

A mechanism of self-organization in a desert with phytogenic mounds

JAN J. QUETS,^{1,†} MAGDY I. EL-BANA,² SAUD L. AL-ROWAILY,³ ABDULAZIZ M. ASSAEED,³ STIJN TEMMERMAN,⁴ AND IVAN NIJS¹

¹Department of Biology, Center of Excellence PLECO (Plant and Vegetation Ecology), University of Antwerp, Universiteitsplein 1, BE-2610 Wilrijk, Belgium

²Department of Botany, Faculty of Science, Port Said University, 42521 Port Said, Egypt

³Department of Plant Production, College of Agriculture, King Saud University, PO Box 2460, Riyadh, Saudi Arabia

⁴Ecosystem Management, Department of Biology, University of Antwerp, Universiteitsplein 1, BE-2610 Wilrijk, Belgium

Citation: Quets, J. J., M. I. El-Bana, S. L. Al-Rowaily, A. M. Assaeed, S. Temmerman, and I. Nijs. 2016. A mechanism of self-organization in a desert with phytogenic mounds. *Ecosphere* 7(11):e01494. 10.1002/ecs2.1494

Abstract. Phytogenic mounds or nebkhas are formed by spatially isolated burial-tolerant plants, which have been trapping windborne sediment within their canopies. They occur in drylands all over the world, and nebkha landscapes are considered intermediate between stable grasslands and unstable deserts with mobile dunes. Depending on the previous state of the landscape, they can thus be viewed both as indicators of desertification and as signs of stabilization. While individual nebkha mounds have been studied extensively, little is known about the organization of nebkha landscapes. In this study, we collected spatiotemporal data of vegetation and topography from four self-made remotely sensed maps, created over a three-year period from a study site in central Saudi Arabia dominated by the nebkha-forming shrub *Rhazya stricta* Decne. Using logistic regressions and *t* tests, we found that the nebkha shrubs grow in topographic depressions, while they shrink on topographic highs and in locations with high nebkha densities. We propose that this spatial variation in nebkha growth is driven by water availability, as the few extreme rain events that typically make up the bulk of precipitation in deserts would spatially redistribute to topographic lows, and as nebkha density would positively correlate with competition for water. Our data suggest a novel mechanism of biogeomorphological self-organization in deserts. The observed nebkha growth in depressions would lead to increased sedimentation on and in between the nebkhas owing to reduced wind speed, which after a time lag might transform depressions into topographic highs on which nebkhas tend to shrink because of water shortage. Shrinking nebkhas, in turn, could provoke soil erosion, on as well as in between the nebkha mounds, which may ultimately transform topographic highs into depressions, thereby closing the cycle of self-organization.

Key words: digital elevation model (DEM); nebkhas; plant shrinkage; *Rhazya stricta* Decne.; Saudi Arabia; spatial ecology; spatial randomization; surface runoff; topography; unmanned aerial vehicle; vegetation pattern.

Received 25 April 2016; **accepted** 12 July 2016. Corresponding Editor: D. P. C. Peters.

Copyright: © 2016 Quets et al. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

† **E-mail:** jqquets@gmail.com

INTRODUCTION

Phytogenic mounds or nebkhas are vegetated hummocks composed of burial-tolerant desert plants, which frequently undergo windborne sediment deposition (Hesp and McLachlan 2000). The mound-forming process is triggered by wind

speed reduction in sediment-laden air inside the nebkha canopy (Danin 1996). Suitable habitats for nebkhas thus rely on the presence of exposed sediments available for eolian transport and are therefore often extensively found in drylands worldwide (Quets et al. 2013). Because nebkhas increase surface roughness (King et al. 2006),

they restrict the eolian sediment flux above the landscape (Danin 1996), thereby reducing sand abrasion stress on plant communities and resisting desert expansion (Okin et al. 2006). Moreover, nebkhas can be significant hot spots of resource concentration (soil nutrients and water) as well as hot spots of biodiversity in an otherwise species-poor desert landscape (El-Bana et al. 2007). Overall, nebkhas thus actively contribute to resource sustainability in drylands and are consequently recommended in restoration projects of degraded rangelands (El-Bana et al. 2003).

Similar to dryland species in general, nebkha host plant species apply different strategies in coping with drought (Batanouny 2001). An overlooked and underrated strategy is the size plasticity found in many long-lived, usually larger desert shrubs (Goldberg and Turner 1986, Salguero-Gomez and Casper 2010), which allows healthy plants to shrink and regrow depending on water availability (Salguero-Gomez and Casper 2011). This protects against mortality from extreme drought and accelerates recovery afterward (Salguero-Gomez and Casper 2010). As precipitation is highly temporally variable in drylands (Warner 2004), the vegetation cover of size-adaptive dryland species temporally oscillates, not so much because of imbalances between recruitment and death rates, but rather through these size fluctuations of already established surviving individuals (Goldberg and Turner 1986). Although rains are scarce in deserts, most of the long-term total amount of rainwater provided to the soil, falls in rain events with intensities much higher than the average, particularly in hyper-arid deserts (Huxman 2004). Runoff generation is therefore not unlikely in deserts (Nicholson 2011). Topography may induce a redistribution of this runoff water, thereby forming ephemeral ponds and streams (Belsky 1986, Klausmeier 1999, Ludwig 2005), as also often seen in Saudi Arabian desert landscapes (e.g., Fig. 1) by the authors from this article. As a consequence, drought stress can vary spatially as well, besides temporally. Finally, landscape parts with high vegetation cover would also invoke drought stress inflicted by root competition for water.

