The influence of competition between lichen colonization and erosion on the evolution of soil surfaces in the Tabernas badlands (SE Spain) and its landscape effects

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ABSTRACT

Badlands often contain a mosaic of soil surface types with contrasting hydrological behaviour which drives their short term geomorphic evolution. The Tabernas badlands, in semiarid SE Spain, show a complex mosaic of bare ground, biological soil crusts and plant covered patches, and high variability of covers and morphologies. Previous work has identified the surfaces that act as sources of runoff and sediments and those that act as sinks; the pathways of runoff between surfaces, and the runoff and erosion at catchment scale. However, surfaces without vascular plants, can be quite dynamic, with important effects on geomorphic processes. This work aims to generate hypotheses about the dynamics of both bare soil (34% of the area) and biological soil crusts (33%), and to provide a first estimation of the growth rate of terricolous lichens (as increase of coverage) and their geomorphological implications.

The dynamics of ten representative soil surfaces were photographically monitored over 13 years, recording the cover and pattern of bare soil and of the two main kinds of biological soil crust: 'brown crust' and 'white crust'. Erosion/deposition were measured by erosion pins in unbounded plots, and the hydrological and erosional behaviour monitored in bounded plots under natural and simulated rainfall. Biological colonization and crust growth were studied from 2004 within cleared plots in four crust communities. Microclimate was continuously monitored in each community.

After 13 years, net erosion was recorded only in previously eroded slopes and divides. Vegetated sites and those covered by biological soil crust remained more or less invariant or recorded sedimentation. In all *white crust* surfaces, whole crust cover increased by 3% on average, while macrolichen cover increased by nearly 30%. Within the driest *brown crust*, macrolichen cover increased by 7%, while the whole crust decreased by 3%. According to previous work, lichen cover, particularly of white crust, is often greater in north to east facing orientations because of the higher slope stability and the longer duration of moisture. However, the increase of the whole biological soil crust can depend more on species composition and previous cover and less or not at all on the aspect, although certain species do grow faster in particular orientations. Within the plots cleared in 2004 the greatest increase occurred in the pioneering brown crust, which reached an average of 26% cover after one year, in spite of it receiving the most insolation. Significant microclimatic differences exist among the communities, mainly in radiation, soil moisture and thallus surface temperature.

Terricolous lichen crusts, primary colonizers of bare, sufficiently stable areas, can grow quickly and, by increasing soil stability and development and modifying surface hydrology, they can influence surface dynamics and ultimately landform dynamics. Crust growth rate probably decreases as its cover increases and it probably also oscillates with microclimatic oscillations. However, the high potential growth rate recorded allows detection not only of climatic changes but also short term (possibly seasonal) periods of stability. Extensive lichen crusts indicate low erosion rates and particular climatic conditions; variations of crust cover could indicate climatic (or land use) variations.

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1. Introduction

Badlands are usually areas with high landform diversity. Vegetation and general ground cover distribution are associated with landform (Lázaro et al., 2000; Cantón et al., 2004a), resulting in a mosaic of soil surface types with contrasting hydrological and erosion behaviour that controls geomorphic evolution. In the Tabernas badlands (semiarid SE Spain) a series of soil surface types has been identified (Calvo-Cases et al., 1991a; Alexander et al., 1994; among others) and the hydrological and erosion responses of the main types have been investigated (Calvo-Cases et al., 1991a; Calvo-Cases and Harvey, 1996; Solé-Benet et al., 1997; Cantón et al., 2001a; 2002), identifying the soil surfaces that constitute the main sources of runoff and sediments and those that act as sinks. The natural pathways of runoff between soil surfaces have been explored, giving a first explanation for the runoff and sediments collected at catchment scale from the surface composition of the catchment (Cantón et al., 2001a). However, these soil surfaces can be quite dynamic, particularly those without generalized vascular vegetation, and, since they have different responses to rainfall, their spatial and temporal changes can have important consequences for geomorphic processes such as runoff and erosion.

Surfaces with little or no vascular plant cover account for 67% (Cantón, 1999) of the total area and are the most susceptible to erosion and consequently to change, playing a key role in controlling badland evolution. Within this group of surfaces, the extremes are represented by bare regolith (the lowest stability) and a full cover of biological soil crust dominated by terricolous lichens (the highest stability). Thus, knowing how biological soil crust is degraded or bare soil is colonized by lichens seems to be a key to understanding the evolution of this badland area. On the other hand, little literature exists about detailed soil surface dynamics, and, particularly, terricolous lichen development and evolution (but see Belnap and Gardner, 1993; DeFalco, 1995; Belnap et al., 2003).

Biological soil crusts are frequent worldwide in inhospitable (or relatively inhospitable) sites (Büdel, 2003); in the Iberian semiarid SE, they are dominated by lichens. Lichen crusts affect hydrology, erosion, soil properties and the recruitment of vascular plants. They generally decrease erosion and increase runoff, redistributing water and increasing soil stability (Alexander and Calvo-Cases 1990; West, 1990; Calvo-Cases et al., 1991a; Eldridge and Greene, 1994; Yair, 2003). Most studies agree that these crusts maintain soil moisture (Perez, 1997, Seghieri et al., 1997, Malam Issa et al., 1999, Cantón et al., 2004b). Moreover, they increase pH (García-Pichel and Belnap, 2003) and the amount and availability of nutrients (Harper and Pendleton, 1993; Mitchell and Fullen, 1994; Belnap and Harper, 1995; Harper and Belnap, 2001); they provide Nitrogen, as up to 70% of the N fixed by cyanobacteria and cyanolichens moves immediately to the soil (DeFalco, 1995; Harper and Belnap, 2001); they provide Carbon and organic mater, as all organisms of the crust secrete Carbon, up to 50% of the total fixed; they increase organic Carbon and Nitrogen, improving soil fertility (St Clair and Johansen, 1993, Jeffries, et al., 1992). They also increase soil polysaccharides and total Carbon by up to 300% (Belnap et al., 2003), these extracellular polysaccharides facilitating the aggregation of soil particles (Lynch and Bragg, 1985; Cantón et al., 2003). These crusts favour vegetation development because, in addition to increasing soil fertility, they act as a trap for seeds, water and organic mater (Harper and St. Clair, 1985; Mücher et al., 1988), mainly by increasing surface roughness. However, the effect of the crusts on plant recruitment is still little known as it depends on very local factors (lichen species, type of seed, soil); and, on the other hand, there is some recent evidence that, at medium spatial and temporal scales, widespread biological soil crust can retard vegetation development (Orlovsky et al., 2004). These crusts are relatively little exigent, persistent, but mechanically fragile (Belnap and Eldridge, 2003).

Due to their very limited capacity to grow in height, lichens can only compete with vascular plants within a narrow window of climatic conditions which favour neither plant growth nor water erosion. Low magnitude and low intensity precipitation as well as high atmospheric humidity and frequent dew would differentially favour lichens (Lázaro, 2004). Due to this and to the crust's fragility, small environmental changes can have important effects on these crusts. In favourable climatic conditions they are able to achieve high cover and their effects are significant. This is facilitated because different species have preferences for different methods of hydration. Cyanobacterial lichens seem to require liquid water to activate photosynthesis (Lange et al., 1993) though some free-living cyanobacteria are able to photosynthesize in almost water-saturated air (Lange et al., 1994). Green algal lichens, however, can hydrate sufficiently for photosynthesis using either water vapour at high relative humidities or liquid water (Lange and Kilian, 1985). Besides, biological soil crusts are primary colonizers (Lázaro et al., 2000). Therefore, they represent an important soil stabilization agent in certain environmental circumstances; and their growth rate will play a decisive role in surface stabilization. The role of this growth rate is important also in terms of soil science, plant ecology, and land restoration.

If human disturbance is absent, lichens can persist for a long time in the same site, constituting evidence of stable conditions and providing information about the minimum stabilization age of the considered surface if lichen growth rate is known (Sancho et al., 2001). However, lichen growth seems very variable in space and time, among species, according to microclimatic conditions and as a function of the previous lichen cover. Abundant information exists on growth rates for certain species of alpine and polar lichens (see Sancho and Pintado 2004). However, lichen growth rates in arid regions are poorly known.

The influence of life on topography is a topic that has remained largely unexplored. Erosion laws that explicitly include biotic effects are needed to explore how intrinsically small-scale biotic processes can influence the form of entire landscapes, and to determine whether these processes create a distinctive topography (Dietrich and Perron, 2006).

Our work has two steps: first, we examined changes in different surfaces by low-frequency, long-term observations; then, as suggested by the results of these observations, we focused on an experimental study of the colonizing capacity and growth rate of the main lichen communities. Our objectives are (i) to generate hypotheses about the spatial and temporal dynamics of both bare soil surfaces and biological soil crusts, and (ii) to provide a first estimation of the growth rate (as increase of soil cover) of lichens and their geomorphological implications, improving the interpretation of key geomorphic processes.

