



Periodic temporal oscillations in biocrust–vegetation dynamics on sand dunes



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ABSTRACT

We show that the system of biocrust and vegetation on sand dunes modeled by two coupled ordinary nonlinear differential equations exhibits self-sustained oscillations. Such oscillations can occur on vegetated linear dunes that are mostly covered by biocrust. The vegetation–biocrust interaction underlies these oscillations and these do not occur if only vegetation dynamics is considered. The oscillations are “relaxation oscillations” which are characterized by two alternating attraction processes to equilibrium states with high low vegetation covers. The complex dynamics of the biocrust–vegetation model leads to unexpected scenarios, such as vegetation rehabilitation induced by drought or by grazing during which the system shifts to one of the bistable state dominated by a higher vegetation cover, or rehabilitation of vegetation that is induced by decrease in precipitation. The oscillation periods range from decades to millennia and they can interact and be affected by the climate system variability.

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1. Introduction

Dune systems cover up to a third of the area of low and mid-latitude arid areas and form important and unique landscapes and ecosystems (Lancaster, 1995; Lancaster, 2013). They are dynamic geomorphic bedforms that are sensitive to climate variability on a variety of spatiotemporal scales (Thomas et al., 2005; Ashkenazy et al., 2012; Yizhaq et al., 2013). Dunes are also a potential source for dust caused by aeolian abrasion emission (Enzel et al., 2010)–dust has an important impact on loess formation (Crouvi et al., 2012) and on the marine ecological system (Bhattachan et al., 2012). In many places around the world, dunes are considered to be a threat since they affect human activity and property (Dong et al., 2005; Khalaf and Al-Ajmi, 1993); yet, in other regions efforts have been made to increase dune activity, in part to enrich biodiversity of psammophile (sand-loving) species (Rubinstein et al., 2013).

Dunes can be active (mobile), semi-active, or fixed (stable), mainly depending on wind, precipitation, and dune cover (vegetation and biocrust) (Thomas and Wiggs, 2008; McKenna-Neuman et al., 1996; Argaman et al., 2006; Ashkenazy et al., 2012; Tsoar, 2013; Kinast et al., 2013). Vegetation and biocrust play an

important role in dune stabilization and they are strongly affected by winds and precipitation. On the one hand, when dunes are covered by vegetation above a certain critical value (30%, Ash and Wasson (1983)), even very strong winds are masked by the vegetation such that they do not reach the ground and thus do not result in sand erosion and dune mobility. On the other hand, when the dunes are bare, even relatively weak winds that are above the threshold velocity (6 m/s, Fryberger (1979)) will lead to sand transport. Winds also directly affect vegetation by exerting stress on it and increasing evapotranspiration, a condition that further reduces vegetation cover, hence leading to enhanced dune activity.

Biocrust can be found on vegetated sand dunes throughout the world (mostly on dune slopes and on interdune areas), including the vegetated linear dunes (VLDs) of Australia, the northern Negev Desert, the Thar Desert and the Kalahari Desert (Hesse and Simpson, 2006; Danin, 1996; Tsoar, 2013; Thomas, 2013). VLDs (Fig. 1) are low compared to unvegetated linear dunes–their height ranges from a few meters up to dozens of meters (Tsoar, 2013). In arid and hyper arid environments, the biocrust is mainly composed of a thin cyanobacteria layer (thickness of 2 mm, Almog and Yair (2007)), but it can also contain lichens and mosses in wetter regions (Almog and Yair, 2007). In the northwestern Negev sand dunes, biocrust consists of filamentous cyanobacteria, which serves as trap for atmospheric dust, since it increase the surface roughness (Veste et al., 2011; Zaady et al., 2014). In turn, the deposited dust can contribute to the development of crust through its physical presence and chemical reactivity (Viles, 2008; Rosenstein et al., 2014). The

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cohesive biocrust is more resistant to wind erosion than bare sand as the filamentous cyanobacteria bind grain particles together. Wind-tunnel experiments showed that this crust resistance to wind erosion depends on the type of the biocrust (McKenna-Neuman and Maxwell, 2002). Due to its resistance to wind erosion and to prolonged droughts, biocrust plays a crucial role in the surface stability of sand dunes (Benlap and Lange, 2001; Siegal et al., 2013; Amir et al., 2014). Destruction of the biocrust by the trampling of grazing animals leads to a sharp increase in aeolian sand transport rates (McKenna-Neuman and Maxwell, 2002) as occurred in the sand dunes on the Egyptian side of the border between Israel and Egypt due to intensive grazing (Tsoar, 2008).

The mutual relations between vegetation and biocrust are complex and depend on the successional stage of the biocrust. It is still debated whether the presence of biocrust enhances vegetation growth or diminishes it (Almog and Yair, 2007). On other soils (such as loess) the crust enhances vegetation growth through the so-called “source-sink” effect, meaning that runoff on the crust flows to sink points where the vegetation is present and the infiltration rate is higher (Shachak and Lovett, 1998). This feedback is also known as “infiltration feedback” and leads to vegetation pattern formation in water limited systems (Meron, 2015).

The activity of sand dunes is sensitive to climatic conditions, mainly to wind power and precipitation (Tsoar, 2005; Hugenhaltz and Wolfe, 2005; Yizhaq et al., 2009; Ashkenazy et al., 2012; Tsoar, 2013; Warren, 2014), although their relative importance is still an open question (Bogle et al., 2014). The activity of aeolian deposits can change usually on time-scales of 10^1 – 10^5 years (Thomas and Wiggs, 2008). By using a luminescence (OSL) dating technique it was shown that the dunes in the Kalahari, Central Asia, Australia, and the Negev (Maman et al., 2011; Roskin et al., 2011) have undergone periods of activity and stability since the Late Pleistocene (the last 40,000 years, for details, see Fig. 6 in Tsoar (2013)). These periods of different types of activity are usually attributed to increased windiness and/or decreased precipitation (Roskin et al., 2011). Dune mobility can also change on decadal and on inter-annual time scales (Lancaster, 2013) due to changes in sediment supply, availability, and mobility that are determined by regional and local climate and by vegetation and biocrust cover.