In this study, we investigate whether the nebkha host plant *Rhazya stricta* Decne. is subject to periodic shrinkage and growth. We hypothesize that the dimensions of such size-adaptive shrubs

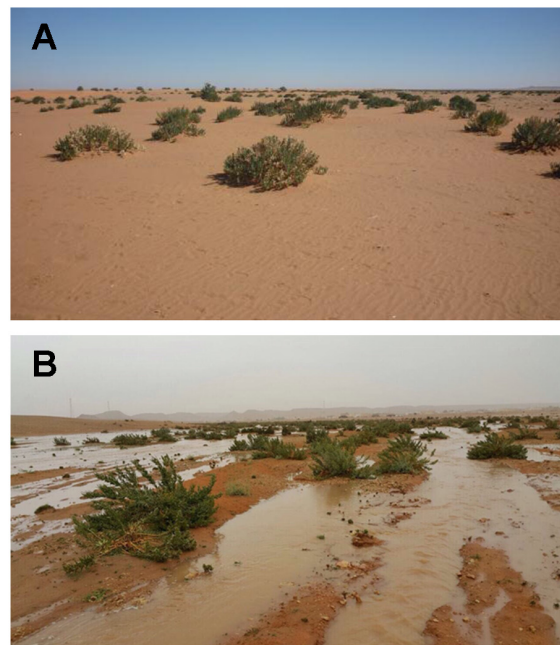


Fig. 1. Landscapes dominated by *Rhazya stricta* in central Saudi Arabia. Site in dry circumstances (A) and a site after a severe rainstorm, with the depressions flooded by runoff water (B) (photographs: Abdulaziz Assaeed).

not only oscillate in time, but also in space in the presence of mobile sediment, leading to a self-organizing mechanism between nebkha vegetation and topography. Indeed, eolian sediment can either erode or settle down in between nebkhas (besides the above-mentioned intra-canopy sediment deposition which creates the nebkhas), depending on whether local nebkha cover is low or high, thereby affecting the surface topography of the internebkha landscape (Gibbens et al. 1983, Field et al. 2012, Sankey et al. 2012). Self-organization would ensue from expansion of the nebkha shrubs in moister topographic depressions and concurrent shrinkage on drier topographic highs and in places with high nebkha cover, even when the nebkha cover over the entire study site remains unchanged. Such spatial reallocation of vegetation cover would in turn reorganize the internebkha topography through sedimentation in areas with expanding nebkhas (owing to lowered wind speed) as opposed to erosion in areas with shrinking nebkhas (owing to enhanced wind speed). Over time, topographic

depressions would thus become elevations and vice versa, closing the feedback loop between nebkha cover and topography.

Biogeomorphological feedbacks between biological and geomorphological systems have been shown to structure several ecosystems (Murray et al. 2008, Reinhardt et al. 2010, Corenblit et al. 2011). We hypothesize that a biogeomorphological feedback between nebkha vegetation and topography can be a driving mechanism for spatial self-organization in nebkha landscapes.

METHODS

Rhazya stricta is a long-lived desert shrub which dominates significant portions of the Arabian Peninsula and is left unaffected by browsers due to its toxicity (Assaeed and Al-Doss 2002). It tolerates sediment-burial and is thereby able to form nebkhas. We selected a 2.56 ha study site (25.510° N, 46.002° E, Fig. 1A), dominated by the unpalatable *R. stricta* owing to camel grazing and browsing on almost all other species, at about 120 km northeast of Riyadh, Saudi Arabia. The largest *R. stricta* nebkhas at the site slightly exceeded 4 m in diameter. No sediment tails were found behind the nebkhas, which indicates the absence of dominant unidirectional winds (Danin 1996). This is also evidenced by literature (Vincent 2008), which reported multidirectional winds in this region.

Long-term averages of annual precipitation and pan evaporation in the region are 83 and 2816 mm, respectively (Vincent 2008), which indicates a hyperarid desert climate (Arnold 1992). However, total rainfall in a particular year can be much higher than average as it greatly varies interannually, for example, from 33 to 317 mm in a 23-yr data series running from 1985 to 2007 as obtained from the meteorological station 40,437 of King Khalid International Airport, Riyadh.

The soil in the study site consists of a CaCO₃ cemented layer with on top a mobile layer of loose unconsolidated sediment, varying in thickness between a few mm to almost one m, also in between nebkhas. Textures of both these soil layers belong to the sandy clay loam class (USDA texture triangle). This soil thus contains a high clay component (>20%), which reduces the infiltration capacity (i.e., the maximum rate of water infiltration) to about 4 mm/h (Rawls et al. 1982). As about 50% of

all rain in most of Saudi Arabia occurs at intensities even higher than 20 mm/h (Jones et al. 1981), it follows that runoff generation in our study site is the rule rather than the exception, which coincides with our experience in the field.

