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# Biogenic crust dynamics on sand dunes

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Sand dunes are often covered by vegetation and biogenic crusts. Despite their significant role in dune stabilization, biogenic crusts have rarely been considered in model studies of dune dynamics. Using a simple model, we study the existence and stability ranges of different dune-cover states along gradients of rainfall and wind power. Two ranges of alternative stable states are identified: fixed crusted dunes and fixed vegetated dunes at low wind power; and fixed vegetated dunes and active dunes at high wind power. These results suggest a crossover between two different forms of desertification.

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Sand dunes have been the subject of active research for many years, largely because of their fascinating shapes and dynamics [1-4]. Current studies have increasingly addressed the question of sand-dune stability in relation to climate change and anthropogenic disturbances [5-7]. Sand dunes are considered "stable" when they are fixed in place.<sup>1</sup> Their stability is strongly affected by the degree of vegetation coverage. High coverage reduces the wind power at the dune surface and thereby acts to immobilize the dunes. The remobilization of fixed dunes, either by vegetation mortality or clear-cutting, often has detrimental effects on the unique ecosystems that develop in stable dunes [8,9], leading to alternative ecosystems associated with active sand [10]. Active dunes may also pose a threat to human settlement as they can block roads and cover residential areas and agricultural fields [11,12].

Sand dunes are also stabilized by biogenic soil crusts. These crusts comprise a variety of organisms, including cyanobacteria, lichens, and mosses, which live at the surface of desert soils [13]. Biogenic crusts enhance the aggregation of sand grains, prevent saltation, and reduce wind erosion. Since most sandy soils are located in drylands, where the vegetation is patchy and generally sparse [3], the role of biogenic crusts in stabilizing dunes is important and often crucial [14]. Despite their significance and vast presence in the Kalahari, Australian, and Central Asia deserts [15–17], soil crusts have rarely been considered in model studies of dune dynamics.

Depending on wind power and precipitation level, different dune-cover states are observed. Figure 1 shows several typical states from regions of relatively weak winds. At very low precipitation levels [Fig. 1(a)], dunes are active due to low crust and vegetation coverage. For higher precipitation levels, the dunes gradually become more stable. At low precipitation levels, the dominant stabilizing agent is the soil crust [Figs. 1(b) and 1(c)], while at high levels, the stabilizing agent is predominantly vegetation [Fig. 1(d)]. Although vegetation and biogenic crusts have similar effects in stabilizing dunes, they are associated with ecosystems that differ vastly in their bioproductivity.

Motivated by these observations, we ask whether the transition from crusted to vegetated dunes along the rainfall gradient is gradual or abrupt and how it is affected by the wind power. Studying these questions is significant for understanding desertification processes, i.e., processes involving the irreversible loss of vegetative bioproductivity [18]. To study these questions, we introduce and analyze a new model, which extends an earlier model for vegetated dunes [19] to include crust dynamics.

The model describes the dynamics of two populations, vegetation and biogenic crust, which are represented by the fractions of surface cover v and b, respectively (0 < v + b < 1). It is a mean field model for a dune field that may cover many dunes. The growth of vegetation and crust is affected by two main environmental factors: precipitation, which promotes growth, and wind, which suppresses growth. In addition, the populations are assumed to compete with each other, as discussed below. The model consists of two coupled ordinary differential equations,

$$\dot{v} = \alpha_v (v + \eta_v) s - \epsilon_v D_p v g(v) s - \gamma D_p^{\frac{4}{3}} v - \phi_v v b \qquad (1a)$$

$$b = \alpha_b (b + \eta_b) s - \epsilon_b D_p bg(v) s - \phi_b bv, \tag{1b}$$

where s = 1 - v - b represents the remaining fraction of bare sand, and the over dot denotes the time derivative. The first terms on the right sides of Eqs. (1a) and (1b) represent logistic growth. Implicit in these growth forms is the assumption that the two life forms, crust and vegetation, locally exclude one another; the presence of crust in a given location prevents the germination of plant seeds, while the presence of vegetation inhibits crust growth by blocking sunlight. The growth rates of vegetation,  $\alpha_v$ , and of biogenic crust,  $\alpha_b$ , are assumed to have the following dependence on annual precipitation (*p*):

$$\alpha_i(p) = \begin{cases} \alpha_{i,\max}(1 - e^{-(p - p_{i,\min})/c_i}) & p \ge p_{i,\min} \\ 0 & p < p_{i,\min}, \end{cases}$$
(2)

where i = v, b,  $p_{\min}$  is a precipitation threshold below which there is no growth, and  $\alpha_{i, \max}$  is the asymptotic growth rate at high precipitation levels. This form is in accordance with field observations [22]. The parameters  $\eta_v$  and  $\eta_b$  represent

<sup>&</sup>lt;sup>1</sup>We distinguish here between *stable dunes* and *stable dune states*. The former term refers to fixed or stationary dunes, whereas the latter refers to asymptotic stability in the sense of dynamical-system theory.