The main goal of this study is to show that the system of biocrust and vegetation on sand dunes modeled by two coupled nonlinear ordinary differential equations (ODEs) (Kinast et al., 2013) exhibits self-sustained oscillations with different periods (between 300 to more than 3000 years) and amplitudes, under constant climatic conditions. Thus, in contrast to the common view, the system of VLDs (or sand ridges, see Tsoar (2013, 2014)) where biocrust is most abundant can introduce oscillations in its activity even without climatic changes. We conjecture that this internal oscillatory dynamics of vegetation and biocrust may interact with the external climatic conditions on various time scales, and may result in richer dynamics of both the dune and climate systems. As VLDs are the majority of dunes utilized in continental desert paleo-aridity studies (Thomas, 2013), because they are more liable to vegetation and biocrust colonization, it is very important to understand the possible various aspects of their complex dynamics—we aim here to study some of such possible aspects through an analytic model for vegetation and biocrust dynamics.

2. Materials and methods

2.1. The model

The mathematical model we used was introduced and studied in the context of the existence and stability ranges of different dune-cover states along gradients of rainfall and wind power

(Kinast et al., 2013; Kinast, 2014). Here we briefly describe the model which consists of two coupled nonlinear ODEs for the vegetation cover v and the biocrust cover b (for more details about the model see Kinast et al. (2013)). The model's equations are,

$$\begin{aligned}\frac{dv}{dt} &= f_1(v, b) = \alpha_v(v + \eta_v)s - (\varepsilon_v g + \gamma DP^{2/3} + \mu_v + \phi_v b)v \\ \frac{db}{dt} &= f_2(v, b) = \alpha_b(b + \eta_b)s - (\varepsilon_b g + \mu_b + \phi_b v)b\end{aligned}\quad (1)$$

where $s \equiv 1 - v - b$ is the bare sand cover. The first term describes a logistic growth modulated by a growth rate parameter which, for $p > p_{\min, v, b}$, depends on precipitation p as follows,

$$\alpha_{v, b} = \alpha_{\max, v, b}(1 - \exp(-(p - p_{\min, v, b})/c_{v, b})) \quad (2)$$

and is 0 for $p \leq p_{\min, v, b}$; $\alpha_{\max, v, b}$ is the maximum growth rate of vegetation and biocrust covers respectively. The other terms are mortality terms due to different effects (Kinast et al., 2013; Kinast, 2014). Both biocrust and vegetation are suppressed by sand transport and sand blasting of saltating particles (Okin, 2013), which is modeled by the function g ,

$$g = \frac{1}{2}DP(\tanh(d(v_c - v)) + 1)s \quad (3)$$

where DP is the drift wind potential which is a measure, in vector units, of the potential sand transport by the wind. It is derived from surface (10 m high) wind above the threshold velocity for sand transport (≈ 6 m/s), through weighting of the sand transport equation. Its definition is: $DP = \langle U^2(U - U_t) \rangle$, where U is the wind speed (in knots: 1 knot = 0.514 m/s) at 10 m height and U_t is the minimal threshold velocity (≈ 12 knots) necessary for sand transport (Fryberger, 1979). There are both theoretical and empirical linear relations between DP and the rate of sand transport (Bullard, 1997). The function g mimics the effect of the critical vegetation cover v_c (i.e., $g = 1$ for $v = 0$ and $g \rightarrow 0$ for $v > v_c$). Other forms of g produced qualitatively similar results, as long as the above mortality term diminishes with vegetation cover or when the spaces between plants decreased in size (Okin, 2008). The sand transport depends on the available bare sand s and it diminishes when the dune is fully covered by vegetation and biocrust ($v + b = 1$).

The other mortality terms ($-\phi_v bv$ and $-\phi_b bv$) stand for non-local competition between the biocrust and the vegetation and mortality due to grazing and trampling ($-\mu_v v$ and $-\mu_b b$ respectively). In addition, there is a mortality term of vegetation $-\gamma DP^{2/3} v$, that accounts for vegetation decay due to direct wind action (this term exists even without sand transport), which increases evapotranspiration and stress, enhances branch breaking, and limits vegetation growth (Hesp, 2002). The two-thirds power aims to represent the wind drag on vegetation which is proportional to the square (Bagnold, 1941) of the wind speed U (while $DP \propto U^3$). γ is a proportionality parameter that may depend on vegetation types (as described in details in Yizhaq et al. (2013, 2009)). Note that the equation for the biocrust does not include such a mortality term since biocrust can withstand very high wind speed (McKenna-Neuman and Maxwell, 2002). More details about the model and its spatial version (which accounts only for vegetation cover) can be found in Kinast et al. (2013) and Yizhaq et al. (2013, 2009).

The study of Kinast et al. (2013) was concentrated on the existence and stability ranges of different dune-cover states as a function of precipitation (p) and wind power (DP). Two ranges of alternative stable states were identified: fixed crust dominated dunes and fixed vegetation dominated dunes at low wind power; and fixed vegetated dunes and active dunes at high wind power (see Fig. 3 of Kinast et al. (2013)). Here we investigate another aspect of the solutions to Eq. (1), namely periodic oscillations.

We study their existence, their dependence on the different model's parameters and the system response to different climatic and anthropogenic scenarios. Kinast (2014) showed that steady mixed dune-cover states may undergo oscillatory instabilities. For $\phi_v = \phi_b = 0$ and $\mu_v = \mu_b = 0$ the oscillations emerge in a super-critical Hopf bifurcation at $d = d_c$, where d is the parameter that controls the wind-shield steepness in Eq. (3). When d is increased beyond the Hopf bifurcation point, d_c , both the period and the amplitude of the oscillations increase. For $d \gg d_c$ the wind-shield function $g(v)$ approaches a step function, the period and amplitude saturate and the dynamics take the form of relaxation-oscillations. Here, we expand the analysis and show results for the full model including the competition and grazing terms.

Long-term oscillations have been reported in other plant population systems. For example, the prairie grassland productivity showed long-term oscillations induced by drought which were sustained under the same climatic conditions (Haddad et al., 2002), although the exact internal mechanism responsible for these oscillations was unknown. In the results presented below, we show that the origin of the oscillations are the feedbacks between vegetation and biocrust. Thus, for the model that captures only the dynamics of the vegetation cover (Yizhaq et al., 2009), such oscillations does not exist as it is known from nonlinear dynamics theory that in one-dimensional systems (first order ODE with a single degree of freedom) non-stationary behaviors must be monotonic in time (Meron, 2015).

2.2. Numerical methods

The model's equations were numerically integrated using a fourth-order Runge–Kutta scheme using time step $dt = 0.005$. The model contains 18 parameters which most of them were adopted from previous publications. The parameters for the vegetation equation were based on Yizhaq et al. (2007, 2009) where their values were validated against the range of bistability of active and fixed dunes. The parameters for the biocrust equation were based on Yizhaq et al. (2013) and Kinast et al. (2013), and Benlap and Lange (2001) where their values used to show the existence and stability domains of different dune-cover states, of fixed biocrust dominated dunes to fixed vegetation dominated dunes (see Table 1 in the Supplementary Material). Here we show that

under almost the same set of parameters the model can represent new solutions of periodic oscillations.

