



# 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 ( $\approx 6$  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 ( $-\phi_v b v$  and  $-\phi_b v v$ ) 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  $DP \propto U^3$ ).  $\gamma$  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.

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