FIG. 1. (Color online) Different types of sand dune cover along a rainfall gradient in Israel (*p* denoting the mean annual precipitation): (a) bare and active dune in hyper-arid region (Kasuy sands); (b) partially crusted and vegetated semiactive dune in arid region (Nizzana, 50% crust cover and 10% vegetation cover [20]); (c) almost fully crusted and vegetated fixed dune in arid region (Halutza, 80% crust cover and 15% vegetation cover [21]); (d) vegetated fixed dune in semiarid region (Nitzanim); (e) the Israel-Egypt border region with crusted fixed dunes on the Israeli side alongside bare and mobile dunes on the Egyptian side.

spontaneous growth rates due to, for example, a bank of seeds and spores in the soil, respectively.

Wind affects the vegetation and the crust, both directly and indirectly. Indirect wind effects include sand transport, which leads to root exposure and burial of plants and crusts by sand. This process is represented by the second terms in Eqs. (1a) and (1b). The parameter  $D_p$ , the *drift potential*, is proportional to the potential bulk of sand that can be transported by the wind, and is given by Ref. [1]:

$$D_p = \langle U^2 (U - U_t) \rangle, \tag{3}$$

where U is the wind speed and  $U_t$  is a threshold velocity that is necessary for sand transport (approximately 12 knots for wind measured at 10 m above the ground). If U is measured in knots (1 knot  $\approx 0.5$  m/s), the units of  $D_p$  are defined as *vector units* (VU).  $D_p$  can generally be classified into low, intermediate, and high energy winds ( $D_p < 200$  VU, 200 VU  $< D_p <$ 400 VU, and  $D_p > 400$  VU, respectively [2]).

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The function g(v) introduces a wind shielding effect created by vegetation. Observations indicate [23] that when vegetative cover exceeds a certain value  $(v_c)$ , it induces a *skimming flow* in which sand is protected from direct wind action. This value depends on various properties, such as plant shape and stem flexibility [24,25]. Based on these studies, we chose a continuous step-like function for g(v):

$$g(v) = \frac{1}{2} \{ \tanh[d(v_c - v)] + 1 \},$$
(4)

such that  $g \to 0$  for  $v \gg v_c$  and  $g \to 1$  for  $v \ll v_c$ . The sharpness of g(v) is controlled by d. Since the indirect wind effect requires the availability of sand, the whole term is multiplied by s.

Direct wind effects are restricted, in the model, to vegetation and are represented by the third term in Eq. (1a). This term accounts for stresses, such as increased evapotranspiration and branch cutting. It does not have a parallel in Eq. (1b) since crust can sustain very intense winds [26]. Wind drag is proportional to the square of the wind velocity, and therefore, this term is proportional to  $D_p^{2/3}$ .

The parameters  $\phi_v$  and  $\phi_b$  represent interactions between vegetation and crust. On one hand, crusts are known to support vegetation growth as a result of the "source-sink" effect [27], i.e., the interception of water runoff generated by the crust ("source") at vegetation patches ("sink"). On the other hand, crust suppresses vegetation by preventing water infiltration and seed germination [28]. Biogenic crust is usually suppressed by plants due to litter from nearby plants that limits light and that may destroy the crust if the litter is toxic [29]. It is still debated whether the net effect of these interactions is positive or negative. Here, we assume that the negative relations are more significant.

The parameter values used in this study are based on Yizhaq *et al.* [19] for the equation of the vegetation dynamics [Eq. (1a)] and on the studies of Belnap *et al.* [13,26] for the crust [Eq. (1b)]. The numerical values are:  $\alpha_{v,\text{max}} = 0.15 \text{ yr}^{-1}$ ;  $p_{v,\text{min}} = 50 \text{ mm/yr}$ ;  $c_v = 100 \text{ mm/yr}$ ;  $\eta_v = 0.2$ ;  $\epsilon_v = 10^{-3} \text{ yr}^{-1}\text{VU}^{-1}$ ;  $\gamma = 8 \times 10^{-4} \text{ yr}^{-1}\text{VU}^{3/2}$ ;  $\phi_v = 0.01 \text{ yr}^{-1}$ ;  $\alpha_{b,\text{max}} = 0.015 \text{ yr}^{-1}$ ;  $p_{b,\text{min}} = 20 \text{ mm/yr}$ ;  $c_b = 50 \text{ mm/yr}$ ;  $\eta_b = 0.1$ ;  $\epsilon_b = 10^{-4} \text{ yr}^{-1}\text{VU}^{-1}$ ;  $\phi_b = 0.01 \text{ yr}^{-1}$ ;  $v_c = 0.3$ ; d = 15.