Based on Kinast et al. (2013), the following set of parameters was used in most of the simulations: $\eta_v = 0.2$, $\alpha_{max,v} = 0.15 \text{ yr}^{-1}$, $\epsilon_v = 0.001 \text{ yr}^{-1} \text{ VU}^{-1}$ (VU are vector unit), $\gamma = 8 \cdot 10^{-4} \text{ yr}^{-1} \text{ VU}^{3/2}$, $\mu_v = 0.02 \text{ yr}^{-1}$, $\phi_v = 0.01 \text{ yr}^{-1}$, $c_v = 100 \text{ mm/yr}$, $v_c = 0.3$, $p_{min,v} = 50 \text{ mm/yr}$, $\eta_b = 0.1$, $d = 15$ for the equation for v , and $\eta_b = 0.1$, $\alpha_{max,b} = 0.015 \text{ yr}^{-1}$, $\epsilon_b = 1 \cdot 10^{-4} \text{ yr}^{-1} \text{ VU}^{-1}$, $\mu_b = 1 \cdot 10^{-4} \text{ yr}^{-1}$, $\phi_b = 0.01 \text{ yr}^{-1}$, $p_{min,b} = 20 \text{ mm/yr}$ and $c_b = 50 \text{ mm/yr}$ for the equation for b . Since the main two factors that affect dune mobilization are wind power and precipitation (DP and p) we mainly study the model's sensitivity to them. We also study the sensitivity of the results to other parameters such as grazing and the mutual competition between biocrust and vegetation as shown in the next section.

3. Results

3.1. The oscillation mechanism

To understand the mechanism that underlies the self-sustained oscillations it is simpler to set the grazing ($\mu_{v,b}$) and the competition ($\phi_{v,b}$) terms to zero. Fig. 2 shows one examples of such a periodic solution. The physical mechanism behind the oscillations is related to the nonlinear suppressing effect of the wind on vegetation which depends on the critical vegetation cover v_c . Following Kinast (2014), we start from a cycle where the initial state defined with $v > v_c$, such that plants suppress the wind effect on both vegetation and biocrust ($g \ll 1$), and thus both can grow at the expense of bare sand. But this growth stops at some point as it depends on the bare soil cover in the logistic terms in Eq. (1). The direct wind stress effect (the term $\gamma \text{DP}^{2/3}$ in Eq. (1)) acts only on vegetation, leading a decrease in vegetation and the further growth of biocrust. As the vegetation cover decreases below the critical vegetation cover ($v < v_c$), the sand transport terms ($g \lesssim 1$) will act on both the vegetation and biocrust (as the wind shield effect is no more effective) and the biocrust will also decline consequently, thus the bare sand portion will increase. At some point, there will be enough sand for regrowth of vegetation and biocrust. The vegetation will grow faster as its growth rate is much



Fig. 1. Vegetation linear dunes in the northern Negev desert near the Israeli-Egyptian border. The interdune area and the slopes are stable and covered with cyanobacterial-green algae crust (Veste et al., 2011) and vegetation while only the crests are bare and active. The mean annual precipitation in this region is $\sim 70 \text{ mm}$.

higher than the biocrust growth rate. Then, a new cycle will begin when the vegetation cover exceeds the critical vegetation cover v_c .

Fig. 3 shows the domain of oscillations in the p -DP phase plane without grazing and competition terms. With these terms the domain of oscillations becomes more complex and confined in a finite area of DP and p space as shown in Fig. 4. For example, for $p \sim 400$ mm/yr, it is possible to find two regions of DP for which there are relaxation oscillations. In addition to these oscillatory solutions, the system (Eq. (1)) has a steady state-solution which depends on the initial conditions shown in Fig. 5. There are two types of bistability (BS): BS Type I is a bistability of two steady states and BS Type II is a bistability of an oscillation solution with a steady state solution related to high v and low b . A bistability similar to Type II was found in a model of thermohaline circulation in response to wind stress amplitude (Ashkenazy and Tziperman, 2007). Fig. 6 shows the different domains of stability for the vegetation cover. This diagram is important for understanding the system response to climatic changes as shown in the next section.

3.2. Mathematical type of oscillations

The oscillations discussed above are “relaxation oscillations” (as in the Van der Pole oscillator or Belousov–Zhabotinsky reaction Meron (2015)) which are characterized by two alternating processes of different time scales (Strogatz, 1994): a relaxation period during which the system approaches an equilibrium point with a higher value of vegetation cover, alternating with a period in which the equilibrium point shifts to a state with a lower vegetation cover. It is possible to gain more information about the nature of the oscillations by plotting the vector field near the fixed point. The direction of the “flow” is obtained by the angle of the vector (f_2, f_1) [see Eq. (1)] in the b, v phase plane while the radius is defined as $r^2 = v^2 + b^2$. The rate of change of r can be obtained by taking the time derivative of r^2 ,

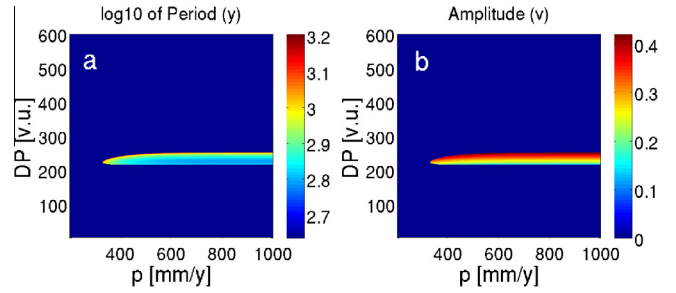


Fig. 3. Periods (a) and amplitude of the oscillations (b) as a function of precipitation, p , and wind power, DP. Parameters: as in Fig. 2 but without grazing and competition terms. Note that for this case the range of oscillations is not confined in the p axis due to saturation of the growth terms for both vegetation and biocrust for high precipitation rates (Eq. (2)).

