

Resilience and recovery potential of duneland vegetation in the southern Kalahari

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Abstract. Many dune fields around the world have undergone alternating periods of mobilization and stabilization in response to changes in wind power and rainfall. However, in modern times disturbances associated with land use are believed to be a dominant factor contributing to the activation of stabilized vegetated dunes in drylands, while the reduction in human activities such as grazing and farming may lead to stabilization of once active dune fields. The Kalahari region of southern Africa has recently begun to exhibit visible signs of dune mobilization, a process that could lead to an activation of aeolian transport in the region with important implications for the biogeochemistry of downwind terrestrial and marine ecosystems. It is still unclear whether the region is poised at a tipping point between its current state (i.e., vegetated fixed linear dunes), and a “degraded” state (i.e., barren and active dunes). Here we investigate the ability of the landscape to recover from the degraded state by assessing the resilience of duneland vegetation and evaluating the vegetation and soil characteristics. Using field observations and soil seed bank experiments, we show that palatable perennial grass cover is reduced while the seedbank is depleted on grazed dunefields. Conversely, the interdunes generally exhibit relatively rich seed banks. Soils from grazed and ungrazed sites show that plant available nutrient contents are not significantly different; therefore, soil nutrients are likely not a major factor limiting the recovery of perennial vegetation in this region. It is observed that the perennial grasses reestablish on the recovering dunes after grazers have been excluded, indicating that the landscape is still able to recover after years of denudation and that any irreversible shift to a stable degraded state is likely during extended periods of disturbance and/or climatic shifts that promote the degraded state. We also find that changes in grass cover, grass community composition, and seed bank can serve as indicators of whether the system has irreversibly shifted from a vegetated to a bare dune state.

Key words: dune reactivation; feedbacks; overgrazing; seed bank; southern Kalahari; vegetation recovery.

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INTRODUCTION

Aeolian activity is a major factor limiting vegetation establishment and growth on sand dunes (Tsoar 1990, Tsoar and Blumberg 2002,

Tsoar 2005) but water availability also plays an important role (e.g., Sarnthein 1978, Lancaster 1988, Forman et al. 1995, Thomas et al. 2005, Telfer and Thomas 2007). Dunes transform from stable (vegetated, immobilized) to active (bare,

mobile) form after vegetation cover is reduced beyond a critical percentage vegetation cover. This process is called “reactivation”; the reverse is known as “stabilization”. It has been suggested that disturbances associated with land use can also reactivate dunes in places with low wind power (Yizhaq et al. 2007, 2009). In many cases, the reactivation of dunefields occurs over shorter temporal scales and is attributed to anthropogenic pressure, especially from grazing and farming. For instance, in the Negev Desert, along the Israel - Egypt border, the Israeli side now has dunes that are stabilized by vegetation while on the Egyptian side dunes are mobile because of overgrazing. Since the establishment of the border in 1982, wood gathering and grazing stopped in the Israeli side and dunes were restabilized within two years (Yizhaq et al. 2007). Similar management practices were introduced in the coastal dunes of Israel in 1949, and the dunes became stable and vegetation cover increased from 4.3% to 17% between 1944 and 1995 (Tsoar and Blumberg 2002).

Vegetation establishment and growth appear to be limited by a number of factors, including loss of soil resources resulting from the intensification of wind erosion and dust emissions from reactivated dunefields (Tsoar 1990, 2005, Duran and Herrmann 2006, Barchyn and Hugenholtz 2012a). Most of these factors could act in a positive feedback with the loss of vegetation (e.g., D’Odorico et al. 2013). For instance, the decrease in vegetation cover causes an intensification of soil erosion; the associated loss of soil resources may impede vegetation recovery (Okin et al. 2006, Turnbull et al. 2008). Moreover, recovery of vegetation may also be seed- or propagule- (e.g., bud bank) limited. Dune vegetation can mitigate against negative effects of erosion through vegetative propagation (Liu et al. 2012, 2013). Likewise, the feedbacks between vegetation cover and dune mobility are well represented in models of evolution of vegetated dune fields (e.g., Hugenholtz and Wolfe 2005a, Duran and Herrmann 2006, Barchyn and Hugenholtz 2012b). These models show that the emergence of vegetation on bare dunes reduces the rate of aeolian activity and the dunes shift from barchan (active) to parabolic (fixed) forms (e.g., Reitz et al. 2010). These positive feedbacks of land degradation may lead to the emergence

of bistable dynamics (Fig. 1). In other words, because of positive feedbacks the landscape may be stable both in a vegetated and in an unvegetated state (Fig. 1B) (e.g., Yizhaq et al. 2007, 2009, D’Odorico et al. 2013). Thus, if dune vegetation is disturbed beyond a critical level, the system diverges from one stable state (Fig. 1A) to the alternative state of bare, mobile dunes. At this point, the landscape would not necessarily recover its initial configuration of stable vegetated dunes by just reducing grazing pressure or other disturbances because its alternative unvegetated state is stable. Thus, the transition to the barren/mobile dune state would be irreversible, at least over relatively short time scales (e.g., decades to centuries) (e.g., Yizhaq et al. 2009). However, it is not clear when a landscape exhibits these bistable dynamics and is therefore prone to such irreversible shifts to a stable barren (“degraded”) state. Therefore, from a management perspective it is crucial to understand whether a landscape is undergoing irreversible transition to degraded conditions and whether a reduction in land use intensity might lead to the recovery of vegetation in active dune fields. While in some grazing systems recovery is achieved when the grazing intensity is lowered (Rietkerk and vandeKoppel 1997), in others degradation continues (Peters et al. 2004), recovery does not occur and the landscape remains devoid of vegetation (e.g., Sinclair and Fryxell