The steady states of Eqs. (1a) and (1b) and their stability properties for low wind powers are presented in the bifurcation diagram shown in Fig. 2. The results are consistent with the general trend shown in Fig. 1 and reported in field observations [13]: a low precipitation range (a) of bare active dunes; intermediate precipitation ranges (b), (c) of dunes with mixed crust-vegetation coverage, semistabilized (b) or almost stabilized (c); and a high precipitation range (d) of stabilized vegetated dunes. In addition, the diagram predicts a bistability range (c) of vegetation-dominated dunes (v > b)and crust-dominated dunes (b > v). The bistability results from the negative vegetation-crust interactions assumed in the model, which relies on the conjecture that a crusted soil prevents the germination of plant seeds and also reduces the infiltration of surface water into the soil, while a vegetated soil provides shading and possibly toxic materials that inhibit the growth of crusts.



FIG. 2. (Color online) Bifurcation diagram of dune-cover states at low wind powers. Solid and dashed lines represent, respectively, stable and unstable steady solutions of Eqs. (1) with  $D_p = 120$  VU, obtained using a numerical continuation method. The thin red line and the thick blue line represent, respectively, the vegetation-dominated and the crust-dominated states. The labels a,b,c,d refer to the corresponding panels in Fig. 1. They represent bare dunes (a); mixtures of crust and vegetation forming semi-stable dunes (b) and stable dunes (c); and stable vegetated dunes (d).

A different type of bistability is known to exist in regions of strong winds and high precipitation [9,19]. This form of bistability results from the wind-shielding effect of the plants. The high wind power makes a bare dune active and suppresses plant growth, despite the high precipitation level. However, once the dune is vegetated, the wind-shielding effect of vegetation allows its persistence. Thus, two forms of bistability, designated here as Type I and Type II, are possible. Type I is associated with the wind-shielding effect of vegetation and occurs at high precipitation and strong winds. In this case, the stable dune states are bare active dunes and vegetated fixed dunes. Type II is associated with vegetation-crust competition, as Fig. 2 shows, and occurs at low precipitation and weak winds. Here, the possible stable dune states are crust-dominated dunes and vegetationdominated dunes. While the bistability of Type I has been identified [9,19], observations of Type II have not yet been reported.

Figure 3 shows the domains of the two bistability forms in the plane spanned by the precipitation p and the wind power  $D_p$ . The two domains are connected to form a continuous domain; proceeding from low to high p and  $D_p$  values, a cross-over from the bistability of Type II to Type I occurs. Bounding the continuous bistability domain are monostability domains of unvegetated dunes (bare or crusted) at low p or high  $D_p$ , and vegetated dunes at high p and low  $D_p$ .

The existence of a biomass productive vegetationdominated state and a less productive crust-dominated state, in the case of Type II bistability, implies the possible occurrence of desertification, i.e., a state transition inducing bioproductivity loss, as well as the feasibility of rehabilitation of vegetation, a state transition resulting in bioproductivity gain. By "bioproductivity," we refer to the total amount of vegetative biomass. Such transitions can be triggered either by



FIG. 3. (Color online) A phase diagram showing the monostability and bistability domains of dune-cover states. The colored domain represents regions of bistability, gradually changing from Type I bistability (active bare state and fixed vegetated state), in the limit of high precipitation and high wind power values, to Type II bistability (fixed vegetation-dominated state and fixed crust-dominated state), in the limit of low precipitation and low wind power values. The different colors represent the maximal cover fraction of crust (between the more and less crusted states). The bistability domain is bounded by a monostability domain of vegetated dunes at high precipitation, and a monostability domain of unvegetated dunes at low precipitation, crusted at low wind power and bare at high wind power.

environmental variability, for example, precipitation or windpower fluctuations, or by anthropogenic disturbances. The disturbance types that are necessary to trigger desertification or the rehabilitation of vegetation can be determined by examining the positions of the two stable states in relation to the boundary between their basins of attraction, as Fig. 4 illustrates. Disturbances involving vegetation removal can induce desertification (transition from point V to point B) only at sufficiently low precipitation levels [Figs. 4(a) and 4(b)]. At higher precipitation levels [Figs. 4(c) and 4(d)], the disturbance should also involve an increase in crust coverage (at the expense of sandy soil), a rather unlikely disturbance scenario. Rehabilitation of vegetation (transition from point B to point V) at relatively low precipitation levels [Figs. 4(a) and 4(b)] cannot be triggered by crust removal only—planting is also necessary. At higher precipitation levels [Figs. 4(c) and 4(d)], crust removal alone can trigger such rehabilitation.