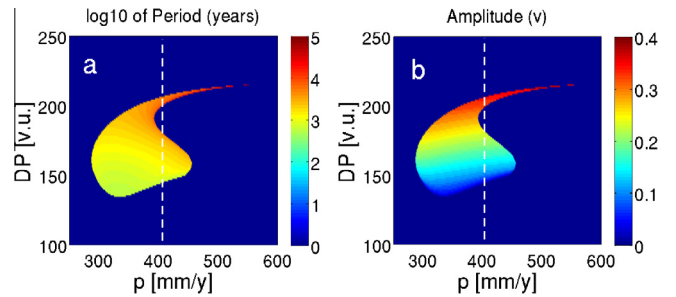


Fig. 4. Periods (a) and amplitude of the oscillations (b) as a function of grazing and competition terms. Parameters: as in Fig. 2 with $\mu_v = 0.02$, $\mu_b = 0.0001$, and $\phi_v = \phi_b = 0.01$. The amplitude of the oscillations is calculated as the difference between the maximal and minimal values. The vertical dashed lines indicated $p = 400$ mm/y where are two regimes of oscillatory solutions.

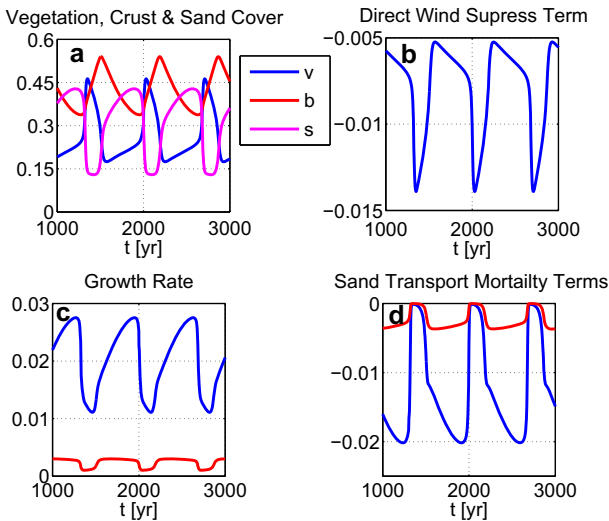


Fig. 2. The different model's terms during a periodic solution. (a) Vegetation cover (v), biocrust cover (b) and bare sand cover ($s = 1 - b - v$); (b) direct wind suppression term that acts only on vegetation ($\gamma DP^{2/3}$); (c) Growth rates of vegetation ($\gamma DP^{2/3}$) and biocrust ($\alpha_b(b + \eta_b)s$); (d) Mortality terms due to sand transport, for vegetation ($\epsilon_v g$) and for biocrust ($\epsilon_b g$) where $g = \frac{1}{2} DP (\tanh(d(v_c - v)) + 1)s$ defines the masking effect of vegetation. Parameters: $\eta_v = 0.2$, $\alpha_{max,v} = 0.15$, $\epsilon_v = 0.001$, $\gamma = 8 \cdot 10^{-4}$, $\mu_v = 0.02$, $\phi_v = 0.01$, $c_v = 100$, $v_c = 0$, $p_{min,v} = 50$, $\eta_b = 0.1$, $\epsilon_b = 1 \cdot 10^{-4}$, $\mu_b = 1 \cdot 10^{-4}$, $\phi_b = 0.01$, $p_{min,b} = 20$ and $c_b = 50$ with $p = 500$ mm/yr and $DP = 230$.

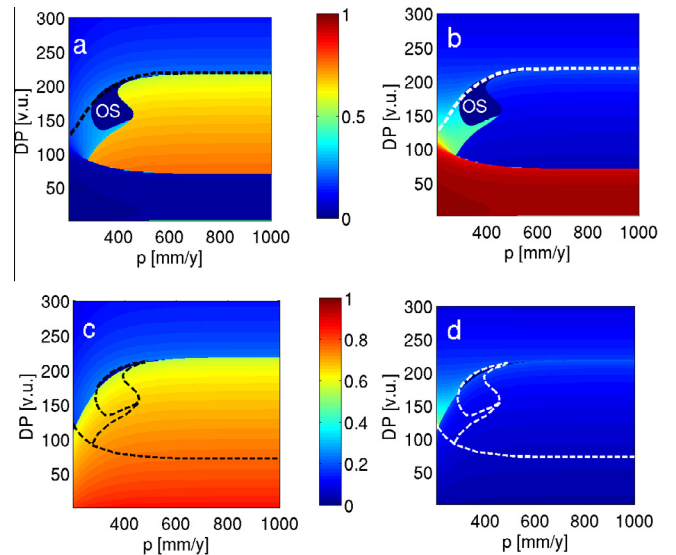


Fig. 5. Steady states solutions for vegetation (a, c) and biocrust (b, d). Parameters: as in Fig. 2 with $\mu_v = 0.02$, $\mu_b = 0.0001$, $\phi_v = \phi_b = 0.01$. OS stands for the oscillations solution domain (see Fig. 4) which is obtained for initial conditions with high value of b and low v . The steady states in panels c and d were obtained starting from high v and low b . The cover fraction for the steady state solutions is indicated by the color bar while the oscillatory state regime is indicated by the blue color (see Fig. 4 for the amplitude and period of the oscillations). The dashed line show the transition lines of the alternative domains of stable solutions. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

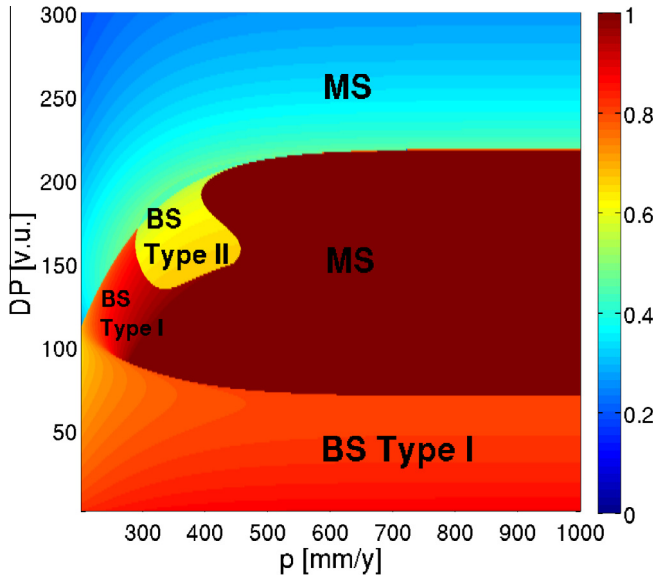


Fig. 6. Different domains of stability and bistability for vegetation cover. MS stands for mono-stable state, and BS (bi-stable) Type I is a domain with two steady solutions whereas, in BS Type II domain, the bistability is of one stationary solution and one oscillatory solution. The different solutions can be found in Fig. 5. *b* exhibits similar diagram.

$$\frac{dr}{dt} = \frac{1}{r}(vf_1 + bf_2). \quad (4)$$

Thus, as r is always positive (by definition), the magnitude of $vf_1 + bf_2$ represents the rate of change of r . Fig. S1 of the supplementary material shows one example of a stable limit cycle where nearby trajectories converge towards the cycle. The convergence to the limit cycle depends on the different values of the parameters as shown in Fig. 7 for two values of v_c ($v_c = 0.3$ and $v_c = 0.24$). As in the Van der Pol oscillator, the linear stability analysis fails to find the limit cycle solutions (Boyce and DiPrima, 2001). A conventional linear stability analysis is not applicable for the model's equations, thus our results are based on extensive numerical simulations where we explicitly compute the periodic solutions.