Initial hypotheses are: (i) from field observation, terricolous lichen growth in SE Spain may be faster than expected, at least in the first colonizing stages; (ii) at least some classes of biological soil crusts are able to colonize places that are completely exposed to solar radiation if erosion rates are low enough; (iii) there are two general and opposite kinds of dynamics including all surfaces: erosion or vegetation, both including positive feedbacks and both having geomorphic consequences. Bare regolith or shrubland are extremes belonging to the first and second dynamics (respectively) and their change requires long stable periods or extreme erosive events. But intermediate surfaces, such as a more or less developed biological soil crust, are critical, as they can move both towards erosion or towards vegetation depending on very local factors in time and space; which, at the present, introduces uncertainty in the spatial and temporal patterns of surface distribution; (iv) from lichen species distribution in space (Lázaro, 1995; Bevan's unpublished data), some species will be pioneers and better adapted to high levels of solar radiation, whereas others will be more demanding of prior conditions and will appear later, replacing the former ones.

2. Study area

The Tabernas' Desert is located in SE Spain, in the Sorbas–Tabernas basin surrounded by several Betic ranges: the Gador, Nevada, Filabres
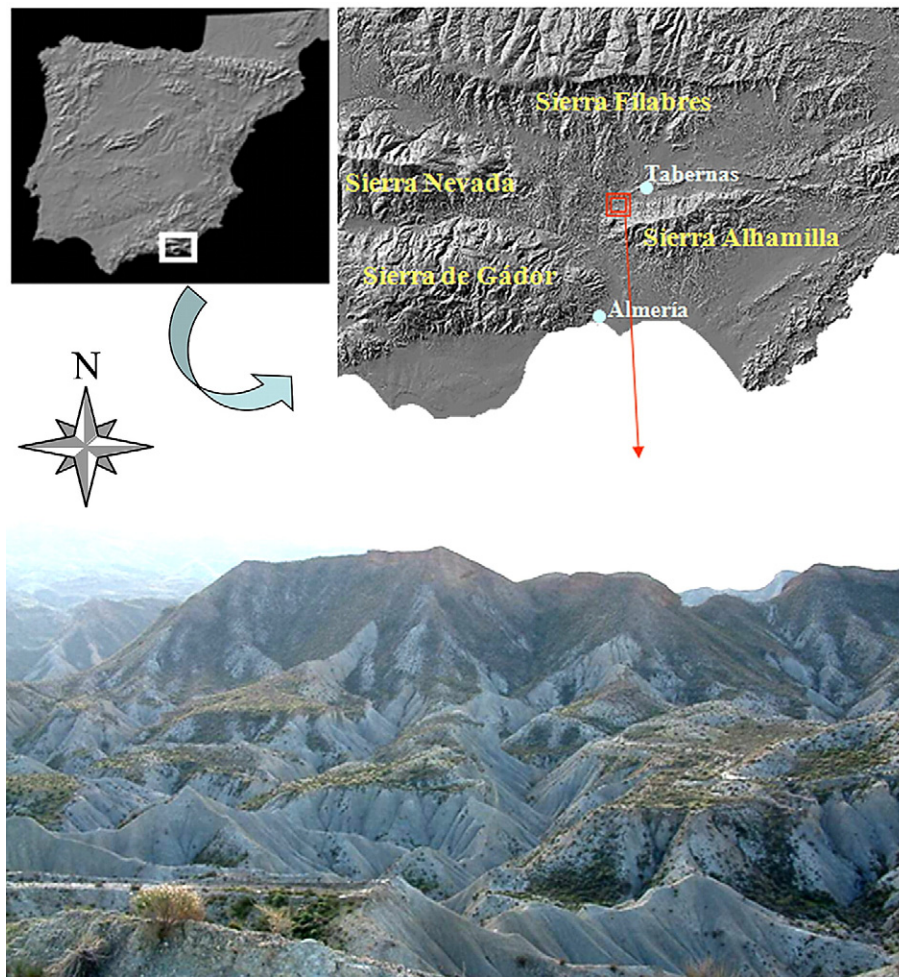
Fig. 1. The study area: Location map and a general view.

and Alhamilla. The first three of these ranges intercept most rainfall fronts, which come mainly from the west, thus explaining the low annual precipitation of around 230 mm.

Fig. 1 shows the situation and a general view of the study area.

The basin is mainly filled by Miocene soft rocks, mostly marls and calcareous sandstones, which, along with the dry climate, have produced an extensive badlands landscape with several encased levels, an important vertical development reaching 150 m and a complex geomorphology developed during the Quaternary (Calvo-Cases and Harvey, 1989). The area studied is in the square kilometre delimited by the UTM X 549 and Y 4096, and between 240 and 300 m a.s.l., and it is roughly formed by a series of parallel catchments. The most obvious features of these badlands are their valley asymmetry and vegetation pattern: S to W facing slopes are normally bare and eroded, while N to E facing slopes almost always have more or less developed soil and are covered by vegetation: grasses, dwarf shrubs, annuals and an important cover of biological soil crust including many species of terricolous lichens and often patches dominated by cyanobacteria (Lázaro, 1995). Between some catchments, more or less flat areas constituting old residual hanging pediments exist. This schematic general morphology results in a complex landscape when observed at large scales, especially when looking at the soil surfaces or ground cover.

Fig. 2 shows the main characteristics of the climate in the area from the meteorological station in the nearby town of Tabernas, with a temporal series of 30 years, and from our weather station in the experimental site (13 years).

The Tabernas diagram shows a semiarid warm Mediterranean climate with a particularly strong water deficit during the summer months. An average annual temperature of 18 °C, an absolute maximum of 45 °C, an absolute minimum of −5.5 °C, and high inter-annual and intra-annual variability for rainfall, are typical climatic features of the area. From our station in the experimental site, the maximum rainfall in 24 h during the study period has been 76 mm; rainfall intensity exceeds 100 mm h^{-1} only when considered for an interval of 5 min, or 150 mm h^{-1} for intervals shorter than 1 min.

3. Methods

This area in the Tabernas Desert, where badlands are very well expressed, was chosen in 1990 as an experimental site for studies in surface hydrology, geomorphology, pedology and plant ecology. A wide variety of soil surfaces or ground cover types, ranging from completely bare regolith to fully vegetated, was identified in previous works (Lázaro, 1995; Lázaro et al., 2000; Cantón, 1999; Cantón et al., 2004a) and can be summarized as:

1 bare regolith with marls at the surface
2 silt deposits, having: bare soil with depositional silty upper layer and mineral crust (2a)

   sites as 2a but with some cover of incipient or degraded biological soil crust (2b)

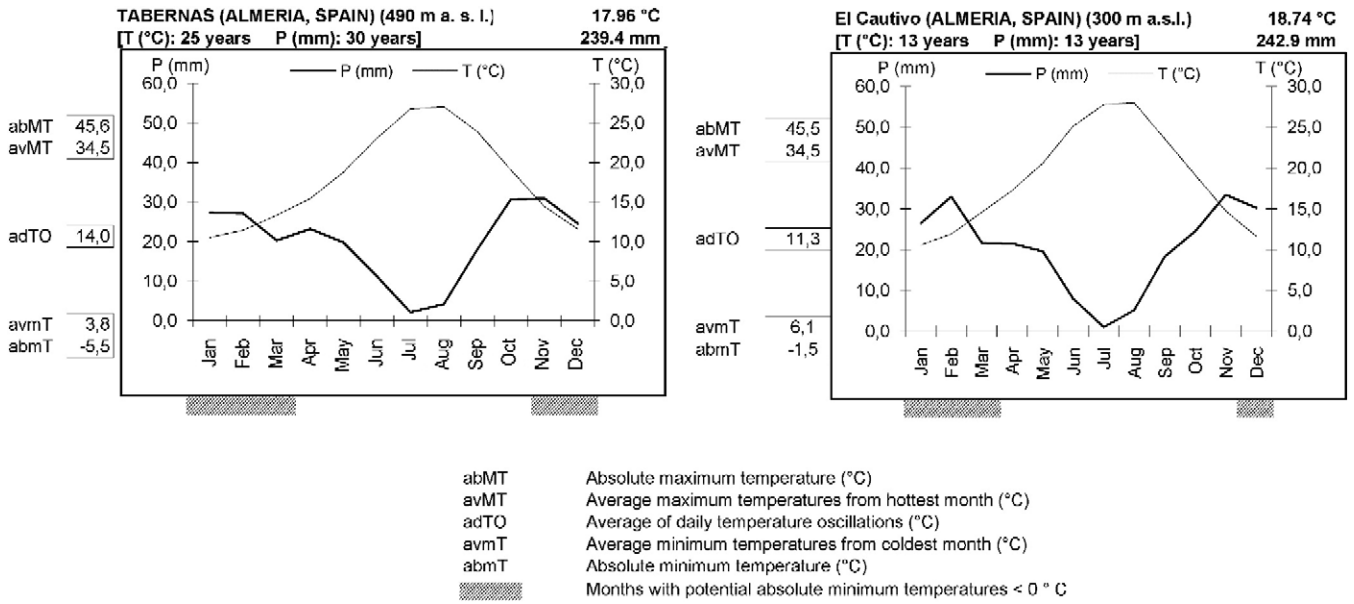   sites as 2a but with pedestals, as small stones protect the subjacent soil (2c)

Fig. 2. Walter–Lieth climatic diagrams from Tabernas weather station (Spanish Meteorological National Institute) and from our own station in the instrumented area.