The study site (Fig. 2) was photographed four times, that is, in December 2010 (t_1), March 2012 (t_2), April 2013 (t_3), and February 2014 (t_4), using a camera attached to an unmanned aerial vehicle (either an Allsopp Skyhook 3.3 m³ helikite, or a MikroKopter Okto-XL drone). Each of these field campaigns yielded a set of partially overlapping high-resolution (>100 pixels/m) RGB pictures, from which orthoimages were produced using photogrammetric software (Agisoft Photoscan Pro, Saint Petersburg, Russia). A digital elevation model of the landscape at t_4 was created with the same software. Orthoimages were downsampled to a resolution of 100 pixels/m, the digital elevation model to 20 pixels/m. A recent comparative study on the accuracy of digital elevation models made from low-altitude imagery (Harwin et al. 2015) showed that the vertical root-mean-square error of a digital elevation model of a 50 m wide beach stroke in Tasmania, made using the same methodology and software as in our study, was lower than 1.2 cm. This gives an indication of the vertical error of the digital elevation model constructed here. Binary maps were created from the orthoimages, to distinguish nebkha vegetation from background bare soil, using Photoshop CS5. Hereto, the canopy edges of individual nebkhas were manually delineated as they appeared on the orthoimages, with high precision as allowed by the aforementioned high spatial resolution of these images (i.e., 100 pixels/m).

To avoid confusion, it is crucial to understand that the topography mentioned in the remainder of this article will never refer to the nebkha mounds themselves, but solely to the internebkha elevations. Nebkhas were therefore removed from the digital elevation model. Hereto, digital elevation model values within nebkha contours (determined from the orthoimages as explained above) were replaced by values interpolated from digital elevation model values just outside these contours using the `inpaint_nans` script (D'Errico 2004) in MATLAB R2011a (MathWorks, Natick, Massachusetts, USA), yielding a nebkha-free digital elevation model. As most topographic elevations and depressions in between the nebkhas were

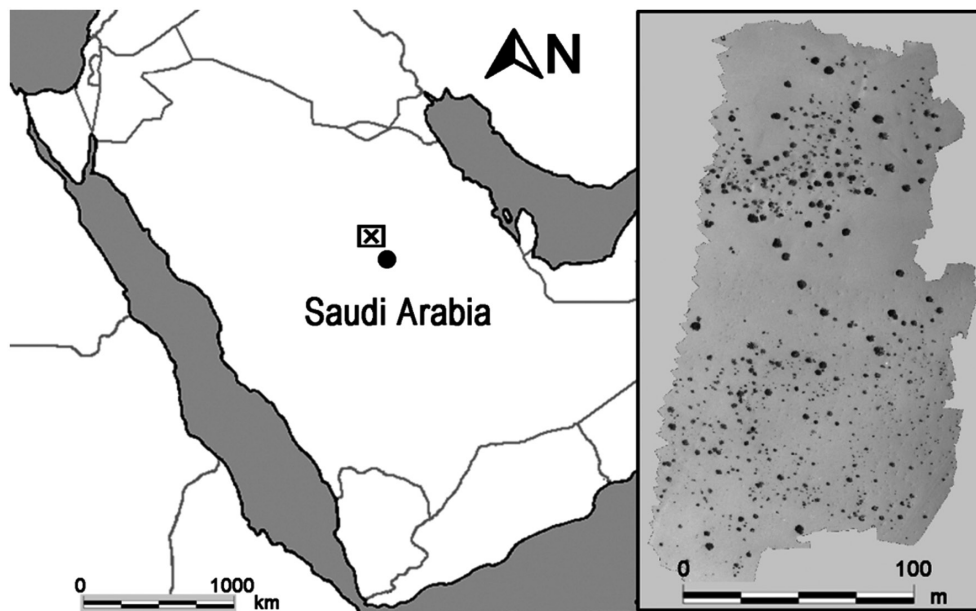


Fig. 2. Study site. Left: Arabian Peninsula and Saudi Arabia. The black dot indicates Riyadh and the crossed box the study site. Right: orthoimage of the study site at t_2 , with nebkha host plants visible in black.

estimated to have extents of about 10 m diameter, a smoothed nebkha-free digital elevation model using a 10 m radius median filter was subtracted from the original nonsmoothed nebkha-free digital elevation model, in order to acquire a map of local topographic deviation (LTD; Head et al. 2002). This map was subsequently classified into deep ($LTD < -10$ cm) and shallow (-10 cm $< LTD < -5$ cm) parts of topographic depressions, and lower ($+5$ cm $< LTD < +10$ cm) and higher ($LTD > +10$ cm) parts of topographic elevations, as well as flat terrain (-5 cm $< LTD < +5$ cm). The borders of those classes were chosen as to divide the landscape into parts of approximately similar size. From the binary images, we first calculated the *R. stricta* mean-field nebkha cover, that is, the fraction of the site covered with nebkha vegetation, as well as the absolute mean-field nebkha cover changes during the time intervals t_{1-2} , t_{2-3} , and t_{3-4} . We also obtained local nebkha cover data by calculating the nebkha cover inside contiguous 10×10 m² grid cells, for t_1 , t_2 , t_3 , and t_4 . Next, we examined whether vegetation patches in the site could both grow and shrink, and if so, whether the proportion of growing or shrinking nebkhas depended on the LTD (because of runoff water redistribution), the local nebkha cover (because of competition), or the nebkha size, the latter of which was observed previously in

desert shrubs (Salguero-Gomez and Casper 2011). Hereto, we performed logistic regressions, separately on t_{1-2} , t_{2-3} , and t_{3-4} data, with the response variable Y , indicating whether a preexisting nebkha had either been growing ($Y = 0$) or shrinking ($Y = 1$) during the time interval under study, and LTD, local nebkha cover (excluding the focus nebkha), and nebkha size as explanatory variables. We further determined whether absolute nebkha cover changes during t_{1-2} , t_{2-3} , and t_{3-4} were negative on topographic highs ($LTD > +5$ cm) and positive in topographic depressions ($LTD < -5$ cm) using one-tailed t tests.