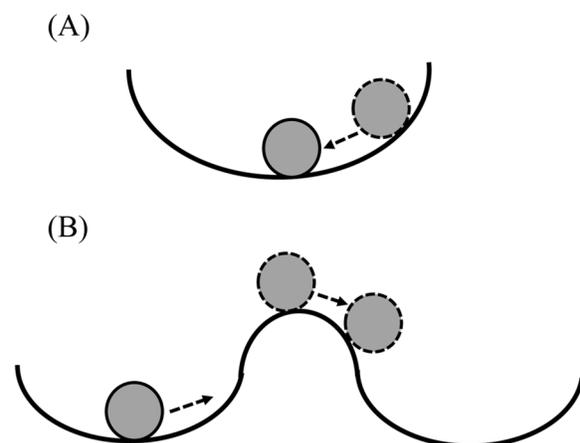


Fig. 1. Schematic representation of A) stable B) and bistable dynamics. In the case of bistable ecosystems, the two alternative states are separated by a potential barrier.

1985).

To evaluate the impact of land use practices on these landscapes it is therefore crucial to assess whether the underlying dynamics are bistable and, if so, to evaluate how far the system is from crossing the threshold (i.e., the potential barrier in Fig. 1) marking the transition to unvegetated, mobile dunes.

Of particular interest is the case of the Kalahari dunelands, where at present there is little scientific evidence concerning whether these dune fields can recover to the preferred stable vegetated state. There is some evidence of ongoing dune mobilization in the region particularly in overgrazed areas close to boreholes and villages (Thomas and Twyman 2004). Soil biological crusts stabilize the soil surface and could offset the negative impact of vegetation loss in the southern Kalahari however, it has been suggested that grazers destroy the crust cover and burial by eroded soil restrict crustal development (e.g., Thomas and Dougill 2007). Recent studies have shown that an increase in aeolian transport associated with dune reactivation may enhance the delivery of soluble iron to the Southern Ocean, with possible impacts on its productivity (Bhattachan et al. 2012, 2013). Previous studies have suggested that the dune-fields in the Kalahari are in a fixed, stable state because wind power (drift potential) is too low to activate these dunes (e.g., Lancaster 1988, Ashkenazy et al. 2012) and the annual precipitation is high enough to allow vegetation regrowth (e.g., Bullard et al. 1996). However, results from modeling studies by Yizhaq et al. (2007, 2009) have shown that even without climatic changes, land use can shift the system from fixed state to the active one. In this study we concentrate on the southern Kalahari and assess the resilience of dune vegetation, which is important for dune-land stability (or bistability).

Land use in the southern Kalahari

The degradation of Kalahari rangeland following Botswana's independence in 1966 is well documented (e.g., Perkins and Thomas 1993, Perkins 1996). The result was an unprecedented acceleration of borehole drilling in areas that were not previously used for raising cattle (Thomas and Shaw 1991:229). The use of boreholes allowed the ranchers to use arid areas

in the Kalahari that were previously grazed only during wet years (Milton and Dean 2000). Therefore, the shift from traditional pastoralism to borehole-dependent ranching resulted in degradation of the Kalahari where the cattle stocking rates usually exceeded the potential carrying capacity (Thomas and Shaw 1991:232). The introduction of cattle grazing appears to have led to shrub encroachment in less than 20 years, and replacement of grasses by scrub and woody vegetation in open grasslands was documented by explorers (Thomas and Shaw 1991:215). Declining cattle productivity from shrub encroachment often led to the establishment of more boreholes, which further enhanced land degradation and shrub encroachment (e.g., Perkins and Thomas 1993). Overall, between 1930 and 1990, the grazed area in the Kgalagadi district (which encompasses the southern Kalahari) increased from 13,000 km² to 32,000 km² and the number of official boreholes increased from eight in 1955 to over 380 in 1990 (Thomas and Twyman 2004).

In the Kalahari, overgrazing has led to an increase in bare ground cover, shrub encroachment in areas around villages, and the replacement of perennial grasses by less palatable, annual grasses (Thomas and Twyman 2004) and often cited as major indicators of land degradation (Perkins and Thomas 1993). As a result of overgrazing, *Acacia mellifera* trees that are unpalatable to cattle are encroaching in the interdune areas at the expense of herbaceous vegetation (e.g., Perkins and Thomas 1993, Reed et al. 2007, Stringer and Reed 2007). The replacement of palatable perennial grasses that stabilize the dune crests by annual grasses which are less effective at dune stabilization because of their shallow, weak and ephemeral root systems (Thomas and Twyman 2004) exposes the dune-fields to erosive action of wind during the dry season (e.g., Milton and Dean 2000). Thus, shrub encroachment, increases in bare ground cover, and loss of perennial grasses could be used as indicators that the landscape is undergoing transition to a degraded state.

In the southern Kalahari, dune mobilization occurs during dry and windy periods when vegetation cover decreases below ~14% (Wiggs et al. 1995), though a dramatic increase in aeolian transport is observed already when vegetation