3 brown crust, biological soil crust dominated by undifferentiated brown crust (mainly cyanobacterial) along with diverse, often small, lichen species
4 white crust, biological soil crust dominated by large, terricolous, mainly white lichens
5 vascular plants dominate the soil cover, mainly annuals and/or dwarf shrubs.

Four sets of plots were initially established, with surface types 1 to 4 being included in all of them. The second set also includes surface type 5, covered by vascular plants:

Set 1. This started in 1991 with 0.5 m × 0.5 m plots for photographic recording (4 to 6 photographs per plot per year during the first years, and then 1 or 2 per year or every 2 years). Monitoring ceased in 2005 and the set constitutes an exploratory preliminary work. It includes 13 plots, with each crusted surface represented in most cases by 2 or 3 plots in contrasted geomorphological positions, as a surface could have different behaviour according to its landform or its relative location.
Set 2. This was established to obtain runoff and erosion data by rainfall simulations, made in 1992 by Solé-Benet et al. (1997) over 17 (including surfaces with vascular plants) small size plots (0.24 m²) which were similarly distributed, but circular and bounded.
Set 3. 10 of the plots used in the simulations of Set 2 were provided with deposits collecting runoff and sediments, to allow further hydrological monitoring under natural rainfall conditions from 1992 to 1999.
Set 4. This included 10 larger (4 m²), unbounded plots with 6 erosion pins in each and, from 1994 to 2005, ground lowering was measured annually, usually in July (dry soil conditions), to avoid the consequences of any possible swelling (Cantón, 1999).

As association exists at the site between cover type and landforms (Lázaro et al., 2000), the different surfaces are not equally distributed through the landforms. Table 1 summarizes the distribution of all plots by surface and landform. Vascular plants were not monitored photographically or by erosion pins due to their higher stability and the difficulty of seeing the soil or measuring the pins beneath plants.

For technical reasons, no plots were established on surfaces steeper than 35°.

When divides are sufficiently wide and stable, they are covered with lichens and with some vascular plants; otherwise, they are eroded and bare, though some contain a boundary between bare soil and lichen crust. In Table 1 there are 12 photographic plots; the 13th was selected for monitoring a clear frontier between lichen crust and bare soil on one of the latter types of divide, E–W aligned, as it seemed particularly interesting to detect the advance or retreat of the lichen crust over time. On stable slopes, there are several plots with white crust because they had different initial white lichen cover. In all, the surfaces examined represent more than 80% of the total area of the badlands site (about 50 Ha). The rest is mainly *Stipa tenacissima* grassland, which occupies the surrounding areas not directly affected by the present drainage network, and also occurs on some of the

Table 1
Distribution of the four sets of plots through the soil surface types and the landforms

Plot distribution through soil surface types and landforms							
Soil surface type		Eroded slope	Stable slope	Eroded divide	Stable divide	Hanging pediment	Recent pediment
1 — Bare regolith		ph rs nr ep					
2 — Silt deposit	a) — With mineral crust	ph 2rs nr ep		ph ep			
	b) — With incipient or degraded lichens	ph 2rs nr ep					
	c) — With stones and pedestals	ph rs ep					
3 — Brown crust				ph rs nr ep		ph rs	ph 2rs nr ep
4 — White crust				3ph 2rs 2nr 2ep	ph rs nr ep		
5 — Vascular plants				2rs nr		2rs nr	

'ph' indicates the photographic set, 'rs', the rainfall simulation set, 'nr' monitoring under natural rainfall and, 'ep' indicates the erosion pins set.

oldest slopes in the catchments examined (Alexander et al., 1994). The surfaces other than those covered by vascular plants account for 67% of the total area (Cantón, 1999).

The analogue photographs were scanned at high resolution, and all were geometrically corrected. A supervised classification was made using Idrisi on the first and last photograph of each plot with relevant crust, selecting several training areas from only two kinds of surface: white crust and brown crust. This classification was used to obtain only rough results but minimizing errors, as automatic classifications are not always a sure method for the differentiation of a lot of surfaces at so detailed a scale. We compare the covers in the first and last photograph of each plot.

In previous unpublished work, some of us defined four main lichen communities by means of multivariate classification of 120 lichen inventories distributed in a partial-random fashion, in which we recorded the frequency and cover of each species. These communities are identified by their dominant or typical lichen species: *Endocarpon pusillum*, *Diploschistes diacapsis*, *Squamarina lentigera* and *Lepraria crassissima*, and will be named from here on 'Endo', 'Diplo', Squa' and 'Lepra', to avoid confusions with the species. The first matches with the brown crust, while the other three are within the white crust. In May 2004, a new series of monitoring plots was initiated, focussing on lichen colonization and growth. This comprised three plots of 30 cm×30 cm in each one of these four main lichen communities. At the beginning of the experiment the biological soil crust was completely removed from each plot, which was judged sufficiently small not to have an important risk of erosion. In May 2005, each plot was sampled by superimposing a 30 cm×30 cm quadrat divided into 36 square cells. From each cell, we recorded the presence and cover of each lichen species and, for the whole 30 cm×30 cm area, the frequency of each species, measured as the number of cells in which it was present. Undifferentiated biological crusts (mainly cyanobacteria and fungi), mosses and liverworts were treated as species. Lichen thalli too small to allow identification were recorded as "white young" or "black young" (as light or dark colour is associated with dominant species in white crust and brown crust, respectively), since they were very frequent and provide information about the density of initial colonization. The use of the grid allows: (i) a wide range of frequencies to be recorded and better estimation of cover (ii) recording of species position because without taking into account the location of colonizing thalli it is not possible to distinguish whether colonization has stopped or is perhaps very active but active erosion is also removing the thalli (iii) to see whether lichens tend to grow close to the border of the unaltered crust or away from it, by comparing the 3 nested rings of cells of the grid, in each community.

In each community the microclimatic conditions are (the experiment is on-going) continuously monitored close to the growth plots by automatically recording the rainfall amount and intensity and, at 20 min intervals, temperature and relative humidity at 20 cm above the soil, temperature on the thallus of the dominant lichen species, soil moisture in the upper soil layer, below the lichen crust, and the photosynthetically active radiation (PAR) reaching the lichen crust. Loggers are HWS from Onset Co. (USA) and sensors are from several trademarks. From the dew point and the lichen temperature data we calculated the duration in minutes of dew deposition. The communities Squa and Diplo have only one pluviometer as they are very close to one another. To compare microclimatic conditions between lichen communities, data were reduced to monthly values, the data of a given variable in a given month being used as variance. Non-parametric Kruskal–Wallis ANOVAs were performed, using StatSoft, Inc. (2005) STATISTICA (data analysis software system), version 7.1. www.statsoft.com, by each variable and month, except for minutes of dew, rainfall amount, number of rainfall days and absolute maximum of rainfall intensity, which are totals or maxima, not averages.

In the instrumented area we have a weather station and four nested catchments gauged by H Flumes since 1991. On rills in eroded

Table 2
Erosion data from unbounded (erosion pins) and bounded (natural and simulated rainfall) plots

Erosion and deposition data from each soil surface				
Soil surface type		Erosion/deposition from pins, mm	Erosion from bounded plots (g m^{-2} year^{-1})	Erosion from rainfall simulations (g m^{-2})
Bare regolith	In slope	−12.49	396.6	439.2
	In divide	−15.19		
Silt deposit	Silty bare soil with mineral crust	2.3	160.9	36.1–567.5
	Silts with pedestals	3.57	375.2	122.3
	Silts with degraded lichens	11.20	156.2	92.9
Brown crust	In slope	8.41	266.8	49.4–122.3
	In pediment	−0.30		122.3
White crust	White crust in slope	−0.79	31.3	18.7
	White crust and annuals in slope	7.32	19.5	5.6
	White crust in divide	−0.13	6.8	7.7
Vascular plants	Lichens+annuals+perennials in hanging pediment	–	3.7	4.6
	Annuals+perennials in slope	–	3.3	0.7

Results from the pins are average differential heights, in mm; negative values correspond to erosion and positive ones to deposition; data correspond to the whole monitoring period (3974 days, near 11 years). Results from bounded plots are averages, or a rank in two cases of simulation experiments with very wide dispersion of values.

slopes additional erosion data were collected using a laser perfilometer. These data are referred to in the discussion.

4. Results

4.1. Series of different surface type plots: photographs, erosion pins, erosion experiments

The *Bare regolith* shows a crack pattern which is not maintained after one year although some features, such as small rock fragments, are still visible after one year, but not after 13 years. In this surface, erosion could be very high, during both natural events and rainfall simulations (Table 2). However, the appearance of the surface remains similar. The average result from erosion pins is 12 mm of erosion, though with a very high variability ranging from 25.4 mm of erosion to 18.9 mm of sedimentation. This high sedimentation is due to the location of the plot with pins near to the base of the slope. In *divide*, this surface also shows a crack pattern which is barely maintained after one year (only the main crack orientation is preserved), and not at all after 13 years. According to the pins, erosion in the divide is even larger than in the slope, both in the average and in the extremes (Table 2).