Rainfall records from Riyadh's King Khalid International Airport meteorological station 40,437 reported an above-average wet time interval during t_{1-2} , and average wet periods during t_{2-3} , and t_{3-4} . The last three months of t_{3-4} suffered from increased human disturbance due to more intense camel herd trampling.

RESULTS

The mean-field nebkha cover in the study site was 3.2% at t_1 , strongly expanded to 4.8% at t_2 , and remained quasi stable thereafter (Fig. 3). For all three studied time intervals, the probability of nebkha shrinkage increased with rising LTD

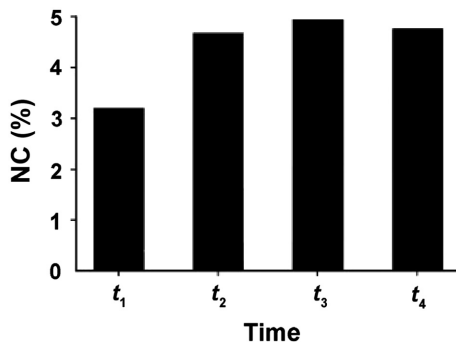


Fig. 3. Nebkha cover (NC) of the study site, measured at t_1 , t_2 , t_3 , and t_4 .

values (i.e., rising height of local topographic highs in the internebkha space, $P < 0.05$) (Fig. 4). However, despite that nebkhas tended to shrink more intensely on topographic elevations, more nebkha cover was found on these locations (Fig. 5); this paradox will be explained in the next section. The probability of nebkha shrinkage (Fig. 4) was also promoted by higher nebkha cover ($P < 0.05$), except in the wet year (i.e., during t_{1-2}). During the last time interval t_{3-4} which suffered from strong human disturbance, the probability of shrinkage was additionally higher for larger nebkhas ($P < 0.05$).

In topographic depressions, changes in nebkha cover were significantly positive for all time intervals, while they were significantly negative on internebkha highs with the exception of t_{1-2} (Fig. 6). Nebkha cover thus spatially reallocated from topographic internebkha highs toward depressions (see t_{2-3} and t_{3-4} in Fig. 6), as the mean-field nebkha cover, as measured over the entire study site, stayed quasi-steady-state during these time periods (Fig. 3).

DISCUSSION

Patterned vegetation is sighted in drylands worldwide (Klausmeier 1999) and has been studied since decades (Watt 1947). Roughly two kinds of processes underlying vegetation mosaics are proposed in literature, depending on whether they occur in homogeneous or heterogeneous environments.

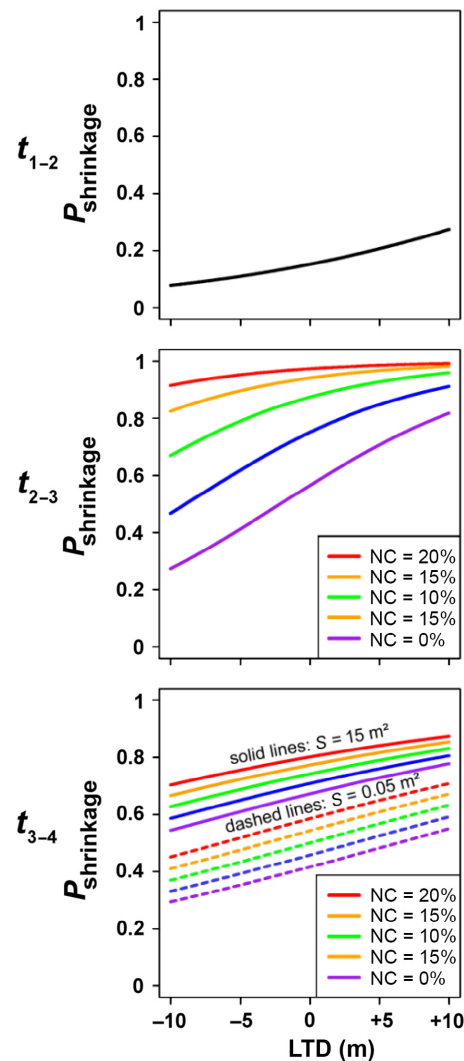


Fig. 4. Stepwise logistic regressions of the response variable “probability of shrinkage of a vegetation patch ($P_{shrinkage}$)” during t_{1-2} , t_{2-3} , or t_{3-4} vs. the explanatory variables local topographic deviation (LTD), nebkha cover (NC), and vegetation patch size (S). The prefix “stepwise” indicates that nonsignificant explanatory variables were omitted from the regressions, starting from the least significant. The logistic regression was simplified by treating the LTD classes (i.e., $]-\infty, -10[$ cm, $]-10, -5[$ cm, $]-5, +5[$ cm, $]+5, +10[$ cm, and $]+10, \infty[$ cm) as values of a continuous LTD variable (i.e., -10 cm, -5 cm, 0 cm, $+5$ cm, $+10$ cm, respectively), as recommended by Campbell (2006).