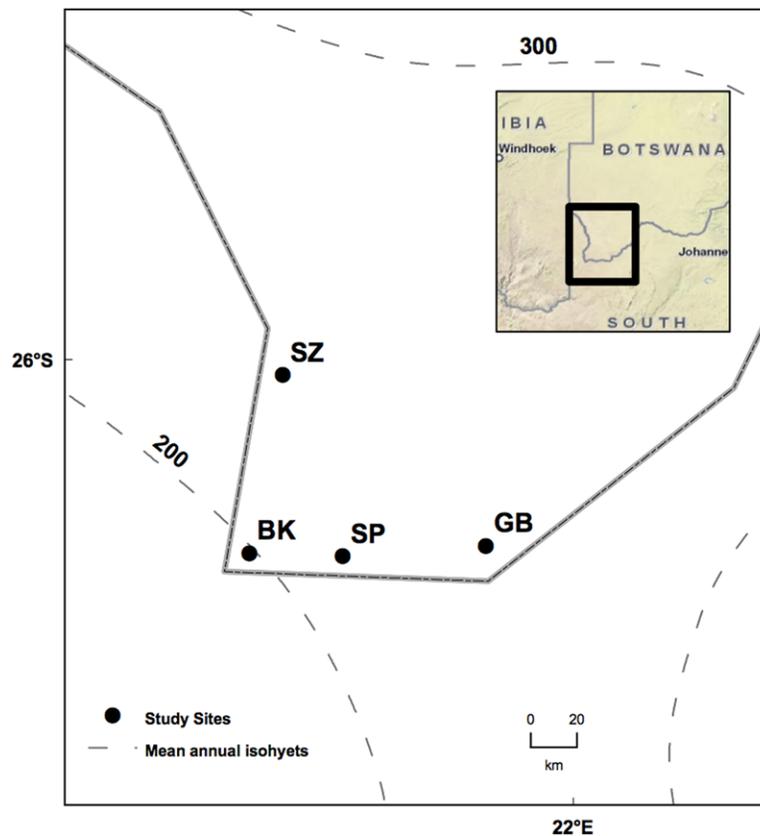


Fig. 2. The study sites (Table 1) were located in Bokspits (BK), Spaarwater (SP), Gakhibane (GB), and Struizendam (SZ). Mean annual isohyets at intervals of 100 mm of annual precipitation are also reported.

cover is less than 40% (e.g., Bhattachan et al. 2013). Indeed, bare, mobile dunes are ubiquitous in the southern Kalahari and are usually found closer to villages on communal lands and overgrazed farms.

Field sites

We investigate resilience of dune vegetation in a region located in southern Botswana at the border with South Africa, about 100 km north of the southern edge of the Kalahari sand deposits. In this region rainfall has an annual mean of 200–300 mm/yr and occurs in the summer months (December–March). The typical vegetation is an open *Acacia* savanna with varying land cover, depending on the land use history. The southern Kalahari exhibits stable linear dunes from 5–25 m high with crest spacing of 200 m to 2 km (Thomas and Leason 2005). The dune vegetation consists of three main classes, perennial grasses

(mostly *Stipagrostis* sp.) growing on dune crests and interdunes, perennial shrubs (e.g., *Rhigozum trichotomum*), and annual grasses (mainly *Schmidtia kalahariensis*) (Thomas and Twyman 2004, Thomas and Leason 2005).

This research was conducted at study sites established on well-managed farms, overgrazed farms, and communal grazed areas near villages (Fig. 2, Table 1). A recovering site existed in one of the study sites (Gakhibane), where a plot (area 140 m by 400 m) was set up 15 years ago by the local community to exclude grazers and limit the movement of the dune. Grass regrowth was observed inside the fence while outside the fence, the dunes remained completely denuded and active (Fig. 3B).

METHODS

Soil sampling

Soil samples (three replicates per land cover

Table 1. Study site locations in the southern Kalahari and the land cover type at each site. Three replicates of soil samples were collected from the top 5 cm of the soil surface at each land cover.

Site	Type	Location
Bokspits	vegetated interdune	26.8208° S, 20.6740° E
	vegetated dune crest	26.8199° S, 21.6749° E
Struizendam	bare dune	26.6750° S, 20.6413° E
	interdune	26.6707° S, 20.6369° E
	recovering dune	26.6737° S, 20.6405° E
Spaarwater	bare dune	26.8476° S, 21.0826° E
	transition	26.8446° S, 21.0831° E
	vegetated interdune	26.8401° S, 21.0825° E
	vegetated dune crest	26.8393° S, 21.0839° E
Gakhibane	inside the plot, recovering dune	26.7211° S, 21.7697° E
	outside the plot, bare dune	26.7194° S, 21.7688° E

per site) were collected from the top 5 cm at all study sites during the dry season between July and August in 2011. The samples from a managed leased farm in Bokspits were collected from vegetated dune crests and vegetated interdunes. In the overgrazed communal land at Struizendam samples were collected from a bare dune, vegetated interdune and recovering dune crest from an enclosed plot that was fenced off to exclude grazers (Fig. 4). The samples collected at a leased farm in Spaarwater were from bare dune, vegetated dune crests, vegetated interdune and a transitional area located between the bare dune and the vegetated dune crests. The samples collected at the recovering site (Gakhibane) were taken from areas located both inside and outside the fenced plot. The land cover characteristics of the areas sampled at each site are summarized in Table 1. At each site, the fractional cover was measured by surveying vegetation along 100 m long line transects. All samples were double bagged and stored to be shipped back to Virginia. Analyses to determine soil seed bank and soil nutrient content were carried out within two months after the sampling.

Greenhouse experiment

Soil samples (three replicates per land cover per site) were spread in trays (15 cm × 25 cm × 2 cm) and placed in a greenhouse. The samples were isolated from other ongoing experiments to limit the transfer and transport of seeds from

other plants. Samples were kept moist throughout the experiment by adding water to the trays every day and all seedlings that emerged were counted. After 4 weeks into the experiment, 50 ppm of fertilizer mixed with water was added to all the samples. Seedlings did not live long enough to be identified. At the end of the experiment (8 weeks, after any new germination had stopped), the soil samples were put in water and the floating ungerminated seeds were counted.