3.3. Sensitivity analysis

The dependence of oscillations on the vegetation critical vegetation v_c for $p = 400$ mm/yr (keeping the other parameters unchanged) is shown in Fig. 8. For smaller values of v_c , higher values of DP are needed for existence of the periodic oscillations and the longer periods the larger are the amplitudes as shown in Fig. 9. The dependence of the oscillations on the intensity of vegetation grazing term (μ_v) is shown in Fig. 10 for $p = 400$ mm/yr and (and for $p = 400$ mm/yr in Fig. S2 of the supplementary material). The oscillations exist for a finite range of μ_v ($0.194 < \mu_v < 0.262$) and for DP values between 150 and 200. For $p = 300$ mm/yr the domain of oscillations becomes even smaller. Fig. 11 shows the dependence of the oscillations on competition term, ϕ_v , for $p = 400$ mm/yr and $\phi_b = 0.01$. Also here, there is finite range of ϕ_v and DP for which the oscillations exist. Clearly, larger values of ϕ_v suppress the oscillations as the system converge to one of the bistable state. The dependence on biocrust competition ϕ_b for $\phi_v = 0.01$ is shown in Fig. S3 of the supplementary material. The dependence on ϕ_v and ϕ_b is asymmetric and it is more sensitive to the values of ϕ_b which are confined to a narrow range between 0.0077 and 0.01. The range of DP values are almost the same for both parameters.

The above sensitivity analysis shows only a small part of the vast space spanned by the model's parameters and it illustrates the impact of the grazing and competition intensities on the oscillations solutions. The main conclusion is that these interesting and new solutions in the context of dune dynamics are obtained for specific range and combination of parameters and outside this range the system is in one of the stationary bistable states. But as the values of the parameters used in the simulations were also used in previous works (Yizhaq et al., 2009; Kinast et al., 2013; Yizhaq et al., 2013), the existence of these internal fluctuations in dune activity can not be neglected. In the next section we show how these oscillations affect the response of dunes to climatic changes.

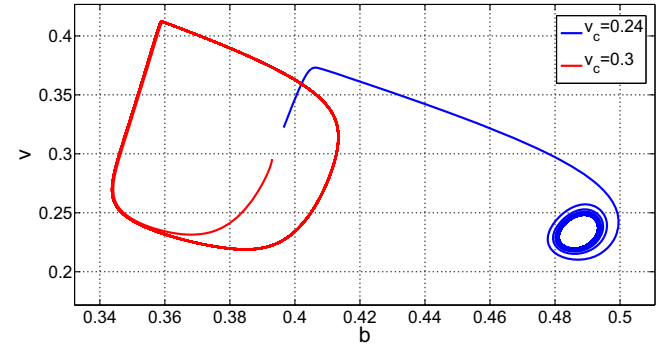


Fig. 7. The convergence to the limit cycle for $v_c = 0.3$ and $v_c = 0.24$. Parameters: As in Fig. 2. The orbits in the phase plane for two different values of v_c . Note that for $v_c = 0.24$ the limit cycle is close to a circle as the oscillations becomes more regular (linear), whereas for $v_c = 0.3$ they are more resemble to relaxation (nonlinear) oscillations type.

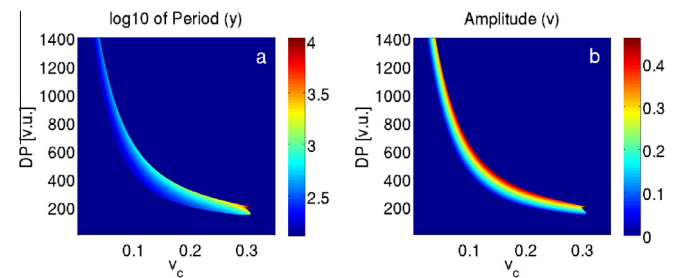


Fig. 8. Sensitivity of the oscillation periods (a) and amplitude (b) to the critical vegetation cover v_c . Parameters: as in Fig. 2 and $p = 400$ mm/yr. The lower is v_c the higher is DP needed to sustain the oscillations and the narrower is the range of DP.

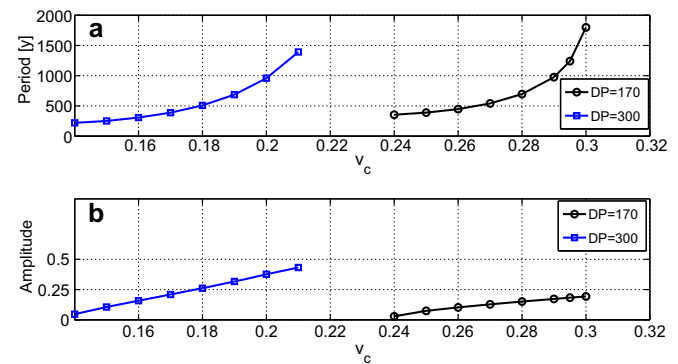


Fig. 9. The periods (a) and amplitudes of the oscillations as a function of v_c , for DP = 170 and DP = 300. Parameters: As in Fig. 2 and $p = 400$ mm/yr. The period grows exponentially with v_c whereas the amplitude grows almost linearly with v_c .

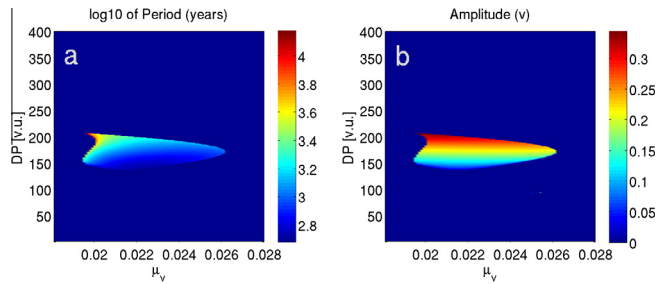


Fig. 10. Sensitivity of the oscillations, periods (a) and amplitude (b) to the grazing intensity parameter μ_v . Parameters: as in Fig. 2 and $p = 400$ mm/yr. The oscillations exist for $0.194 < \mu_v < 0.262$ and for DP values between 150 and 200.