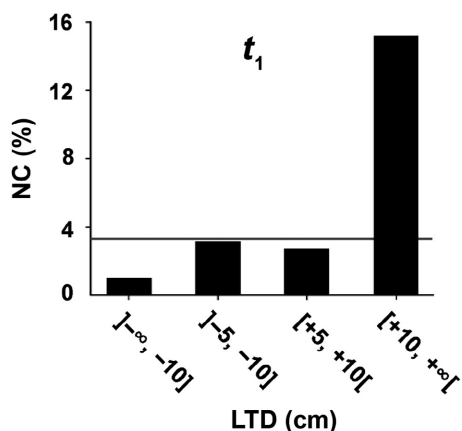


Fig. 5. Nebkha cover (NC) in function of local topographic deviation (LTD), as observed in t_1 . The gray horizontal line marks the NC value spatially averaged over the study site.

In homogeneous environments, vegetation mosaics can emerge when plants are ecological engineers, which introduce heterogeneity in a previously homogeneous environment. A popular example of such type of process involves the spatial redistribution of plant resources (e.g., soil water) by opposing scale-dependent feedbacks between vegetation and the resource levels in their near surroundings (Lejeune et al. 2002, Meron et al. 2004, Rietkerk et al. 2004). According to this theory, facilitation takes place nearby vegetation, for example, owing to better soil water retention driven by locally increased soil organic matter content (Schlesinger et al. 1990), while inhibition occurs at further distances from vegetation patches, for example, because of underground root competition for water (Firbank and Watkinson 1987, Miriti et al. 2001, Belkheiri and Mulas 2013). This would eventually lead to a stable, static, self-organized, and spatially regular distribution of equally sized vegetation patches with regular interdistances (Gilad et al. 2007). Such regular patterns have been observed in several desert landscapes worldwide (Deblauwe et al. 2008). However, many vegetation patterns in deserts also strongly deviate from such a regular configuration (Anderson 1971), one of them being the pattern explored in the current study which is spatially highly irregular (Fig. 2) and has a pronouncedly skewed patch size distribution (Quets et al. 2014). Therefore, we infer that

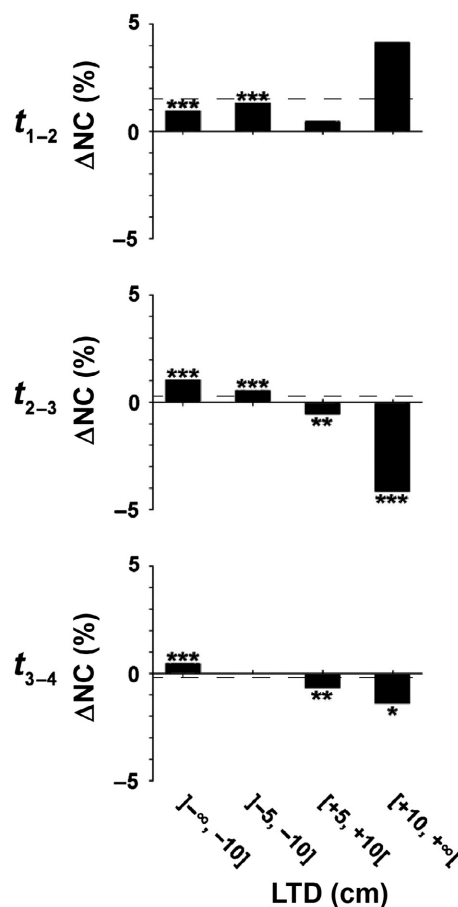


Fig. 6. Absolute changes of nebkha cover (ΔNC) for each class of local topographic deviation (LTD), as occurred during t_{1-2} , t_{2-3} , and t_{3-4} . The dashed line indicates the nebkha cover change over the entire study site. Significances of deviations from zero are indicated by * ($P < 0.05$), ** ($P < 0.01$), or *** ($P < 0.001$).

the vegetation pattern observed in our study site did not emerge from above-mentioned opposing scale-dependent feedbacks, at least not in the first place.

On the other hand, vegetation mosaics can also simply arise when conditions sufficient for plant growth and survival are a priori heterogeneously distributed in space. For instance, topographic deviations can introduce soil moisture heterogeneity as mediated by runoff water redistribution, causing vegetation patterns to visualize those soil moisture patterns that sustain plant life (Belsky 1986, Klausmeier 1999, McGrath et al. 2012). In our study site, the varying topographic

relief and high runoff potential of the soil surface significantly influenced the vegetation pattern of nebkhas as well. However, we did not find that topographic highs had the lowest vegetation cover and topographic lows the highest, in fact we found the opposite (Fig. 5). This may seem at odds with runoff water flowing from highs to lows. However, such a relationship is consistent with our proposed theory of biogeomorphological self-organization, which relates topographic heterogeneity with presence of nebkhas, as explained in the next paragraph. Nevertheless, more nebkhas shrunk on topographic internebkha highs as compared to internebkha depressions, which lead to a pronounced decrease and increase of vegetation cover at these respective locations. This happened while the spatially averaged change of nebkha cover over the entire study site was negligible. Only in a wet year the pattern was broken, which makes sense as water limitation is then lifted throughout the landscape, leading to a significant increase in total nebkha cover. To our knowledge, no study hitherto demonstrated a spatially explicit link between growth or shrinkage of vegetation cover and topographic setting at constant spatially averaged overall vegetation cover.