4.1.1. Silty deposits with mineral crust

Cracking patterns vary almost every season. Susceptibility to erosion is high from natural events and from rainfall simulation (Table 2) and quite variable depending on silt thickness and other factors. However, erosion pins show slight deposition, as is expected in a site with a depositional origin, and a quite high homogeneity during the first 11 years. In the last two years, extremes become highly divergent, from 25 mm of erosion to almost 30 mm of sedimentation. *Silts with pedestals* has maintained some stability, though the cracking pattern changes rapidly, almost seasonally, as the cracks can only occur between the stones and runoff and erosion are concentrated between pedestals. The micro topography indicates active erosion, as the soil around the rock fragments has been eroded, and the susceptibility to erosion is moderately high according to data from

rainfall simulations and bounded plots (Table 2). However, the erosion pins show a slight overall net deposition as expected on a silty surface, and a high spatial and temporal homogeneity in the records. The pattern of the rock fragments remains stable over several years, but after 13 years it has changed. *Silts with degraded lichens* is north-facing but almost bare because the main channel of the catchment has reached the base of this slope which is now eroding. This plot is in the

lower part of that slope, in an inter-rill area, with sediments coming from upslope. Cracks develop every year but not always in the same season, as they essentially depend on the antecedent soil moisture conditions; their pattern is usually heterogeneous. Susceptibility to erosion is moderately high (Table 2). However, it is here that the largest average deposition is recorded, and the extreme pin values follow the same pattern. Lichen growth is probably restricted as the

a) Silts with degraded lichens, 1992   Silts with degraded lichens, 2005

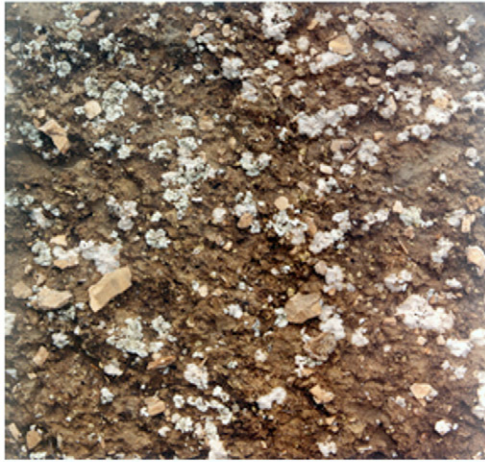b) Brown living crust, 1992   Brown living crust, 2005
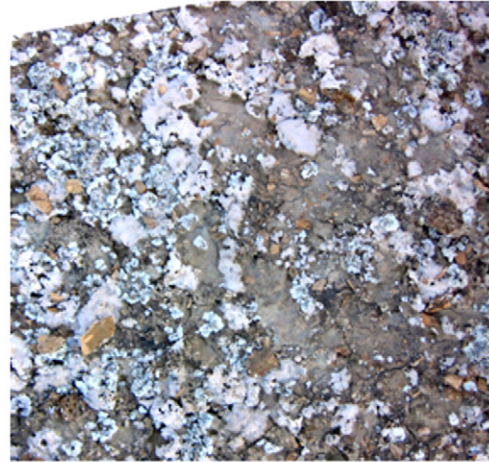
c) Crust frontier in a narrow divide, 1992   Crust frontier in a narrow divide, 2005

Fig. 3. Pairs of initial and final photographs from a selected set of the photographic monitoring plots.
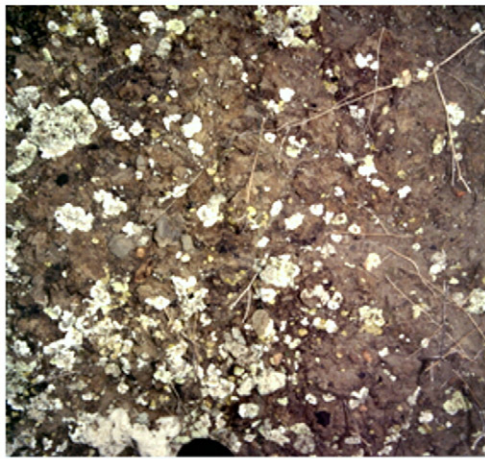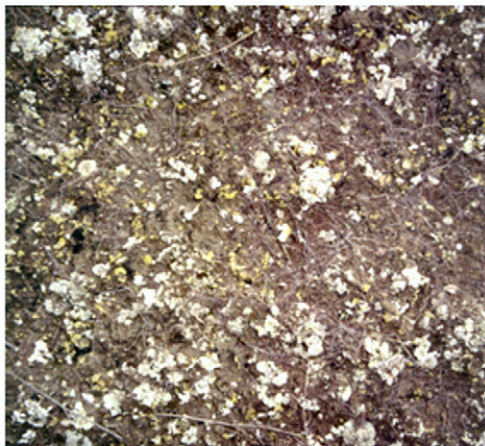
d) White lichens in divide, 1992   White lichens in divide, 2005

e) White lichens 24% initial cover, 1992   White lichens 24% initial cover, 2005

f) White lichens 27% initial cover, 1992   White lichens 27% initial cover, 2005

Fig. 3 (*continued*).

surface undergoes significant sedimentation. Fig. 3 shows a selected set of photographs from long long-term monitoring plots and Table 3 shows the quantitative changes in percentage cover of both brown crust and white crust from the same set of photographs. Fig. 3a is from Silts with degraded lichens and shows an important decrease in the brown crust which is also evident in Table 3.

Brown crust *in slope* shows a cracking pattern which is maintained after one year, but not longer. This surface is highly susceptible to erosion, though with very variable responses (Table 2). However, the crust only decreased very slightly. The average of erosion pins shows important deposition (Table 2), though extreme values range from 15 mm of erosion to 20 mm of deposition. Here lichens must deal with

Table 3
For each main surface covered with biological soil crust, data about percentage covers of both brown crust and white crust (the main classes of crust) in the first and last years of the series is given

| Changes in the biological soil crusts from long-term photography				
Surfaces with some biological soil crust	Year	White crust	Brown crust	Total biological soil crust
Silts with degraded lichens (degraded brown crust)	1992	0	24	24
	2005	0	8	8
Brown crust (south slope with lichens)	1992	5	87	93
	2005	12	78	90
White crust in divide	1992	18	74	91
	2005	48	48	96
White crust (24% initial cover) in north slope	1992	24	75	99
	2005	55	44	99
White crust (70% initial cover) in north slope	1992	70	27	97
	2005	87	12	99
Lichens (north)–bare soil (south) boundary	1992	20	43	63
	2005	20	33	53

quite an active soil surface and, despite this, they manage to resist as only a very slight overall decrease of the whole cover was recorded after 13 years. In fact, the white lichens grew and the main changes in the crust were due to an appreciable replacement of brown crust by white crust (Table 3). Thus, this crust shows successional development (Table 3; Fig. 3b) although it is probably near to the environmental limits. Brown crust *in pediment*, in which the main cover is also undifferentiated biological soil crust, shows only slightly developed cracks, perhaps because lichens and the microphytic crust maintain cohesion and retain soil moisture. Crack pattern is heterogeneous both in space and time. Brown crust here also shows a high susceptibility to erosion (Table 2) as this kind of crust is often not very robust. However, according to the erosion pins, it is clearly a stable surface, due to its geomorphological situation, as its overall erosional behaviour after 13 years is near zero.

Bare regolith and silty deposits are cracked surfaces and brown crust is often cracked also. However, surfaces covered by white crust

are much less cracked. In general, cracking patterns are mostly seasonal, remaining from a few months to one year. Their change suggests that anisotropy of soil surface properties (tensile strength, *etc*) becomes random over the long term (several years). Cracking cycles are strongly influenced by the climate, with very dry summers and a fuzzily-located rainy season. Cracks reach their maximum development after the summer and they are almost always completely closed at the end of the rainy season; in the following summer, cracks appear in another location.

White crust includes four photographic plots: one in a stable and relatively wide divide and the other three in north to east facing slopes, one with 24% of initial white lichen cover, one with about 70% and the third with 27% and some annuals (very low cover). The behaviour of all these surfaces was quite similar: Susceptibility to erosion was much lower than in the surfaces described above and erosion pins reflect high stability with a balance near to zero or even light deposition. The growth of the biological crusts as a whole was limited due to the high initial covers. However, increase of white lichens was considerable; on average, they increased by nearly 30% of the plot surface, except where initial white crust cover was 70% (though there was still an increase of 17% in this case). The increase occurred by replacement of the brown crust. The pattern of white crust changed after a few years due mainly to species replacement; changes were smaller when the initial white lichen cover was high. (Tables 2, 3; Fig. 3d, e, f). Others differences between these plots were that, in the divide, erosion reached a maximum of 10 mm; and, in the plot 'with annuals', erosion pins show a small overall deposition; the extremes ranged between 10 mm of erosion and 15 mm of deposition.