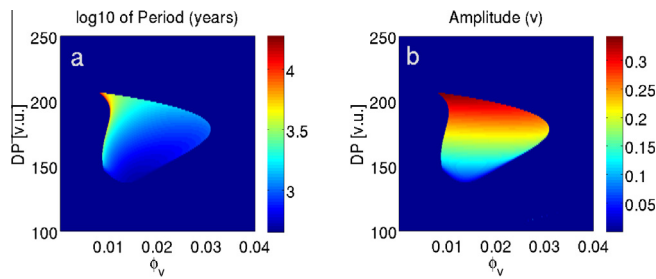


Fig. 11. Sensitivity of the oscillations, periods (a) and amplitude (b) to the parameter representing the competition between vegetation and biocrust, ϕ_v . Parameters: as in Fig. 2 and $p = 400$ mm/yr and $\phi_b = 0.01$. The oscillations exist for a finite domain of ϕ_v and DP.

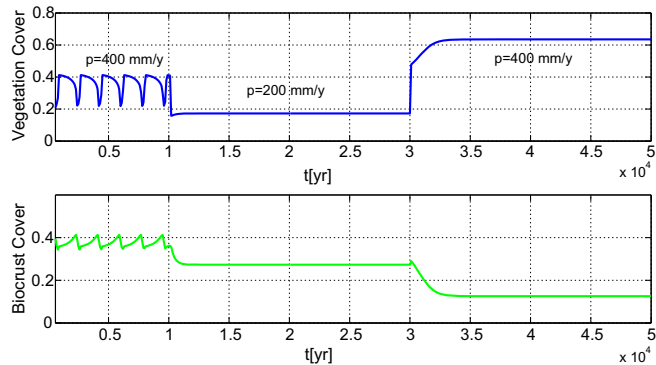


Fig. 12. Rehabilitation modulated by a climatic change (period with low p). Parameters: as in Fig. 2 with DP=170. The system starts in the oscillation state with $p = 400$ mm/y, then the precipitation drops to 200 mm/yr and the system shifts to one of the bistable states with low vegetation cover and high biocrust cover. When the precipitation returns to its initial value the system converges to the alternative bistable state with higher vegetation cover and lower biocrust cover.

3.4. System response to different climatic scenarios

We used the model (1) to explore the system response to different scenarios of climatic and anthropogenic changes to gain a better insight on the system's dynamics. These scenarios are quite artificial and aim to suggest conceptual responses to climatic (precipitation and wind power) and anthropogenic changes. The complex dynamics of the biocrust–vegetation model leads to interesting and counterintuitive behaviors, such as vegetation rehabilitation induced by drought (Fig. 12): When the system is initiated from the self-sustained oscillation state, reduction in precipitation from $p = 400$ mm/yr to $p = 200$ mm/yr shifts the system to a biocrust-dominated stable state. Increasing the precipitation again to its initial value shifts the system to a vegetation-dominated steady state

which coexists with the oscillatory solution (BS Type II). Thus, this decrease in precipitation triggered the transition of the system to a more productive state (higher vegetation cover). In most of the research of desertification (e.g., D'Odrico et al. (2013)) a dry period is associated with degraded state of the system. The bistability of the oscillation state with a vegetated dominated state allows this interesting response of the system.

The situation is even more interesting as the system dynamics depends on the initial conditions. In the domain in which both the oscillatory and the steady-state solutions exist (BS Type II), the system can converge to either one of these two states depending on the initial values of v and b . Fig. 13 (panels a and b) shows a sequence in which the precipitation alternates between $p = 400$ and $p = 300$ mm/yr. The system remains in the periodic solution with a longer period for $p = 400$ mm/yr. But the same sequence can shift the system to the vegetation dominated state (panels c and d). This behavior depends on the exact value (phase) of v and b at the time that the precipitation increased again to $p = 400$. In the first simulation the change occurs when v decreases after it reached its maximum value, whereas in the second simulation it occurs when v is at its maximum value. Thus, different initial conditions (phases) lead to different convergence (which is common in nonlinear systems). Fig. S4 helps in understanding the dependence of the dynamics on the initial conditions. For example for $p = 400$ mm/y, when starting from $b_0 > 0.4$ the system converges to the oscillatory state whereas for $b_0 < 0.4$ the system converges to the stationary state (vegetation dominant). For $p = 300$ mm/yr the critical threshold is about 0.3. Thus, for $b > 0.3$ the system converges to the oscillatory state as shown in Fig. 13 (panels a and b).

Climatic changes can also involve changes in the wind power, DP. In Fig. S5, counter-intuitively, an increase in the wind power shifts the system from the oscillatory state to the stationary solution with a higher value of vegetation cover. This is due to the coexistence of oscillatory and stationary stable states for DP = 200. As for the precipitation example shown above (Fig. 13), the phase at which the transition in DP occurs is important and may lead to the original oscillatory state instead of the higher vegetation steady state.

3.5. System response to different anthropogenic scenarios

The anthropogenic influence on vegetation and biocrust can be modeled by changing the intensity of “grazing” (or “trampling”) parameters, μ_v and μ_b . Fig. 14 shows a sequence of simulations with various values of μ_v (between 0.02 and 0.03). Increasing the grazing intensity results in the transition from the oscillatory state to a lower productivity state with low levels of biocrust and vegetation covers (this is the only stable state in this case). But again reducing the value of μ_v to 0.02 shifts the system to the state with a higher vegetation cover instead of returning to its initial oscillatory state because the change occurs when v is low. Decreasing μ_v to 0.025 shifts the system to the oscillatory state which is the only stable state for this set of parameters, thus it does not depend on the phase of v or b . Therefore, the system is shifted to a higher productivity state by applying the perturbation of intense grazing. This behavior is interesting since grazing activity is usually regarded as a factor responsible for vegetation destruction that can shift the ecological system to a lower a productive state (Okin, 2013), as in the case of the dunes in the Egyptian side of the border between Israel and Egypt where grazing is permitted (Tsoar, 2008).

The above examples demonstrate that the system's response to climatic and anthropogenic changes depend on the state/phase of the system during the time the change or the disturbance occurs, and on the multi-stability of states for a specific set of the model's parameters.