We suggest that the formation of mounds by nebkha-forming plants in our study site may generate a feedback cycle of events that leads to self-organization (Fig. 7), which is different from the self-organizing principle emerging from scale-dependent feedbacks. The cycle starts with the reduction of wind speed in areas with high local nebkha cover, owing to their greater surface roughness compared to more barren areas. The resulting sedimentation (deposition of particles, also between the nebkhas) elevates these landscape parts with abundant nebkhas, thereby converging the runoff water during rainfall events in topographic depressions with lower local nebkha cover. As a consequence, soil moisture progressively improves over time in areas with few nebkhas while it deteriorates in areas highly covered with nebkhas, respectively, promoting and suppressing the growth of existing nebkhas and the emergence of new seedlings. Topographic lows may thus eventually become abundant in nebkhas, which subsequently elevates these areas. The nebkhas on topographic highs, on the other hand, decline, which might bring erosion

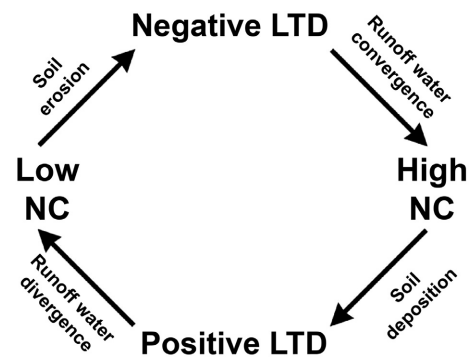


Fig. 7. Proposed feedback loop between nebkha cover (NC) and local topographic deviation (LTD) in deserts with phytogenic mounds.

and eventually topographic depression. Here, the cycle recommences (Fig. 7). Rates of sedimentation, erosion, plant growth, and shrinkage may all have an impact on the loop frequency of this feedback cycle: Higher rates of such processes should lead to faster feedback cycles because the steps inside the loop would take less time. Sedimentation and erosion rates may depend on wind velocity, availability of source material of eolian sediment, vegetation cover, and also on the morphology and sizes of individual nebkhas. Rates of plant growth and shrinkage are dependent on the size plasticity of the plant species involved, and on meteorological conditions.

The fact that topographic highs have the highest vegetation cover and topographic lows the lowest (Fig. 5) is consistent with our theory (Fig. 7). Indeed, although shrinkage or growth can be an immediate response to changing soil moisture levels (Li et al. 2015), it may take more time for nebkhas to grow above (or shrink under) a certain threshold level. Therefore, while values of vegetation cover decline on topographic highs, they may be still high, as an inheritance resulting from the former inversed topography.

Our findings and proposed feedback loop may not be generalizable to all nebkha fields on Earth. For topography to be able to redistribute runoff, runoff has to be generated in the first place. Both highly intense rainfall events and low-infiltration soils encourage runoff production, and both were present in our study site. Although highly intense rainfall is common in most deserts worldwide, especially in hyperarid climates (Nicholson 2011), soils with textures of low-infiltration capacity

may be less prevalent. Nevertheless, soil microbial crust and soil trampling by cattle may underlie runoff generation in deserts as well (Laity 2008). In more coarsely textured sediments lacking microbial crust, most rainfall will probably infiltrate, thereby suppressing the production of runoff. However, when such a surface layer is shallow and lays on top of a cemented layer less permeable than the top soil, soil moisture will likely concentrate in depressions too, because of water logging above the cemented layer.

The nebkha plants in our study site were able to significantly shrink in adverse circumstances while staying healthy. Without this size plasticity, the feedback loop shown in Fig. 7 would not work. Although size plasticity has been observed in many desert shrub species, this feature is at present understudied (Salguero-Gomez and Casper 2010), so its worldwide prevalence in nebkha fields is yet unknown. Shrinking can also occur from browsing or grazing by cattle, without being related to topography. However, in our study there was no browsing because the nebkha host plant *R. stricta* is toxic for animals. The findings in our study indicate that the growth or shrinkage of nebkha shrubs is dependent on surface soil moisture. This implies that the root system of *R. stricta* would be mostly superficial. In general, root systems of desert shrubs are highly variable. They can have varying extents of lateral roots and a prominent taproot may be present or absent. The importance of surface soil moisture may weaken when nebkhas have access to groundwater via taproots.

Although many self-organized ecosystems are deemed to be at risk of catastrophic shifts toward a degraded ecosystem state (Kéfi et al. 2014), we did not find liable mechanisms leading to such catastrophic shifts in the proposed self-organizing patchy nebkha landscape. Indeed, the main concentration mechanism of precipitation water—which supposedly controls the hot spots for regeneration and growth of nebkha vegetation—is driven by topographic variation, which is inherent to deserts with mobile sediment, even without vegetation (Bagnold 1941). Therefore, a regime shift of deserts with nebkhas toward deserts without vegetation does not seem as irreversible as in other self-organized ecosystems. However, seed limitation in landscapes without vegetation could make the degraded ecosystem

state difficult to reverse. Nevertheless, the obstacle of seed limitation in reversing empty deserts to greener drylands is not specific to the self-organizing principle in this study.