In the additional photographic plot in a narrow divide which was selected for the clear boundary, marked by a small step, between bare soil in its south-facing part and a well developed lichen crust in its north-facing part, we observed a decrease in the total lichen cover (though mainly at the expense of the brown crust, white lichens seeming more resistant) as well as a change in the lichen boundary (Fig. 3c). The clear boundary from 1992 is now quite fuzzy as the clear step between the two soil surfaces and orientations has almost
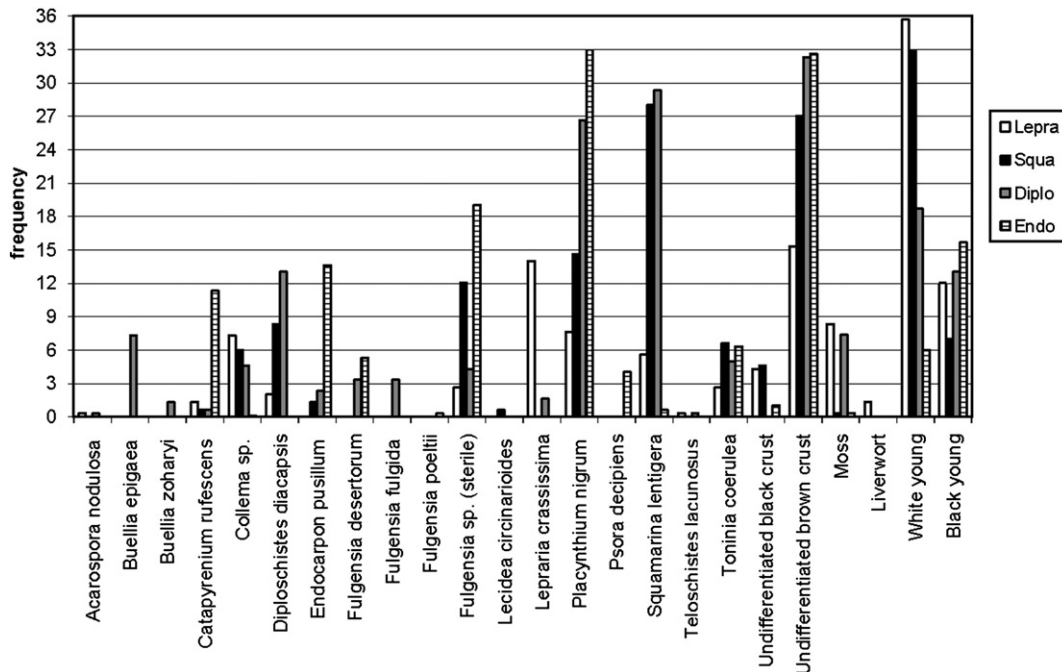
Fig. 4. Average frequencies of each lichen species found in the cleared plots of each lichen community after 1 year; three plots per community. 36 is the maximum possible frequency. Undifferentiated crusts (mainly cyanobacteria and fungi), mosses, liverworts, 'white young' and 'black young' are also included. Bar textures indicate different communities.
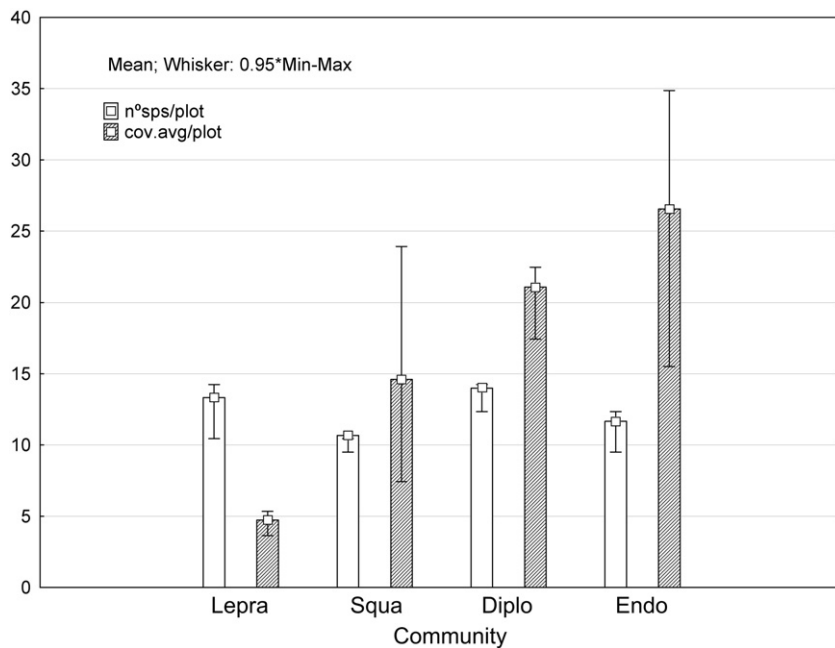
Fig. 5. For each community and after one year, average number of species per plot, undifferentiated brown and black crusts, mosses, liverworts, 'white young' and 'black young' being treated as species (void columns), and average total biological crust percentage cover per plot (grey columns). Whiskers mark maximum and minimum values.

disappeared. As lichens grow mostly over some thickness of fines, when they degrade substrate thickness decreases and, inversely, when soil thickness decreases, lichens probably degrade.

In the photographs in Fig. 3 we can also observe the most frequent features of lichen cover evolution in the Tabernas badlands in recent years:

(i) a slight overall increase in lichen cover; (ii) a change in lichen pattern which includes both very local increases and decreases in lichen cover and mainly changes in lichen species, generally replacing brown crust by white macrolichens.

4.2. Lichen colonization and growth

We include here the results from the cleared plots after the first year, which consist of data on primary colonization and growth of individual species in terms of thallus frequencies and coverage, as well as the spatial pattern of colonization in each community.

In Fig. 4 we show the average frequency of each lichen species found in the cleared plots of each community after one year. Although each of the dominant species and particularly *S. lentigera*, is able to colonize its own community, some species, mainly *Placynthium nigrum*, are clearly more able to colonize bare sites. But the best colonizing capacity taking into account all communities is shown by the brown undifferentiated living crust. The frequencies of 'white young' and 'black young' show that, at least in the case of white lichens, the number of thalli that initially try to colonize is much higher than the number which actually establish themselves, particularly in the communities in which the crust development is slower (Lepra); thus they appear but do not establish. In Fig. 5 we show the average total lichen cover and the average frequency of all lichen species in every community.

The number of lichen species per cell of the sampling grid differs significantly between the communities ($p<0.0000$) and with distance from the cell to the border of the plot ($p<0.000$); the interaction between both factors is also significant ($p<0.000$). The total lichen cover per cell of the sampling grid also shows significant difference between the communities ($p<0.0000$). In Table 4 we show, for each community, the significance of non-parametric ANOVAs, (Kruskal–

Wallis) and Median tests, of the number of lichen species per cell and total lichen cover per cell, using distance to the plot border as a factor in both cases. Note that Squa is the only community in which development is independent of the spatial position with regard to the border of unaltered crust. The remaining communities show opposite behaviours: while in Lepra new lichens appear near to the border, in the others, the new lichens prefer the void area. Note that the number of lichen species and the total lichen cover show the same pattern through the communities.

Microclimatic variables from each community, summarized as monthly values, are assembled in Table 5, which shows differences in some variables, despite the spatial proximity of the areas (a few hundreds of metres between them). Table 6 shows the significance of the Kruskal–Wallis analyses performed for each month and each averaged variable, always using the lichen community as a factor. The largest differences between communities were found, in descending order, for PAR reaching the lichens, soil moisture below the lichen crust, temperature of the crusts and duration of dew deposition.

The number of rainfall days also showed a difference between the communities. There were 55 for Lepra, whereas Squa and Diplo received 42 and Endo 44, even though the total rainfall for the measured period was almost 5 mm lower for Lepra than for the other areas. Rainfall intensities did not show significant differences, and air temperature and humidity were only different in some months in spring and winter. For

Table 4
For each community, the significance of Kruskal–Wallis and Median tests, of the number of lichen species per cell and total lichen cover per cell, using in both cases the distance from the plot border as a factor

	Differences in number of lichen species and total lichen cover according to distance from the plot border			
	Number of lichen species per cell		Total lichen cover per cell	
Community	Kruskal–Wallis test	Median test	Kruskal–Wallis test	Median test
Lepra	$p<0.0000$	$p<0.0000$	$p<0.0000$	$p<0.0000$
Squa	$p=0.2993$	$p=0.5097$	$p=0.6552$	$p=0.7057$
Diplo	$p=0.0020$	$p=0.0041$	$p=0.0048$	$p=0.0057$
Endo	$p=0.0206$	$p=0.0021$	$p=0.0000$	$p=0.0012$

Table 5
Monthly averages of: lichen temperature (Tlic, °C), air temperature (Tair, °C), air relative humidity (RHum, %), photosynthetically active radiation (PAR, µE), soil moisture (SoMo, % v/v), daily minutes of dew (Dewm avg), mean rain intensity per rainy day (I avg, mm/h) and average of daily maximums of rain intensity (I avg max, mm/h)