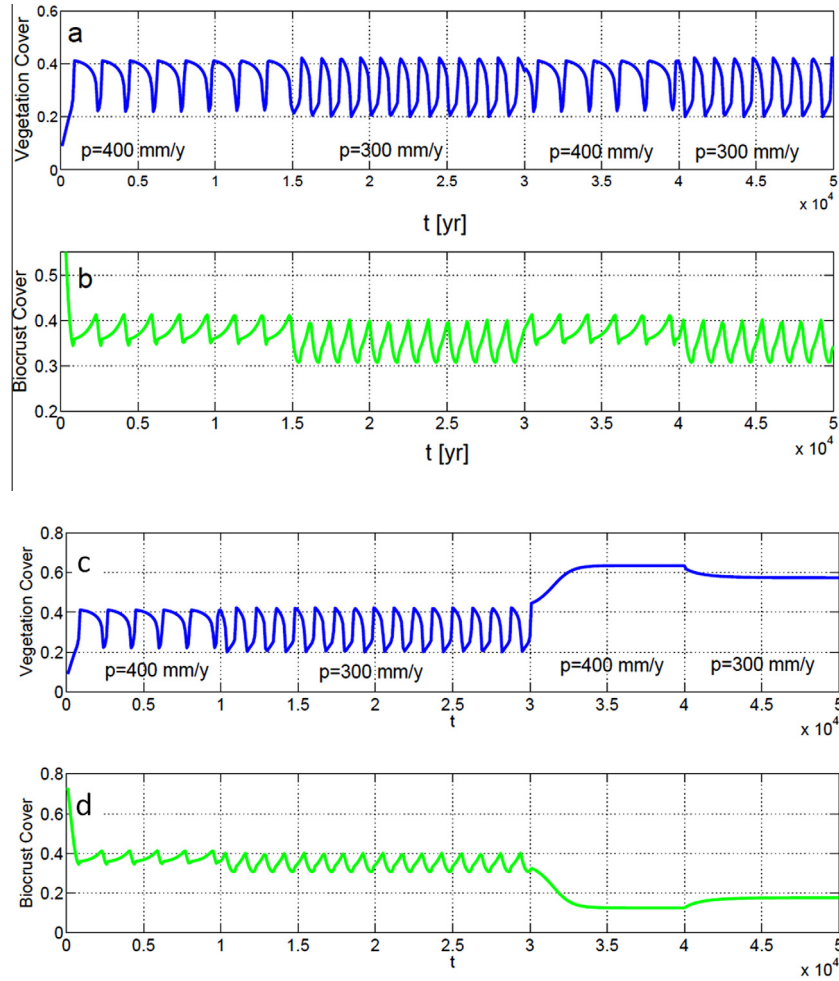


Fig. 13. Variations in precipitation that do not lead to a transition to steady stable state. Parameters: as in Fig. 2 with $DP = 170$. The system remains in the oscillatory state under precipitation cyclic changes from $p = 400$ mm/yr to $p = 300$ mm/yr, although the period and amplitude of the oscillations change (panels a and b). (c) The sequence of precipitation is the same as panel (a) except that the increase in precipitation occurs when b is in its maximal value, resulting in the convergence of the system to the a state with large v and low b (panel d).

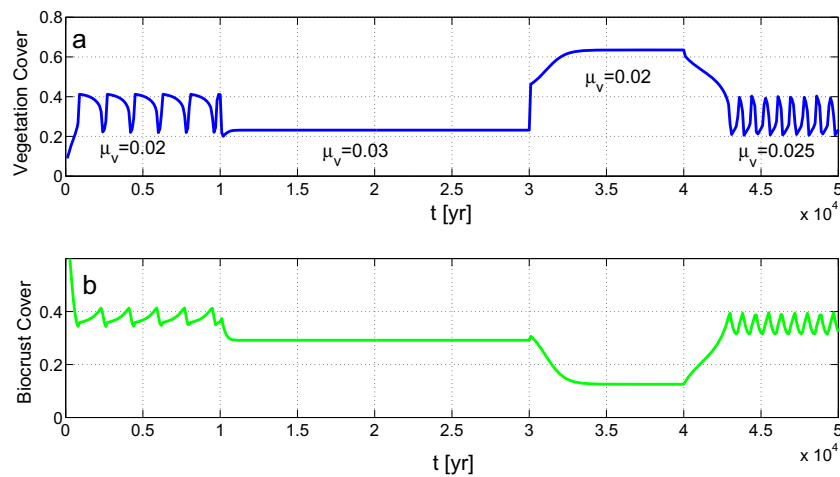


Fig. 14. Rehabilitation induced by grazing. Parameters: As in Fig. 2 with $P = 400$ mm/yr. The initial conditions are in the oscillations state. Increasing the grazing intensity parameter (from $\mu_v = 0.02$ to $\mu_v = 0.03$) shifts the system to the lower bistable state. When decreasing the grazing to its initial value, the system shifts to the higher, vegetation dominant productive state. The system then return to the oscillatory state when the grazing intensity is increased to $\mu_v = 0.025$.

4. Discussion

We find that under fixed parameters representing climatic factors (wind and precipitation) a model for vegetation and biocrust

covers on sand dunes exhibits self-sustained oscillations with periods between 300 to more than 3000 years depending on the different model's parameters. The variations in the vegetation and biocrust covers induce a new intrinsic time scale in dune activity