Future research, more focused on measuring changes of topography induced by the presence or absence of vegetation is needed to further support our above-inferred theory of biogeomorphological self-organization, in order to test its importance for causing vegetation patchiness in nebkha landscapes. Long-term temporal studies on space or airborne imagery might search for spatiotemporal oscillations of vegetation cover in nebkha landscapes, in order to detect the self-organizing mechanism proposed in this study. Observation of such oscillations could detect catastrophic shifts from grassland to nebkhaland post factum. Modeling work incorporating feedbacks between topography and vegetation cover might further reveal yet unknown implications for the vulnerability and stability of nebkha ecosystems under climate change.

CONCLUSIONS

Nebkha growth was positive in depressions, interpreted as the result of better soil moisture conditions, and negative, mostly even leading to strong size shrinkage, on topographic highs, understood as the outcome of low available soil moisture. These findings imply that the vegetation cover in landscapes with phytogenic mounds can be spatially rearranged between years, at least in deserts with high runoff potential, yielding a dynamic equilibrium where nebkha cover and topography oscillate both in time and space.

ACKNOWLEDGMENTS

We thank Dmitry Semenov and Alexey Pasumansky from Agisoft, for their excellent customer service on Agisoft software. We are also grateful to B.A. Dar, who was of tremendous help in most aspects of the fieldwork. This project was supported by the NSTIP strategic technologies program in the Kingdom of Saudi Arabia, as project 11-ENV1471-02, and project G014709N of Research Foundation—Flanders (FWO).

LITERATURE CITED

Anderson, D. J. 1971. Pattern in desert perennials. *Journal of Ecology* 59:555–560.

- Arnold, E. 1992. World atlas of desertification. UNEP, London, UK.
- Assaeed, A. M., and A. A. Al-Doss. 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.
- Bagnold, R. A. 1941. The physics of blown sand and desert dunes. Methuen, London, UK.
- Batanouny, K. H. 2001. Plants in the deserts of the Middle East. Springer, New York, New York, USA.
- Belkheiri, O., and M. Mulas. 2013. Effect of water stress on growth, water use efficiency and gas exchange as related to osmotic adjustment of two halophytes *Atriplex* spp. *Functional Plant Biology* 40:466–474.
- Belsky, A. J. 1986. Population and community processes in a mosaic grassland in the Serengeti, Tanzania. *Journal of Ecology* 74:841–856.
- Campbell, M. J. 2006. Statistics at square two. Second edition. Blackwell, Malden, Massachusetts, USA.
- Corenblit, D., A. C. W. Baas, G. Bornette, J. Darrozes, S. Delmotte, R. A. Francis, A. M. Gurnell, F. Julien, R. J. Naiman, and J. Steiger. 2011. Feedbacks between geomorphology and biota controlling Earth surface processes and landforms: a review of foundation concepts and current understandings. *Earth-Science Reviews* 106:307–331.
- Danin, A. 1996. Plants of desert dunes. Springer, Berlin, Germany.
- Deblauwe, V., N. Barbier, P. Couteron, O. Lejeune, and J. Bogaert. 2008. The global biogeography of semi-arid periodic vegetation patterns. *Global Ecology and Biogeography* 17:715–723.
- D'Errico, J. 2004. Inpaint_nans. MATLAB central file exchange. MathWorks, Natick, Massachusetts, USA.
- El-Bana, M. I., Z. Q. Li, and I. Nijs. 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., I. Nijs, and A. H. A. Khedr. 2003. The importance of phytogenic mounds (nebkhas) for restoration of arid degraded rangelands in northern Sinai. *Restoration Ecology* 11:317–324.
- Field, J. P., D. D. Breshears, J. J. Whicker, and C. B. Zou. 2012. Sediment capture by vegetation patches: implications for desertification and increased resource redistribution. *Journal of Geophysical Research. Biogeosciences* 117:G01033.
- Firbank, L. G., and A. R. Watkinson. 1987. On the analysis of competition at the level of the individual plant. *Oecologia* 71:308–317.
- Gibbens, R. P., J. M. Tromble, J. T. Hennessy, and M. Cardenas. 1983. Soil movement in Mesquite dunelands and former grasslands of southern New-Mexico from 1933 to 1980. *Journal of Range Management* 36:145–148.
- Gilad, E., M. Shachak, and E. Meron. 2007. Dynamics and spatial organization of plant communities in water-limited systems. *Theoretical Population Biology* 72:214–230.
- Goldberg, D. E., and R. M. Turner. 1986. Vegetation change and plant demography in permanent plots in the Sonoran Desert. *Ecology* 67:695–712.
- Harwin, S., A. Lucieer, and J. Osborn. 2015. The impact of the calibration method on the accuracy of point clouds derived using unmanned aerial vehicle multi-view stereopsis. *Remote Sensing* 7: 11933–11953.
- Head, J. W., M. A. Kreslavsky, and S. Pratt. 2002. Northern lowlands of Mars: evidence for widespread volcanic flooding and tectonic deformation in the Hesperian Period. *Journal of Geophysical Research Planets* 107:5003. <http://dx.doi.org/10.1029/2000JE001445>
- Hesp, P., and A. McLachlan. 2000. Morphology, dynamics, ecology and fauna of *Arctotheca populifolia* and *Gazania rigens* nabkha dunes. *Journal of Arid Environments* 44:155–172.
- Huxman, T. E. 2004. Precipitation pulses and carbon fluxes in semiarid and arid ecosystems. *Oecologia* 141:254–268.
- Jones, K. R., O. Berney, D. P. Carr, and E. C. Barrett. 1981. Arid zone hydrology for agricultural development. FAO, Rome, Italy.
- Kéfi, S., V. Guttal, W. A. Brock, S. R. Carpenter, A. M. Ellison, V. N. Livina, D. A. Seekell, M. Scheffer, E. H. van Nes, and V. Dakos. 2014. Early warning signals of ecological transitions: methods for spatial patterns. *PLoS ONE* 9:e92097.
- King, J., W. G. Nickling, and J. A. Gillies. 2006. Aeolian shear stress ratio measurements within mesquite-dominated landscapes of the Chihuahuan Desert, New Mexico, USA. *Geomorphology* 82:229–244.
- Klausmeier, C. A. 1999. Regular and irregular patterns in semiarid vegetation. *Science* 284:1826–1828.
- Laity, J. E.. 2008. Deserts and desert environments. Wiley-Blackwell, Oxford, UK.
- Lejeune, O., M. Tlidi, and P. Couteron. 2002. Localized vegetation patches: a self-organized response to resource scarcity. *Physical Review E* 66:010901.
- Li, F., W. Zhao, and H. Liu. 2015. Productivity responses of desert vegetation to precipitation patterns across a rainfall gradient. *Journal of Plant Research* 128:283–294.
- Ludwig, J. A. 2005. Vegetation patches and runoff-erosion as interacting ecohydrological processes in semiarid landscapes. *Ecology* 86:288–297.
- McGrath, G. S., K. Paik, and C. Hinz. 2012. Microtopography alters self-organized vegetation patterns