Ion chromatography

The soil nutrient content was quantified in terms of plant available anionic nitrogen (nitrate + nitrite) and phosphorus (phosphate). To this end, water extractable anions were analyzed using 2 g of sediment on a subset of sediments collected per land cover per site, shaken for 30 minutes in 10 ml of deionized water and centrifuged for 10 minutes at 3600 rpm. The concentrations of anions (NO_3^- and NO_2^- , PO_4^{3-}) were measured on a Dionex ICS-2000 ion chromatograph.

RESULTS

The dune crests are stabilized by perennial grasses (mostly *Stipagrostis amabilis*) and the interdunes exhibit a mix of perennial and annual grasses (Table 2). The fractional cover in the vegetated interdune of the leased farm sites (Bokspits and Spaarwater) was denser than in the recovering sites (i.e., enclosed plots of Struizendam and Gakhibane). Moreover, these recovering sites had a lower vegetation density than the vegetated dune crests in the leased farm sites (Bokspits or Spaarwater) and were mostly covered by perennial grasses. Of the 36% grass cover at the transition site in Spaarwater, only 5% was contributed by perennial grasses (Table 2).

Seed germination and the emergence of shoots were only observed at sites with vegetation except the recovering dune in Gakhibane (Fig. 5A). The samples from vegetated interdunes in the leased farm sites (Bokspits and Spaarwater) yielded the largest number of shoots. ANOVA was used to determine if there was significant difference between the number of shoots from the vegetated and bare dunes. The mean number of germinated seeds from the interdune in

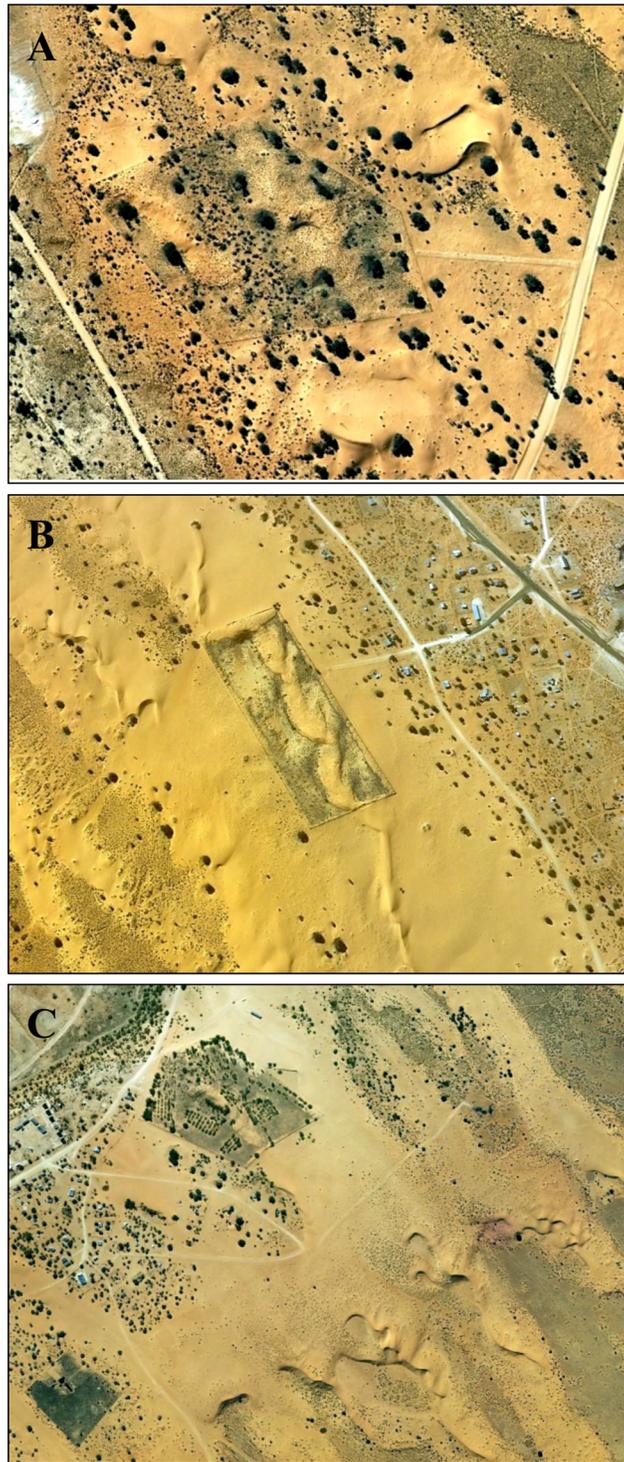


Fig. 3. The recovering dunes in (A) Bokspits, (B) Gakhibane and (C) Struizendam. Map Data: Google, 2013 AfriGIS (Pty) Ltd.

