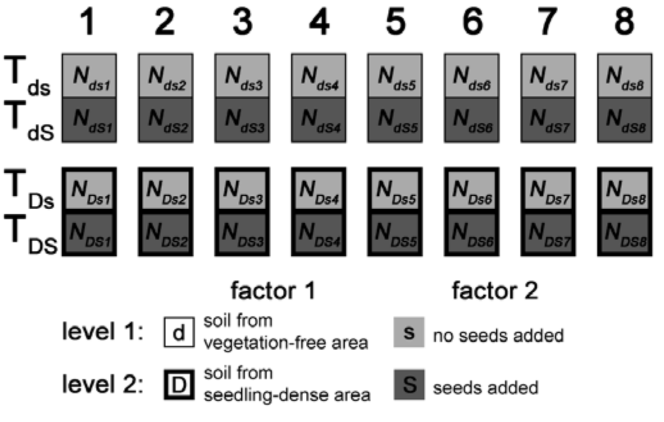


Figure A.1 Experimental design of the two-factorial two-level germination experiment. Rectangles symbolize trays filled with soil samples. Sixteen pooled soil samples were taken from either recruit-free

areas (trays with thin borders in the figure; level 1 of factor 1, denoted by 'd') or from recruit-dense areas (trays with thick borders in the figure; level 2 of factor 1, denoted by 'D'). Each tray was split in two parts, either receiving no seeds (light grey in the figure; level 1 of factor 2, denoted by 's'), or an additional 100 *R. stricta* seeds (dark grey in the figure; level 2 of factor 2, denoted by 'S'). The four treatments T_{sd}, T_{Sd}, T_{sD}, and T_{SD}, signify all possible factor level combinations. N_{xyi} represents the number of emerged recruits for level $x \in \{d, D\}$ of factor 1, level $y \in \{s, S\}$ of factor 2, and replicate $i \in \{1, 2, \ldots, 8\}$.

The soil samples for the seed experiment were acquired by first selecting 16 non-overlapping 7 × 7 m sized plots in the study site. Eight of these plots were strategically placed as to not contain recruits or any other vegetation, while in the other eight plots within-plot recruit densities were chosen to be high (i.e. lying in the upper quartile of recruit densities occurring in the study site, as measured in a grid with 7 × 7 m cells). Nebkhas were avoided as much as possible inside all 16 plots. Within each plot, soil was sampled in four randomly placed 0.5 × 0.5 m quadrats, which were pooled into one soil sample and placed in a tray. These quadrats were laid at least 2 m from *R. stricta* adults if present. Soil was never sampled deeper than 0.05 m, as most seeds of desert shrubs generally reside in the upper most soil layer.

The number of emerged recruits from trays generally peaked four to five weeks after seed planting (not shown), but recruit numbers were censused until eleven weeks after the start of the experiment. Significantly more recruits emerged from tray parts with added seeds compared to the tray parts without seed addition, both for trays filled with soil sampled in vegetation-free [$E(n) = 6.50$ versus 0.25; $p = 0.02$] and recruit-dense [$E(n) = 3.75$ versus 0.13; $p = 0.03$] areas. Tray parts without seed addition did not significantly differ ($p = 0.66$) in recruit emergence density between soil from vegetation-free and recruit-dense areas, probably because few recruits emerged in those tray parts which made the statistical power of these tests inadequate. These results strongly indicate that recruit emergence may be enhanced in all parts of the study site by adding more seeds to the soil.

Appendix B: Field campaign details

During each field campaign, we firstly placed ground control points with known coordinates in the study site; secondly we attached and gyro-stabilized a digital camera underneath the aircraft of use (a Ricoh GX200 during t_1 and t_2, and a Canon IXUS 220 hs during t_3 and t_4); and thirdly we navigated this aircraft along parallel linear tracks, either with the help of people acting as guides in case of the tethered helikite, or using waypoint software (i.e. MikroKopterTool) in case of the drone.

Aircraft altitudes were kept below 22.5 m to ensure image resolutions of at least 100 pixels per meter. During flights, consecutive pictures considerably overlapped, thereby making each part of the study site visible on at least two different pictures, which was a requirement for subsequent photogrammetric modeling. Pictures shot during field campaigns were next post-processed, using photogrammetric software (Agisoft PhotoScan Professional), into orthoimages based on t_1, t_2, t_3, and t_4 data, and a digital elevation model of the inter-nebkha using t_4 data. The digital elevation model was chosen to be constructed from t_4 data as it made use of the most ground control points.

Four ground control points were placed in t_1 and t_2, eight in t_3, and ten in t_4. Ground control points were the corners of a carpet with known dimensions (i.e. 2.9 m × 1.9 m) in t_1, and centers of rubber doormats spread over the study site in t_2, t_3 and t_4. Doormat centers were marked with fluorescent duct tape.

During the last three campaigns (i.e. in t_2, t_3, and t_4) ground control point coordinates were measured with a total station (Leica Builder 405) placed above a fixed geodetic control point (i.e. the ground-level center of a transmission tower 230 m south to the study site's southeast corner), which served as the origin of a local reference system. Another fixed control point (a transmission tower located 430 m to the southeast of the former one) formed together with the location of the total station a fixed direction, which served as one of the two perpendicular axes of the aforementioned local reference system. In this way, ground control point coordinates were measured in identical local metric coordinate systems for the last three field campaigns.

The metric coordinates of the ground control points were later transformed into geographical coordinates (i.e. latitude and longitude data), using the known geographical coordinates of the total station (as measured with a Garmin Foretrex 401 GPS device in 2010), and the known azimuth (i.e. the angular deviation from the north) of the shadow of a vertically leveled stick on a horizontally leveled plate (using a self-made sun shadow tool placed inside the study site). Indeed, since produced pictures were provided with date and time stamp, solar positions as occurring during camera shots could be calculated from aerial pictures. Therefore, the stick shadow of the sun shadow tool allowed us to correctly align imagery along the North-South axis.