- in water-limited ecosystems. *Journal of Geophysical Research. Biogeosciences* 117:G03021.
- Meron, E., E. Gilad, J. von Hardenberg, M. Shachak, and Y. Zarmi. 2004. Vegetation patterns along a rainfall gradient. *Chaos, Solitons and Fractals* 19:367–376.
- Miriti, M. N., S. J. Wright, and H. F. Howe. 2001. The effects of neighbors on the demography of a dominant desert shrub (*Ambrosia dumosa*). *Ecological Monographs* 71:491–509.
- Murray, A. B., M. A. F. Knaapen, M. Tal, and M. L. Kirwan. 2008. Biomorphodynamics: physical-biological feedbacks that shape landscapes. *Water Resources Research* 44:W11301.
- Nicholson, S. E.. 2011. *Dryland climatology*. Cambridge University Press, Cambridge, UK.
- Okin, G. S., D. A. Gillette, and J. E. Herrick. 2006. Multi-scale controls on and consequences of aeolian processes in landscape change in arid and semi-arid environments. *Journal of Arid Environments* 65:253–275.
- Quets, J. J., S. Temmerman, M. I. El-Bana, S. L. Al-Rowaily, A. M. Assaeed, and I. Nijs. 2013. Unraveling landscapes with phytogenic mounds (nebkhas): an exploration of spatial pattern. *Acta Oecologica* 49:53–63.
- Quets, J. J., S. Temmerman, M. I. El-Bana, S. L. Al-Rowaily, A. M. Assaeed, and I. Nijs. 2014. Use of spatial analysis to test hypotheses on plant recruitment in a hyper-arid ecosystem. *PLoS ONE* 9:11.
- Rawls, W. J., D. L. Brakensiek, and K. E. Saxton. 1982. Estimation of soil water properties. *Transactions of the ASAE. American Society of Agricultural Engineers* 25:1316–1320.
- Reinhardt, L., D. Jerolmack, B. D. Cardinale, V. Vanacker, and J. Wright. 2010. Dynamic interactions of life and its landscape: feedbacks at the interface of geomorphology and ecology. *Earth Surface Processes and Landforms* 35:78–101.
- Rietkerk, M., S. C. Dekker, P. C. de Ruiter, and J. van de Koppel. 2004. Self-organized patchiness and catastrophic shifts in ecosystems. *Science* 305:1926–1929.
- Salguero-Gomez, R., and B. B. Casper. 2010. Keeping plant shrinkage in the demographic loop. *Journal of Ecology* 98:312–323.
- Salguero-Gomez, R., and B. B. Casper. 2011. A hydraulic explanation for size-specific plant shrinkage: developmental hydraulic sectoriality. *New Phytologist* 189:229–240.
- Sankey, J. B., S. Ravi, C. S. A. Wallace, R. H. Webb, and T. E. Huxman. 2012. Quantifying soil surface change in degraded drylands: shrub encroachment and effects of fire and vegetation removal in a desert grassland. *Journal of Geophysical Research. Biogeosciences* 117:11.
- Schlesinger, W. H., J. F. Reynolds, G. L. Cunningham, L. F. Huenneke, W. M. Jarrell, R. A. Virginia, and W. G. Whitford. 1990. Biological feedbacks in global desertification. *Science* 247:1043–1048.
- Vincent, P.. 2008. *Saudi Arabia and environmental overview*. Taylor & Francis/Balkema, London, UK.
- Warner, T. 2004. *Desert meteorology*. Cambridge University Press, Cambridge, UK.
- Watt, A. 1947. Pattern and process in the plant community. *Journal of Ecology* 35:1–22.