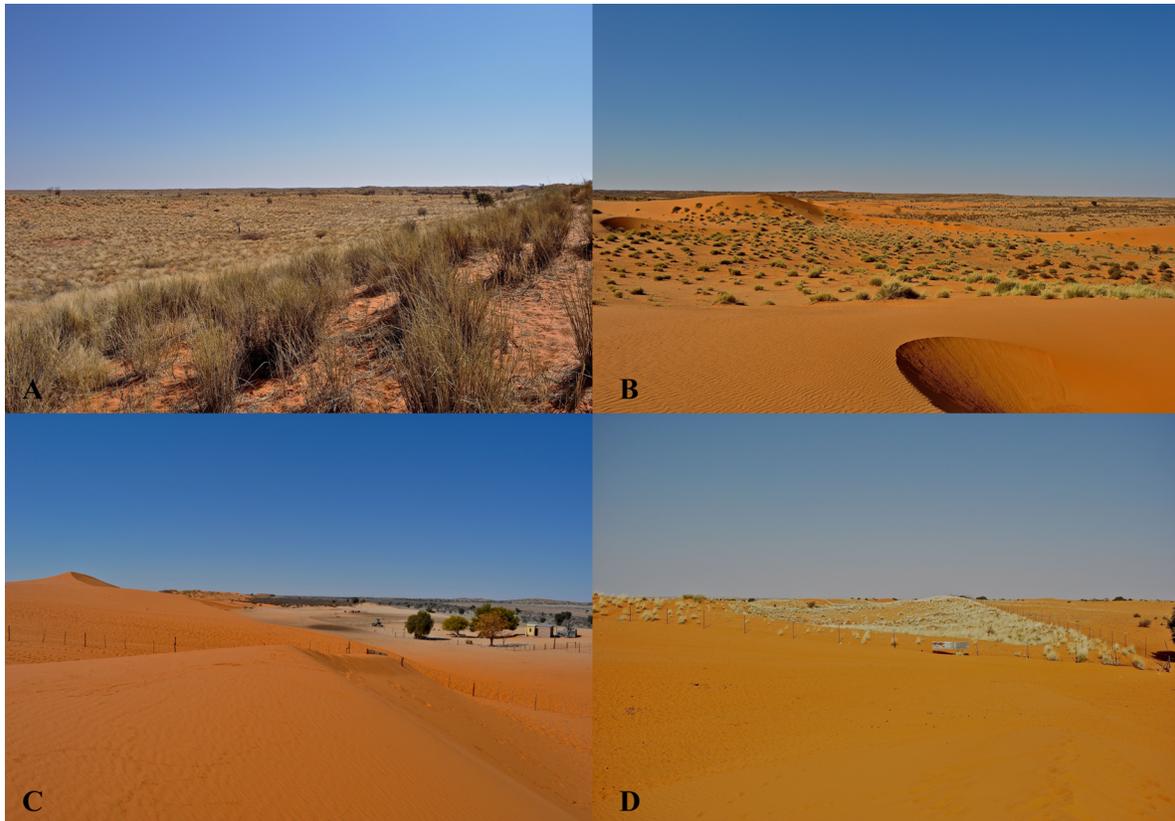


Fig. 4. (A) View from the crest of a linear dune in Bokspits. The interdune is covered by grasses. (B) The dunes close to the village of Struizendam are mobile. (C) A tall mobile dune in Spaarwater. Note the farmer's house to the left of the image, which is being encroached upon by the moving dune. (D) A fence separates the bare dune with no vegetation and a recovering dune with vegetation in Gakhibane.

Bokspits is statistically significantly different from the bare dunes (Fig. 5A). For the ungerminated seed counts, Spaarwater interdune had the greatest number of seeds followed by the transition site in Spaarwater (Table 3). All bare dunes (in Struizendam, Spaarwater and Gakhibane) were devoid of germinable seeds. However, the interdune site in Struizendam without grass cover had ungerminated seeds. The seed counts were higher at those sites where annual grasses (*S. Kalahariensis*) were observed to have higher fractional cover (i.e., interdune site in Spaarwater, and transition site in Spaarwater (Table 2)).

The soil nutrient analyses (i.e., $\text{NO}_3^- + \text{NO}_2^-$, and PO_4^{3-} contents) show that there are no significant differences between the pools of plant available nutrients in soils from bare and vegetated dunes, except for the bare dunes

outside the fenced plot in Gakhibane, which exhibited the highest nitrate content (Fig. 5B). The phosphate contents are slightly greater in vegetated dunes and interdunes than in bare dunes, though the only significant difference was detected in the interdune in Struizendam (Fig. 5B).

DISCUSSION

Dune fields around the world have undergone alternating periods of stabilization and remobilization as a result of changes in climate. Some of the deserts that formerly existed in the Pleistocene are presently much wetter and exhibit sand dunes stabilized by vegetation (e.g., Sarnthein 1978, Goudie 2006). Some examples include the southern Sahara, the Mega-Thar (India), the High Plains (US), the Kimberlies (Australia), the

Table 2. Vegetation composition at the study sites. The cover fraction is calculated from 100-m line transects.

Dune	Site	Percent cover	Species	Species-specific percent cover	Grass type			
Transition	Spaarwater	36	<i>Schmidtia kalahariensis</i>	76	annual			
			<i>Aristida obtusa</i>	16	annual			
			<i>Stipagrostis obtusa</i>	5	perennial			
			<i>Rhynchelytrium repens</i>	3	annual			
Vegetated interdune	Bokspits	77	<i>Schmidtia kalahariensis</i>	100	annual			
	Spaarwater	61	<i>Schmidtia kalahariensis</i>	60	annual			
			<i>Stipagrostis obtusa</i>	21	perennial			
			<i>Rhynchelytrium repens</i>	15	annual			
			<i>Eragrostis lehmanniana</i>	3	perennial			
			<i>Aristida obtusa</i>	1	annual			
Vegetated dune crest	Bokspits	45	<i>Stipagrostis amabilis</i>	95	perennial			
			<i>Stipagrostis obtusa</i>	2	perennial			
			<i>Schmidtia kalahariensis</i>	3	annual			
	Spaarwater	46	<i>Stipagrostis amabilis</i>	77	perennial			
			<i>Schmidtia kalahariensis</i>	16	annual			
			<i>Eragrostis lehmanniana</i>	3	perennial			
			<i>Stipagrostis obtusa</i>	3	perennial			
			<i>Aristida obtusa</i>	1	annual			
			Recovering	Gakhibane	23	<i>Stipagrostis obtusa</i>	96	perennial
				Struizendam	13	<i>Schmidtia kalahariensis</i>	4	annual
<i>Stipagrostis amabilis</i>	85	perennial						
<i>Stipagrostis obtusa</i>	14	perennial						
<i>Schmidtia kalahariensis</i>	1	annual						

Llanos and the Pampas (S. America), and the Kalahari (southern Africa). These regions experienced changes in either wind or rainfall regime that led to the alternating periods of dune stabilization and mobilization (e.g., Goudie 2006, Thomas and Wiggs 2008). The ongoing dune mobilization in the Kalahari appears to be more complex because it coincides with a period of intensification of land use for livestock grazing (Thomas and Shaw 1991), while climatic factors alone appear to be unable to explain the recent increase in aeolian transport and dune mobility in this region (Bullard et al. 1996, Yizhaq et al. 2007, 2009).