Crust type	Month	Tlic	Tair	RHum	PAR	SoMo	Dewm avg	I avg	I avg max	Dewm total	Rain total	Rain N days	I abs max
Lepra	Jul-04	31.85	29.96	55.27	314.13	2.15	0.00	0.00	0.00	0	0.00	0	0.00
Lepra	Aug-04	30.01	28.94	48.28	313.32	1.58	0.00	0.00	0.00	0	0.00	0	0.00
Lepra	Sep-04	24.16	24.26	62.17	172.06	2.86	2.00	13.88	39.65	60	3.97	2	68.68
Lepra	Oct-04	18.85	19.57	56.93	89.46	2.25	2.58	0.24	0.52	80	0.74	1	0.52
Lepra	Nov-04	10.23	11.22	70.84	42.26	2.41	240.67	0.43	1.46	7220	9.67	7	9.20
Lepra	Dec-04	8.51	9.82	73.25	39.95	16.25	63.87	0.67	1.08	1980	48.61	11	5.55
Lepra	Jan-05	4.15	5.85	73.34	30.18	7.03	470.32	0.01	0.01	14,580	1.74	7	0.01
Lepra	Feb-05	5.63	7.13	71.11	53.09	12.71	138.57	1.41	3.18	3880	51.58	11	14.40
Lepra	Mar-05	11.30	12.55	70.98	124.05	17.34	52.90	0.71	1.70	1640	42.16	9	7.63
Lepra	Apr-05	14.83	15.28	59.26	188.48	8.60	1.82	9.05	36.41	20	11.16	4	127.54
Lepra	May-05	24.54	22.91	37.39	302.73	1.43	0.00	4.38	14.45	0	1.74	3	42.51
Squa	Jul-04	33.46	30.39	55.93	504.79	2.18	16.00	0.0004	0.0004	160	0.24	1	0.0004
Squa	Aug-04	32.39	29.74	47.03	509.64	1.60	14.84	0.00	0.00	460	0.00	0	0.00
Squa	Sep-04	26.11	25.36	55.79	350.86	2.91	86.00	23.09	55.27	2580	5.04	2	78.55
Squa	Oct-04	19.95	20.84		235.37	2.28	21.29	0.00	0.00	660	0.00	0	0.00
Squa	Nov-04	10.21	12.35	78.08	123.48	2.45	296.67	0.76	2.53	8900	7.92	3	7.58
Squa	Dec-04	8.49	10.54	74.08	87.05	16.63	246.45	4.77	22.09	7640	52.08	6	45.47
Squa	Jan-05	4.05	7.13	72.10	101.54	7.19	501.94	0.01	0.01	15,560	1.20	5	0.01
Squa	Feb-05	6.33	8.53	69.52	173.21	13.00	224.29	1.40	3.22	6280	55.92	12	15.71
Squa	Mar-05	12.53	12.70	75.15	299.77	17.98	169.03	1.03	3.00	5240	43.92	7	10.67
Squa	Apr-05	20.43	14.41	61.15	480.83	6.15	44.67	10.78	35.22	1340	8.40	3	78.55
Squa	May-05	25.97	17.58	57.12	512.46	2.60	6.45	2.13	5.42	200	1.20	3	15.16
Diplo	Jul-04	32.56	29.54	54.28	558.82	1.94	44.00			440			
Diplo	Aug-04	31.64	28.95	43.81	575.57	1.54	23.87			740			
Diplo	Sep-04	26.20	24.66	57.82	414.03	2.48	144.67			4340			
Diplo	Oct-04	21.09	20.55	51.31	318.35	2.10	89.68			2780			
Diplo	Nov-04	12.04	12.58	63.25	226.94	2.20	472.67			14,180			
Diplo	Dec-04	9.85	10.84	67.09	163.68	15.10	424.52			13,160			
Diplo	Jan-05	6.40	7.58	64.70	229.28	8.26	712.26			22,080			
Diplo	Feb-05	7.96	8.54	62.21	277.21	12.17	489.29			13,700			
Diplo	Mar-05	13.45	12.97	65.95	380.16	17.41	429.03			13,300			
Diplo	Apr-05	19.67	17.85	44.98	561.75	6.26	99.33			2980			
Diplo	May-05	24.55	22.51	38.25	600.53	1.91	27.74			860			
Endo	Jul-04	32.42	28.32	50.16	633.41	1.35	0.65	0.0005	0.0005	20	0.26	1	0.0005
Endo	Aug-04	32.67	29.08	46.14	571.79	0.98	1.29	0.00	0.00	40	0.00	0	0.00
Endo	Sep-04	27.73	25.15	58.24	427.73	1.82	16.00	17.69	37.90	480	4.70	2	58.73
Endo	Oct-04	22.82	21.22	51.13	338.83	1.42	3.87	0.32	0.78	120	0.78	1	0.78
Endo	Nov-04	14.42	13.52	62.63	251.87	1.52	185.33	0.85	2.40	5560	9.14	4	7.64
Endo	Dec-04	11.62	11.53	65.90	200.30	10.53	100.00	2.52	10.97	3100	51.94	11	39.15
Endo	Jan-05	9.81	8.97	61.42	273.50	4.53	277.42	0.0028	0.0028	8600	0.52	2	0.0038
Endo	Feb-05	10.05	9.18	62.04	288.55	8.23	101.43	1.14	2.94	2840	55.33	10	9.49
Endo	Mar-05	15.30	13.15	68.48	393.59	10.43	78.06	1.00	2.59	2420	43.07	7	8.70
Endo	Apr-05	21.47	18.00	47.66	533.56	3.57	14.00	10.18	38.24	420	9.40	3	104.40
Endo	May-05	26.43	22.75	40.49	571.87	1.70	5.81	0.25	0.37	180	1.04	3	0.74

Monthly totals of: minutes of dew (Dewm total), precipitation (Rain total, mm) and number of rainfall days (Rain *N* days). Monthly absolute maximum of rainfall intensity (I abs max, mm/h). In Diplo there are no rainfall data because Diplo and Squa have the same rain gauge.

two microclimatic variables with large differences between the communities, PAR (Fig. 6) and soil moisture (Fig. 7), we show graphically the values during the year from each community.

5. Discussion

After 13 years erosion was only important in bare regolith, whereas lichen-covered surfaces remained stable. Significant lichen increase has occurred in all sufficiently stable landforms with important previous biological soil crust cover. Lichen patterns have varied, mainly through replacement of brown cyanobacterial crust by white macrolichens. This agrees with the successional stages stated by Belnap and Eldridge (2003). Here the cyanobacterial soil crusts and part of the small, often dark, colonizing lichen species such as *Collema* spp., *E. pusillum*, *Fulgensia* spp., *P. nigrum* and others, are replaced by white macrolichens such as *S. lentigera*, *D.diacapsis*, *Buellia* spp. and others. A lichen-covered surface represents an important spatial heterogeneity and different types of lichens have different hydrological and erosive properties (Alexander and Calvo-Cases, 1990). Therefore, the variation of lichen crust composition and covers over time can have important consequences for hydrological and erosive

processes. In turn, hydrology and water source can determine the presence of a particular lichen species, as species have different metabolic responses at high thallus water content or to a given incoming PAR, as well as different abilities to obtain hydration from liquid water, dew or fog (Lange et al., 1999). So, there is a reciprocal interaction between species composition and hydrology. Maestre et al. (2005) provided empirical evidence, just from biological soil crusts, linking the spatial pattern of a community and ecosystem functioning. In our area, lichen cover has decreased only in two soil surfaces: in silts with degraded lichens and in the plot on the frontier between the eroded slope and crusted slope in a narrow divide. In both cases crust decrease was due to very local factors and both surface types have limited extent.

Our growth plots confirmed brown crust as a primary colonizer. However, it has much higher susceptibility to erosion than white crust (Table 2), as confirmed by our result in the plot on a crust frontier in a divide, since almost all of the decrease suffered by the crust occurred in the brown crust (Table 3).

In stable zones, lichens are relegated to the worst sites, such as the upper part of the slopes, due to competition with vascular plants, which need run-on sites in this climate (Lázaro et al., 2000). The effect

Table 6
Significance of the Kruskal–Wallis ANOVAs performed with the microclimatic monthly data of: lichen temperature (Tlic), air temperature (Tair), air relative humidity (RHum), photosynthetically active radiation (PAR), soil moisture (SoMo), daily minutes of dew (Dewmin), mean rain intensity per rainy day (IntAvg) and average of daily maximums of rain intensity per rainy day (IntMax), using lichen community as factor