The desertification form discussed above should be distinguished from that occurring in Type I bistability. In Type II bistability, both the productive and unproductive states (i.e., vegetated and crusted) represent stable, immobilized dunes, while in Type I, the nonvegetated (unproductive) state represents a mobile dune. Thus, desertification in the case of Type I bistability not only involves the loss of vegetation (bioproductivity) but may also lead to detrimental effects associated with dune mobility.

The model can be extended to study the effect of grazing on sand dune stabilization. Such study is motivated by a phenomenon that has been observed at the Israeli-Egyptian border, where sand dunes on the Egyptian side are active, while



FIG. 4. The phase space v,b for the bistability of Type II at increasing precipitation values ( $D_p = 120$  VU). The black dots B and V denote the crust-dominated state and the vegetation-dominated state, respectively. The line between the dots represents the boundary between the basins of attraction of the two alternative stable states. The arrows represent disturbances or manipulations capable of inducing state transitions (see main text for details).

on the Israeli side, dunes are semistabilized. This difference in dune activity is the result of a vast cover of biogenic crust on the Israeli side and its absence on the Egyptian side. The phenomenon is clearly visible across the border line [see Fig. 1(e)] due to different albedo values for crust and sand. It has been argued that biogenic crust is absent from the Egyptian dunes due to grazing activities that have led to crust trampling and erosion [30].

Several studies have addressed the question of modeling grazing activities [31,32]. Here, grazing stress affects both vegetation and crust; while plants are being consumed by herbivores, the crust often breaks under their hoofs [33]. For simplicity, we assume that both processes are linearly dependent on the cover fraction and add the terms  $(-\mu_v v)$  and  $(-\mu_b b)$  to the right-hand side of Eqs. (1a) and (1b), respectively, where the parameters  $\mu_v$  and  $\mu_b$  represent the decay rates of vegetation and crust due to grazing

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 $[(\mu_{v,b}) = (yr^{-1})]$ . Following Ref. [19], we set  $\mu_v = 0.01$  and choose  $\mu_b = 0.01$ , assuming the crust decay rate is similar.

Applying the extended model to the Israeli-Egyptian border region ( $p \approx 100 \text{ mm/yr}$ ,  $D_p \approx 120 \text{ VU}$ ), we find that grazing activity can yield bare dunes with low cover of crust and plants ( $b = 0.09, v = 0.11 \rightarrow s = 0.8$ ), while the absence of grazing yields crust-dominated dunes ( $b = 0.5, v = 0.1 \rightarrow s = 0.4$ ). These results are in qualitative accordance with field observations [Fig. 1(e)]. We note that the absence of grazing can also yield vegetation-dominated dunes (Fig. 2, thin red line). However, this alternative stable state is not observed in the Israeli-Egyptian border region. We conclude that introducing grazing activity at low precipitation levels may have a major effect on the fraction of bare dunes, doubling it in the numerical example presented above.

Further analysis of the model reveals that the competition terms  $\phi_v vb$  and  $\phi_b vb$  in Eqs. (1a) and (1b), respectively, do not affect the qualitative results; the phenomena described above remain valid even when the competition terms are completely removed. We choose to keep these terms to allow the association of the model behaviors with different mechanisms of vegetation-crust competition.

In summary, a mathematical model was introduced to analyze the effect of biogenic crusts on sand dunes. Although simple, the model is able to capture important aspects of the complex dynamics of biogenic crusts and vegetation on sandy soils. Most significantly, it predicts a new form of bistability in which the two alternative stable states correspond to stabilized dunes with different proportions of vegetation and crust coverage. This bistability form (Type II) prevails at low precipitation and wind power values and differs from the bistability of bare dunes and vegetated dunes at high precipitation and wind power values (Type I) [9,19]. The two bistability forms merge in the  $p - D_p$  parameter plane to form a single continuous domain with a small crossover zone. The model sheds new light on the vulnerability of sandy regions to desertification and on the means to restore degraded vegetation.

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