As noted in the previous section, annual grasses are mainly found in interdunes. Once the perennial grasses are lost, the interdunes exhibit a low vegetation cover with annual grass patches bordered by bare soil areas, while the lack of vegetation on the dune crests leads to sediment removal and loss of fine soil particles, which are partly trapped by the annual grasses, indicated by hummocking within the grass patches. The transport of wind-blown sediment is expected to cause the loss of soil nutrients (e.g., Li et al. 2007, Bhattachan et al. 2013), though our data show that the loss of plant available nutrients is still undetectable (Fig. 5B) at the research sites considered in this study. The nitrate content in soil sampled from the bare dune in

Gakhibane is relatively higher than the soil nitrate content along the Kalahari Transect (about $1\text{--}2\ \mu\text{g g}^{-1}$, Feral et al. 2003). This could be due to the ability of livestock waste to sustain soil nutrient levels in proximity to water points despite the overall ongoing degradation of the surrounding landscape (Fig. 5B).

Based on the observations, we can recognize that the degradation of overgrazed dunelands in the Kalahari undergoes a few distinct stages as shown in Fig. 6. As grazing pressure increases, a reduction in perennial grass cover is observed on the dune crests and interdunes because of the higher palatability of perennial grasses with respect to the “sour” annual grasses (e.g., Thomas and Twyman 2004). If grazers are completely excluded, perennial grasses can still recover through vegetative reproduction from perennating buds, rhizomes, and meristems and the system can shift back to the original undegraded state (stage II to I, Fig. 6). However, if the grazing pressure is sustained, the movement of sediments by wind further hampers grass regrowth. At this point, only annual grasses are found on the interdunes (stage III), while perennial grasses are almost completely removed from dune crests and interdunes. The disturbance of annual grasses by livestock foraging after the loss of perennials, and increased aeolian activity (i.e., abrasion, burial,

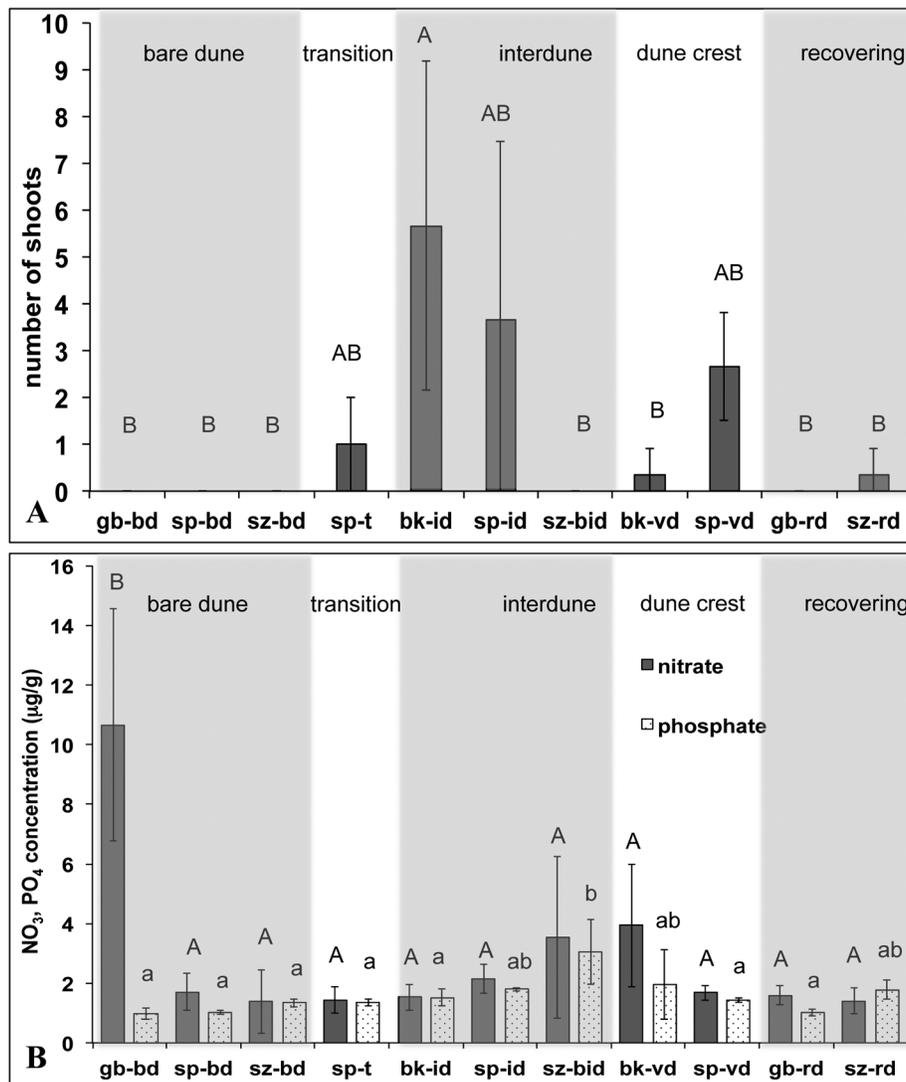


Fig. 5. (A) Shoot counts from the greenhouse experiment and (B) soil nitrate and phosphate concentrations. The results of one-way ANOVA and post hoc Tukey test of the number of shoots and nitrate and phosphate concentrations (± 1 SD) in the soil. The significant differences (at $p < 0.05$ level) are indicated by different letters. Abbreviations are: gb-bd, Gakhibane-bare dune; sp-bd, Spaarwater-bare dune; sz-bd, Struizendam-bare dune; sp-t, Spaarwater-transition; bk-id, Bokspits-vegetated interdune; sp-id, Spaarwater-vegetated interdune; sz-bid, Struizendam-bare interdune; bk-vd, Bokspits-vegetated dune crest; sp-vd, Spaarwater-vegetated dune crest; gb-rd, Gakhibane-recovering dune; sz-rd, Struizendam-recovering dune.