Significance of the Kruskal–Wallis tests with microclimatic monthly data using the biological soil crust community as factor							
	Tlic	Tair	RHum	PAR	SoMo	Dewmin	IntAvg	IntMax
July 2004	0.8530	0.0015	0.2089	0.0000	0.0000	0.0036	0.3679	0.3679
August 2004	0.0000	0.2601	0.2149	0.0000	0.0000	0.0424	1.0000	1.0000
September 2004	0.0001	0.2777	0.1805	0.0000	0.0000	0.0003	0.5647	0.6514
October 2004	0.0002	0.1455	1.0000	0.0000	0.0000	0.0000	0.3679	0.3679
November 2004	0.0000	0.0267	0.0025	0.0000	0.0001	0.0125	0.4120	0.4484
December 2004	0.0000	0.1115	0.0676	0.0000	0.0000	0.0000	0.1286	0.0980
January 2005	0.0000	0.0002	0.0006	0.0000	0.0000	0.0003	0.3650	0.3650
February 2005	0.0000	0.0165	0.0542	0.0000	0.0035	0.0001	0.9219	0.8953
March 2005	0.0196	0.8091	0.1065	0.0000	0.0000	0.0000	0.5242	0.5242
April 2005	0.0000	0.0000	0.0005	0.0000	0.0000	0.0427	0.8150	0.8150
May 2005	0.0009	0.0000	0.0009	0.0000	0.0000	0.3304	0.7326	0.7326

of the water on the lichens and the water dynamics depends on the features of the species; for example the degree of wettability is closely related to surface texture (Valladares, 1994). The processes affecting the lichen crust are mainly mass movement and rill erosion. All the sampling methods used here record the same set of erosion processes (splash, inter-rill diffuse erosion, rill erosion and eventual micro-mass movements; pipes being infrequent in the area). However, the influence of runoff is much greater in the erosion pins because the plots are unbounded and their contributing areas are substantially larger. The erosion values from rainfall simulations and field monitoring in natural rainfall provide information about the susceptibility to erosion of each surface type, with a certain independence from their spatial location, as these plots are small and bounded. The values from erosion pins, however, are not only a function of the surface properties but also, and importantly, a function of the relative spatial situation. Because of this, surfaces such as silts with degraded lichens and brown crust can show important deposition in spite of their high susceptibility to erosion.

Lichen crusts are able to extend onto surfaces of all orientations if the soil is sufficiently stable (Lázaro, 1995; Lázaro et al., 2000; Bevan's unpublished data) although, the white macrolichen species often present a shorter period of activity (grow more slowly) in sunny than in shaded situations (Pintado et al., 2005). However, erosion in this area shows a strong concentration in southerly and westerly aspects, and silt-covered south-facing slopes with important biological soil crust cover are infrequent (Lázaro, 1995; Cantón et al., 2001a, 2002, 2004a). On the other hand, the stable south-facing sites often constitute the footslope rather than the slope proper, with the upper part of the slope (very often eroded) acting as a source of sediment. Due to all these factors we found stronger deposition processes in south-facing crusted surfaces than in north-facing ones.

After 13 years, there is a larger frequency of unvegetated surfaces showing stability or deposition processes than surfaces showing erosion; but the total extent of the two is similar, crusted stable about 33% and bare soil being eroded, 34% of the total extent (Cantón, 1999). The remaining third is vegetated. However, this does not necessarily suggest that the badlands of the Tabernas Desert have been in a period of stabilization in recent years; rather it is evidence that erosion is concentrated in the already eroded areas. The large erosive events probably have a return period which is long enough to allow the lichen crusts to colonize a significant proportion of the area, producing an impression of stability, but these lichen crusts do not provide sufficient protection against the erosivity of major rainfall events. According to Lázaro et al. (2001) the return period for extreme rainfall events of 50 mm in one day is 5 years and for 100 mm in one day, at least 30 years.

Erosion on the south-facing slope has produced a fuzzy frontier between bare regolith and biological crust in the plot on a narrow divide showing a clear boundary in 1992. The clarity of the 1992 frontier could be the result of a particularly stable period on this south-facing slope, which reduced the frequency of erosive events at the divide below a certain threshold allowing the extension of lichen cover to occupy the entire available habitat. According to the growth rate (as increase of covers) recorded in our plots, as little as one year or even less, of stability would be necessary. The clear soil step, coinciding with the border of the lichen crust in 1992 (Fig. 3c), is now lower and fuzzier.

As is frequently the case in dry areas (Yair et al., 1982; Gallart et al., 2002), overall erosion rates are much more moderate than the appearance of the landscape leads one to expect. The main catchment in our study area collects less than 4 t ha^{-1} year^{-1} (H flume). Although the steep and bare S-SW oriented slopes can produce an average of more than 100 t ha^{-1} year^{-1} (laser perfilometer and erosion pins, own unpublished data); while plant covered N-NE oriented slopes give very low sediment yields, less than 0.6 t ha^{-1} year^{-1} (H flume). Overall erosion rates are lower than in other areas of the Spanish semiarid region (Calvo-Cases et al., 1991b; Calvo-Cases and Harvey, 1996) because intense rainfall events are less frequent here (López Bermúdez, 1990). On the other hand, the scarcity of water limits the erosion not only by
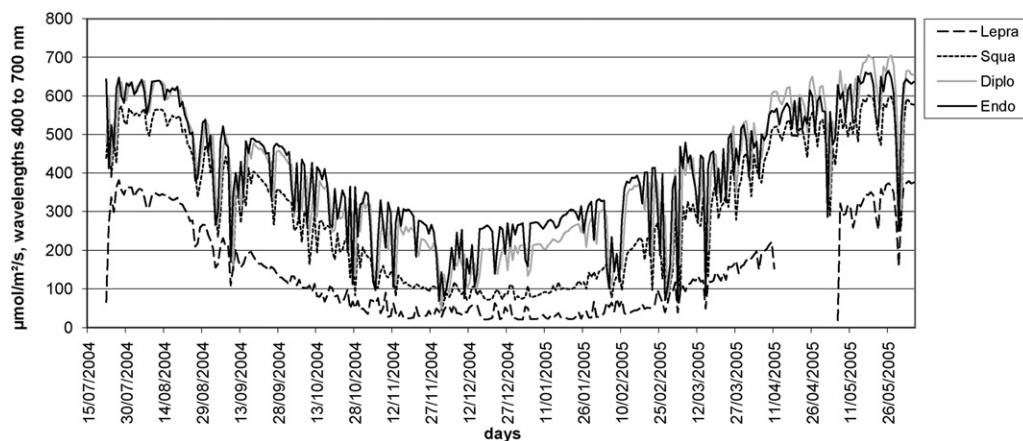
Fig. 6. Daily average of photosynthetically active radiation reaching soil surface in each lichen community.
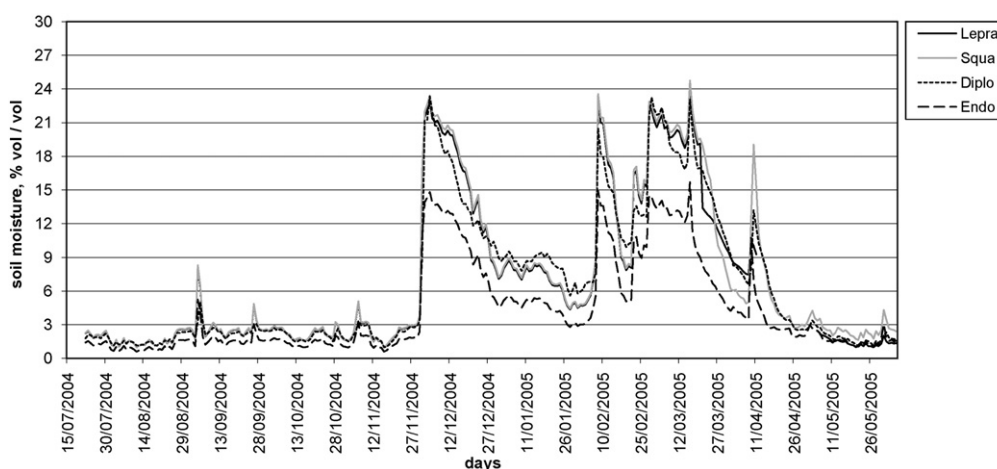
Fig. 7. Daily average of soil moisture immediately below the different lichen crust communities.

limiting the erosivity of the rainfall but also by limiting the transport of materials: the large differences between maximum and minimum values of erosion pins found in bare marls and silts suggest that the distance travelled by the eroded material is often short, as after several years, both erosion and sedimentation are recorded in the same plot, which is 2 m in length. According to Cantón et al. (2001b), weathering is also limited by transport. Thus, landform evolution is slow.

In contrast, biological soil crust development is faster than expected; although it is possible that the first year of monitoring was particularly favourable. Recovery rate of the different communities agrees well with the expected successional order, as the primo-colonizer brown crust is the fastest and, the hypothesized late-successional community, Lepra, much slower. Belnap and Eldridge (2003) also observed brown crust being the first colonizer. The ability of the different communities to develop at some distance from the border of the remaining crust is also consistent with both growth rate and succession order.

Reported recovery rates of biological soil crusts following disturbance vary widely, as they depend on climate, soil type, and severity of disturbance. Experiments and subsequent extrapolations show that a severely disturbed crust in most semiarid or arid landscapes usually requires many decades, or even centuries, for full recovery (Belnap and Lange, 2003). However, all published estimates of crust recovery time are based on linear extrapolations of observed recovery rates and it is not known under what conditions this method is valid. For example, on the Colorado Plateau, scalped plots were reassessed 2–5 and 10–14 years after disturbance; after 2–5 years, cyanobacterial cover was predicted to recover in 45–110 years, whereas it recovered within 14–34 years; thus extrapolations based on 2–5 years greatly overestimated recovery time (Belnap and Eldridge, 2003). In central Karakum desert, Turkmenistan, biological soil crusts are widespread after 40 years in the protected areas with a lack or minimal amount of grazing (Orlovsky et al., 2004). The increase of crust cover in growth plots during the second (present, at time of writing) year seems to be clearly slower than that recorded during the period May 2004–May 2005. Rainfall is, in general, more intense during the present year, and this probably hinders the appearance of new thalli in bare soil. It is not possible to make reliable estimates of crust recovery times from the limited data we have collected so far. However, despite the inter-annual oscillations, our results to date indicate that crusts can grow sufficiently rapidly to detect short stable periods of a year or even just of a season.