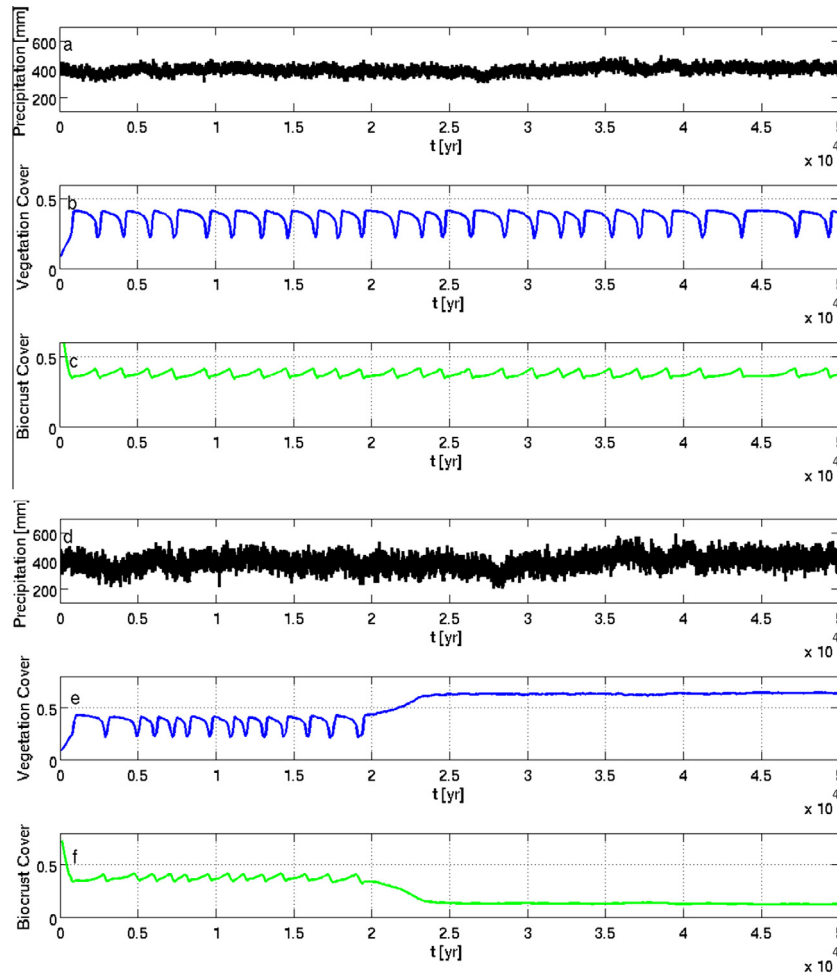


Fig. 15. System response to temporally correlated precipitation ($\sigma = 25$ mm/yr). Parameters: As in Fig. 2 with $\langle p \rangle = 400$ mm/yr. The system starts in the oscillatory state. For low value of σ the system remains in the oscillations state with variable period (panels a and b). For higher value of σ the changes in precipitation are large enough to shift the system to one of the bistable states (panels c and d). Thus, fluctuations in precipitation which are common in arid environment can mask the self-sustained relaxation oscillations of the biocrust–vegetation system on sand dunes.

which is dictated by the mutual relations between biocrust and vegetation. The climate system can affect dune dynamics on this intrinsic time scale.

Climate variables often exhibit long-range temporal correlations on time scale spanning from days to hundreds of thousands of years (Pelletier, 1997; Huybers and Denton, 2008). Motivated by this, we simulated a long-range correlated precipitation time series by Fourier transforming an uncorrelated time series, multiplying its power spectrum by a power law function ($f^{-\beta}$ where f is the frequency) and then transforming it back. Fig. 15 depicts the model's dynamics under such a variable and more realistic precipitation time series with correlation exponent $\beta = 0.5$ and mean \pm one standard deviation precipitation of $p = 400 \pm 25$ mm/yr. For this case the system converges to periodic oscillations with variable periods (panels a and b). For larger standard deviation of 50 mm/yr, the system converges to an almost stationary state, dominated by high vegetation cover (Fig. 15, panels c and d). Thus, larger climate variability eliminates the model's oscillations and shifts the system to one of the bistable states. This result suggests that it will be difficult to observe these predicted oscillations in reality due to their long period and the interaction with the external variability of climate. A similar behavior was shown in coupled vegetation–climate model with random environmental fluctuations that turn a bistable deterministic dynamics into a system with only one stable state (Bathiany et al., 2011) and thereby enhancing ecosystem resilience

as it prevents the critical transition between the vegetation dominated state to the biocrust dominated state.

The climate system exhibits long-range temporal correlations, covering many orders of magnitudes (Pelletier, 1997; Ashkenazy et al., 2003; Huybers and Denton, 2008). These correlations are stronger for longer times scales, up to the time scales of glacial–interglacial oscillations. The underlying mechanism for these stronger temporal correlations is still not fully understood. The model's results described above indicate oscillatory behavior on time scales of thousands of years. Since the sand system can affect the climate system via changes in albedo (Otterman, 1974), precipitation recycling, change of surface roughness and soil moisture (D'Odrico et al., 2013), the reported oscillations may underlie the power of climatic time series at these time scales.

Another important aspect of the periodic oscillation solutions is that they exhibit an intermediate state in the shift of the system during desertification process. According to the common view, desertification is associated with an abrupt transition between two alternative states in response to climate changes or human disturbances (D'Odrico et al., 2013; Meron, 2015). As shown in Fig. 15 the system response to abrupt increase in grazing intensity shifts the system from the non-degraded state to the oscillatory state rather than to the degraded state. This intermediate state exists only in non-variational systems which poses sustained oscillations (Meron, 2015).

Many studies have been devoted to revealing past aeolian activity (Tefler and Thomas, 2007; Roskin et al., 2011; Tsoar, 2013; Thomas, 2013). Variations in sand dune activity was almost solely attributed to the climate variability of wind and precipitation (Warren, 2014). Intrinsic oscillations in the activity of sand dunes such as the one predicted by our model was not considered. We conjecture that such intrinsic dune variability may partially underlie past variations in sand dune activity, thus weakening the direct link between dune activity and decrease in precipitation and/or increase in wind power. Interestingly, most of the models of vegetated aeolian systems overlooked the important role of biocrust. As the vegetated linear dunes are the most common dune types in the study of paleo-climate (Thomas, 2013) and most of these dunes are partially covered by biocrust, it is necessary to include its effect in models. For example, it was shown that after a prolonged drought in the dunes of the western Negev at the border between Israel and Egypt, the average vegetation cover was sharply decreased (Siegal et al., 2013). However, due to the resistance of biocrust to drought, the dunes remained stable.

We believe that the existence of periodic solutions should be considered in the research devoted to studying paleoclimate variability that is based on sand dunes mobility using luminescence dating techniques (OSL). Cycles of activity and stability of sand dunes are not necessarily related to climate variability, but can be a result of the interaction between biocrust and vegetation as predicted by our model. Our results show that the interpretation of OSL dating should include also the possibility of intrinsic self-sustained oscillations in addition to climate variability (Thomas, 2013).

5. Summary and conclusions

We show that the complex dynamics between vegetation and biocrust leads to intrinsic oscillations that emerge solely from the dynamics of the system and not from climate (parameter) variability. These oscillations lead to interesting scenarios where the system responses to climate and anthropogenic changes. These new predicted oscillations are of importance to the study of the vegetated linear dunes which many of them are partially covered by biocrust. These kind of dunes are abundant in the Kalahari, Australian and Central Asian deserts. More advanced spatial models that include coupling to the atmospheric dynamics may help to quantify the relative role of the atmospheric variability and intrinsic dune variability in past and future sand dune activity. According to the nonlinear dynamics theory such spatial non-variational systems can show interesting types of behaviors such as sustained oscillations, traveling waves and various forms of chaotic dynamics.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.aeolia.2015.10.005>.

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