uprooting and lack of stable seed bed for seed germination) are expected to lead to a decline of annual grasses as well. It is possible that the interdune site in Struizendam lost its grass cover by livestock foraging and after a few years of increased aeolian activity on bare, mobile surface the seed bank would be depleted and the

recovery of annual grasses is therefore impeded (stage IV, Fig. 6). This is consistent with other studies that have shown that aeolian processes reduced the soil seed bank (e.g., Li et al. 2007, Alvarez et al. 2012) and impede seed germination in mobile sand beds or cause abrasion damage and burial in grasses and shrub seedlings (e.g.,

Table 3. Results of one-way ANOVA and post hoc Tukey test of the number of seeds per m² (± 1 SD) in the soil. The different capital letters indicate differences between number of seeds for Tukey test.

Dune	Site	Seed density (no./m ²)
Bare	Gakhibane	0 ^A
	Spaarwater	0 ^A
	Struizendam	0 ^A
Transition	Spaarwater	507 \pm 141 ^{AB}
	Bokspits	151 \pm 94 ^A
Vegetated interdune	Spaarwater	1591 \pm 1232 ^B
	Struizendam	80 \pm 71 ^A
Interdune	Bokspits	36 \pm 31 ^A
	Spaarwater	213 \pm 167 ^A
Vegetated dune crest	Gakhibane	27 \pm 46 ^A
	Struizendam	18 \pm 31 ^A

Okin et al. 2006, Li et al. 2009). The fact that grazing exclusion in the fenced plots at Gakhibane and Struizendam (Fig. 3, Table 2) led to a recovery of perennial grasses indicates that at

this stage, there are still live perennating buds, rhizomes or stolons buried in the soil. Thus, the loss of perennial grass cover is still reversible and a decrease in grazing pressure leads to the restabilization of the dune crests.

Other studies have shown how the recovery of perennial grasses in grazed systems may be possible after exclusion of grazers (Valone et al. 2002, Valone and Sauter 2005, Mata-Gonzalez et al. 2007); however, there is also evidence that after longer time periods of overgrazing, the exclusion of grazers may not lead to the recovery of herbaceous vegetation (e.g., Hennessy et al. 1983, West et al. 1984, Peters et al. 2004). Moreover, studies reporting a successful recovery of grasses often exhibited a time lag between reduction in grazing pressure and recovery. For example, in southeastern Arizona perennial grass cover only started to increase significantly after 20 years of grazing exclusion (Valone et al. 2002).