The strong influence of microclimate on lichens is well known and many directly or indirectly related studies have been carried out from a variety of viewpoints (for example, Sancho and Valladares, 1993; Green et al., 1994; Lange et al., 1997; Palmqvist and Sundberg, 2000; Gaio-

Oliveira et al., 2004). In our area, the four lichen communities show clear differences in terms of incident PAR and are arranged in successional order; the sunniest one being the primary colonizer brown crust (Endo), and the least sunny being the late-successional community (Lepra) that often develops in spaces among perennial grasses and shrubs (Lázaro, 1995). Soil moisture is clearly lower under brown crust than under white crust; this agrees with Cantón et al. (2004b) who proposed a role for lichens in soil moisture conservation even when the properties of the soil beneath do not favour water storage. But our results also indicate that brown crust is more waterproof. Surface temperatures are modified and dew deposition is much greater in large, thick lichens than in the rest of the surfaces. Dew duration is only slightly longer in Lepra than in brown crust, as *L. crassissima* has a slender thallus, but in Squa it is nearly double that in Lepra and, in Diplo, nearly double that in Squa. *D.diacapsis* is a robust crustose lichen with a thick and contorted thallus which often separates from the soil forming caverns between the thallus and the soil. This has physical implications, such as changes in thallus temperature regime and in the water dynamics. In fact, although lichen temperatures are quite closely related to the received PAR, *D. diacapsis* often maintains relatively low temperatures taking into account its relatively sunny location. However, macrolichens grow more slowly in fully illuminated locations, as suggested by the changes recorded in brown crust compared to those recorded in white crust (Table 3). Detailed laboratory tests of the metabolic activity of thalli of *D. diacapsis* collected from contrasting sun and shade sites in our study area, showed the importance of microclimatic conditions: considerable metabolic and morphologic differences were found even though the thalli were from the same species. The thalli from sunny locations were smaller, structurally poorly developed but with higher assimilation rates (Pintado et al., 2005).

Some of the microclimatic differences between lichen communities are produced by the lichens themselves; particularly, the soil moisture beneath the crust, the temperature over the thallus and the amount of dew condensed. Undoubtedly, lichens modify the surface hydrology and erosion rates. Alexander et al. (1994) have already proposed lichen crusts as part of a natural stabilization mechanism in this area. Cyanobacterial crusts and, particularly, lichen crusts increase soil stability and reduce erosion according to results from many regions of the world (Alexander and Calvo-Cases, 1990; Greene et al., 1990; Solé-Benet et al., 1997; Eldridge, 1998, 2003; Warren, 2003). Eldridge and Greene (1994) showed that sediment removal by splash erosion fell from 300 g m^{-2} to 50 g m^{-2} when crust cover reached about 50% and Alexander and Calvo-Cases (1990) reported a decrease of sediment concentration in runoff from more than 45 g/l in bare soil to less than 10 g/l for lichen cover as low as 20%; erosion seems to decrease exponentially as lichen cover increases. Also, the larger the crust cover, the longer the period between erosive events able to dismantle the

crust becomes, allowing additional lichen crust extension and an opportunity for vascular plant recruitment. So, cyanobacterial crust and macrolichen crusts constitute the first and second steps in a feedback process of natural stabilization of some surfaces, which agrees with that proposed by Belnap and Eldridge (2003).

These differences in the development of lichens according to the microclimate of their site could trigger small initial differences between surfaces in opposite orientations. This could be critical for the divergent development of those slopes through feedback mechanisms, ultimately forming the present landscape pattern: asymmetric catchments with shorter, steeper and eroded sunny slopes and longer, vegetated, relatively shaded slopes with lower gradients mainly in the footslope. Deposition at the base of eroded slopes is often ephemeral, as sediments are removed by the stream channel more frequently than is the case at the base of the stabilized and vegetated slopes. Plant recruitment is more successful in the already crust-covered and stabilized landforms. The asymmetry, also observed in this area by Gallart et al. (2002), progresses by lateral movement of the channel. Although a complete understanding of this asymmetry requires further work, because catchments often start as a bare and symmetric gully, the first colonizers able to improve soil stability will play a key role.

Since no lichen crust exists where erosion processes are active, and high lichen cover is associated with quite low erosion or deposition rates, we can hypothesise that extensive crust of terricolous lichens at the landscape scale constitutes an indicator of low overall erosion rates because, although they contribute to soil stabilization, they are physically unable to resist major erosive events, particularly when they are developing. Besides, they are favoured by the aridity together with a high frequency of low rainfall events, as well as by a high number of days with dew (Lázaro, 2004), that is to say, a climate with low erosive capacity. Under similar erodibility, the differences in extent of biological soil crusts with comparable floristic composition could be an indicator of differences in rainfall erosivity along a rainfall gradient across a region.

The possibility to use biological soil crusts as a sensor of climatic changes has wider interest because some investigations into monitoring biological soil crust cover using remote sensing have already been carried out (Karnieli et al., 2003; Alexander et al., 2004). The remotely sensed imagery has a pixel size much larger than the lichens, but large crust patches can probably be distinguished as belonging to some of the main classes of biological soil crust, such as the white crust or brown crust distinguished here.

While this study was under review for publication, an article by Belnap (2006) appeared in which a classification of biological soil crust into four general types, based in their general floristic, morphological and ecological characteristics is proposed at a planetary scale, with each type having a different hydrological role. Our brown crust is assimilable to the *rugose crust* of Belnap, whereas a part of our white crusts seems to correspond to the *pinnacled crust* (cyanobacteria still dominates but there is up 40% lichen cover) and the other part seems to correspond to the *rolling crusts* as it is dominated by lichens, although our area is not in a cold nor a low potential-evapotranspiration region.

6. Conclusions

Soil surface features differ spatially and surfaces show different dynamics through time. The dynamics, in turn, generally reinforce the initial features of each surface, evidencing the presence of feedback processes. Stabilization processes dominate in the main part of the Tabernas badlands surfaces, including those that are vegetated and those covered by biological soil crust. Erosion is concentrated in the bare regolith of the already eroded surfaces, which account for about a third of the total extent.

The main erosive processes are concentrated runoff, micro-mass movement and splash. Patterns of soil surface cracks change seasonally, and in some cases annually. Bare regolith and silt deposits

have much larger susceptibility to erosion than surfaces with biological soil crusts.

After 13 years, all landforms that were sufficiently stable showed some growth of biological soil crust if the previous cover was not complete, and a clear growth of white macrolichens (near to 30% of the plot surface in white crust; about 7% in brown crust) at the expense of the undifferentiated crust (mainly cyanobacteria and fungi), which implies a succession. Biological soil crust decreased at only a few points, due to very local factors.

Biological soil crust can grow rapidly in cleared areas, reaching more than 25% cover on average in a single year. However, colonizing capacity and growth rate are very variable among species; those more able to colonize were *P. nigrum* and *S. lentigera*. Also, the cover of lichen crust after one year colonizing an initially bare area is significantly different according to the lichen community in which it occurs. Undifferentiated ('brown') crust (mainly cyanobacteria and fungi) is the first step in colonization and the fastest to develop, although it also exhibits the highest susceptibility to erosion.

Dominant lichen species show different colonizing capacity according to the community. *L. crassissima* and *E. pusillum* only colonize significantly in their own areas. *S. lentigera* and *D. diacapsis* reach their highest values in their own communities.

The greatest biological crust development is reached in the most sunny habitat, covered by brown crust (Endo community), and the smallest, in the mature Lepra community, which occurs on shaded slopes in spaces among vascular plants. The number of lichen species appearing during the colonization is also significantly higher in Endo (although in Diplo it is similar).

The brown crust and the white crust from Diplo preferably colonize bare sites far from the border of the pre-existing crust, whereas the Lepra community extends from its border and Squa develops equally both from its border and at distance from it.

In spite of their spatial proximity, microclimatic differences exist among the lichen communities. Particularly, PAR, soil moisture, temperature at the surface of the thalli of the main species and dew deposition are different.

The rate of development of these lichen crusts was higher than expected in the first year of monitoring. Although data being obtained at the present show that the crust development rate can be quite variable between years, this high potential rate allows detection not only of climatic changes but also of short term periods of stability associated with oscillations of one or a few years and maybe even with seasonal oscillations.

Presence of extensive terricolous lichen crust indicates low erosion rates, at local as well as at landscape scale. This suggests that, in a regional rainfall gradient, within a given erodibility (similar lithology, topography, hillslope scale, etc), differences in lichen crust cover would indicate different rainfall erosivity, though this relationship could be fuzzy if relative humidity or dew have a spatial pattern different from that of the rainfall.

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