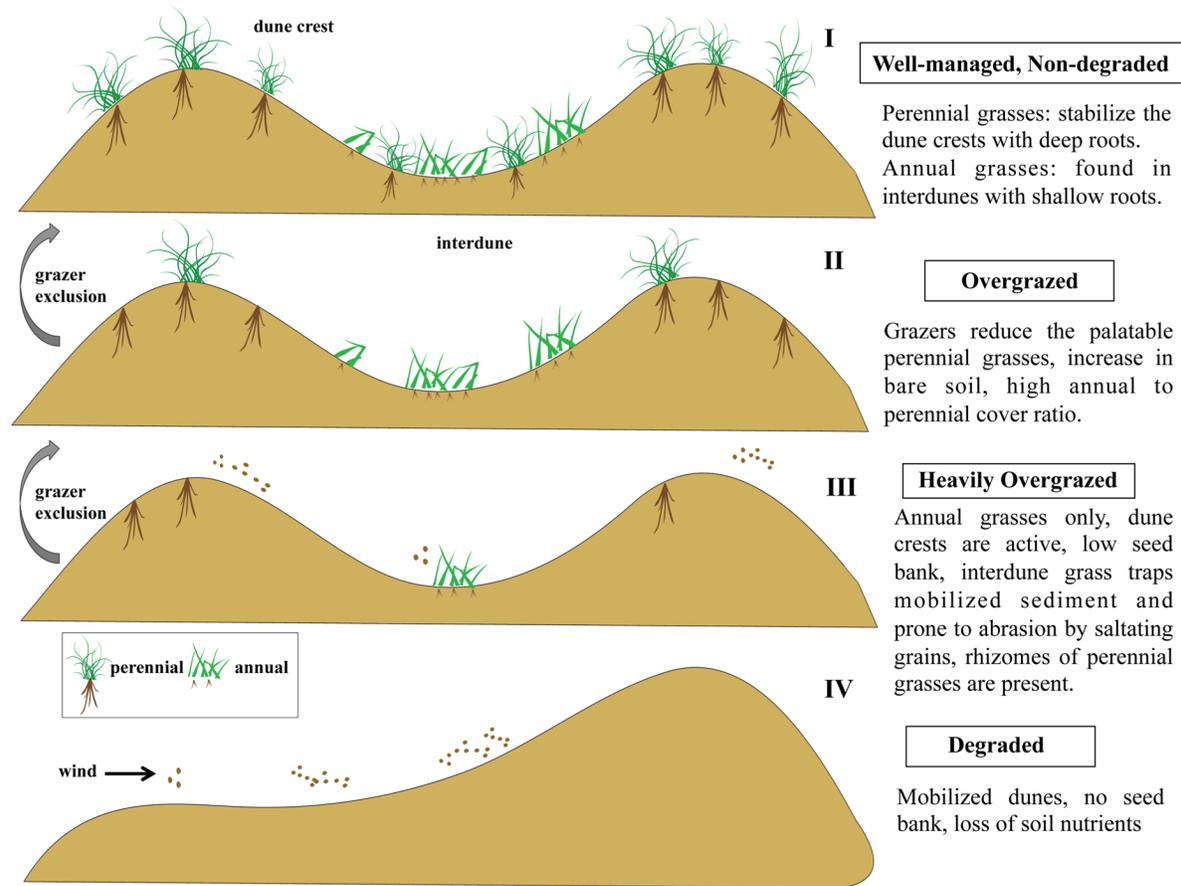


Fig. 6. The effect of grazing on vegetation cover and composition and sediment transport on the dune fields.

A lag of 10–50 years is common in vegetation recovery in semi-arid, or arid grazed systems (Havstad et al. 1999, Guo 2004). Similarly, the response of Kalahari vegetation to diminished rainfall is not instantaneous but appears to exhibit a lag (Milton and Dean 2000).

It should be noted that changes in climate could greatly affect grass recovery even if the grazing pressure was largely reduced. In fact, even though in the Kalahari vegetation loss is mostly due to overgrazing in the proximity of boreholes, its recovery rates strongly depend on available soil moisture, which in the absence of access to groundwater is mainly contributed by rainfall. Therefore, enhanced dune activity was observed in the southern Kalahari in the 1980s when rainfall dropped below 50% of the 30-year mean for the 1960–1990 period (Lancaster 1988, Bullard et al. 1997). However, rainfall is not the only climatic variable controlling the stabilization/mobilization of sand dunes. Winds also play an important role (Lancaster 1988). In northeastern Brazil, mobile barchans and stabilized dunes coexist in the same landscape even though the region is humid with average annual rainfall exceeding 1000 mm. Here, strong winds explain why vegetation recovery does not occur on these mobile dunes (Yizhaq et al. 2007, 2009, Tsoar et al. 2009). Modeling results, however, suggest that in the Kalahari stronger winds are needed to cause a permanent dune reactivation (Yizhaq et al. 2007). The recovery and persistence of perennial grasses in the grazing exclusion plots confirm this assessment (Fig. 3; Table 2). If trends in globally increasing wind speeds continue, at least over the oceans where they are more easily measurable (Young et al. 2011), increasing windiness in the region has the potential, along with potential aridification (Thomas et al. 2005) to increase the potential of the bare dunes to become irreversibly mobilized.

CONCLUSIONS

Unlike other systems, under the existing wind regime the tipping point for land degradation in the Kalahari is not controlled by the maximum sand blasting tolerance of perennial grasses, but by their ability to regenerate after prolonged periods of overgrazing (e.g., Barchyn and Hugenholtz 2012a). Should climate change lead to

an increase in frequency and intensity of winds, disturbances induced by aeolian activity could start playing a more crucial role as suggested by some more general models of coupled dune-vegetation dynamics, whereby, once reactivated, the dunes would not revert back to their fixed/vegetated state (Yizhaq et al. 2009). Likewise, under climate change conditions duneland degradation by a slight increase in grazing pressure could shift the system to an active state from which it would not recover even if the grazing pressure is significantly reduced (Yizhaq et al. 2009).

On the basis of this interpretation of the processes underlying duneland degradation in the southern Kalahari, under current conditions the tipping point is exceeded only when perennial grasses permanently lose their ability to regenerate either clonally or via the seed bank after prolonged periods of overgrazing. Thus, the permanent transition from a vegetated to an unvegetated state is less abrupt and catastrophic than what classic models based on bistability theory (e.g., Scheffer 2009, D’Odorico et al. 2013) would suggest. This means that in the course of such a transition to an unvegetated/mobile dune state, the system is found in intermediate stages in which grass loss is not necessarily irreversible (Fig. 6). Moreover, dune field stabilization likely occurs with significant lag between reestablishment of vegetation cover and complete stabilization (Hugenholtz and Wolfe 2005a, Barchyn and Hugenholtz 2012b), as evidenced by direct measurements of dune stabilization for longer time scales (e.g., Tsoar and Blumberg 2002, Hugenholtz and Wolfe 2005b). Thus, changes in grass cover and grass community composition, seed bank depletion, loss of perennial grass rhizomes or stolons, and decline in soil nutrient content can be used as indicators to determine if this system is reaching a tipping point towards permanent landscape degradation. Moreover, these indicators are useful in assessing the stages of land degradation (Fig. 6). This study shows that in southern Kalahari, the vegetated dunes have not yet irreversibly shifted to the stable bare dune state as indicated by the resurgence of perennial grasses in the recovering plots in Gakhibane and Struizendam. In the context of dryland ecosystems undergoing vegetation loss, these factors appear to be more useful as leading

indicators of state shift than precursors of phase transition based on phenomena such as critical slowing down, rising variance and increasing autocorrelation of the state variables (e.g., Strogatz 2001, Carpenter and Brock 2006, Dakos et al. 2008, 2012, Scheffer 2009). Despite their recent application to other ecosystems in which the transition is more abrupt and high frequency measurements are feasible (Carpenter et al. 2011), these phenomena seem to be more difficult to apply to the “desertification” process (D’Odorico et al. 2013). Conversely, indicators of the state of the system with respect to trajectories of degradation (Fig. 6) could be effective early warning signs of state shift.

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