Do vehicle track disturbances affect the productivity of soil-growing lichens in a fog desert?

J. S. LALLEY† and H. A. VILES

Oxford University Centre for the Environment, Dyson Perrins Building, South Parks Road, Oxford OX1 3QY, UK

Summary

1. The re-establishment of soil-crust lichens following disturbances may be enhanced or discouraged by human-altered microtopographies. This research asks whether such microtopographic changes alter microclimates significantly, and whether changes affect metabolically active periods of recolonizing lichens.

2. In the fog-driven Namib Desert, the water relations of five lichen species were investigated and photosynthetic activity (PSII) was assessed via chlorophyll *a* fluorescence under natural and altered conditions, based on measured microclimates in vehicular disturbances.

3. Surface temperatures in vehicle tracks were significantly higher than controls by up to 2 °C. Fog deposition was significantly lower in tracks, and evaporation rates were higher.

4. Foliose and fruticose lichens retained fog moisture for long periods, and carried out PSII at low relative moisture contents. Desiccation rates of lichens were estimated to increase by 36% in tracks, which reduces PSII durations by as much as 50% in the critical hours following sunrise. *Lecidella crystallina* was least affected due to a pre-existing low water-holding capacity. Extreme temperatures (>45 °C) halted PSII in certain species.

5. These results illustrate the importance of temperature–moisture ratios on desert soil surfaces. Reduced periods of photosynthesis caused by human-induced microtopographic changes, as predicted here, may have important ecological implications by reducing productivity in lichen communities.

Key-words: biological soil crust, chlorophyll *a* fluorescence, Namib Desert, photosynthesis

Introduction

The low rainfall of arid environments has afforded vast areas for the domination of lichen growth in the form of biological soil crusts. Lichens are able to use scarce water resources in deserts more regularly than higher plants, so are important primary producers in some deserts (Cable & Huxman 2004). Lichens can thrive on fog, dew, water runoff and even periods of high humidity (Lange & Tenhunen 1982). Without the ability to store water, lichens are active only when moisture is available, and are otherwise desiccated and dormant (Lange & Tenhunen 1982; Kershaw 1985). In hyper-arid deserts such restricted periods of activity are essential to the subsistence of these organisms, and hence to the many organisms that depend on lichens for nutrient cycling, soil stabilization, thermoregulated habitat and sustenance (Beymer & Klopatek 1991; Evans & Johansen 1999; Lalley *et al*. in press).

If moisture regimes are affected by disturbances to lichen microhabitats, the productivity of soil-crust lichen communities could change and have negative cascading impacts on the environment. Assessments of human disturbance in deserts have revealed the difficulties of restoring soil-crust lichen communities, due to their slow dispersal and growth rates, and also suggest that altered microtopographies influence regrowth (Belnap & Warren 2002; Johansen & St Clair 1986). Some lichen species may be favoured by altered surfaces, while others may never recover, as shown by estimated recovery rates of vehicle tracks ranging from a few to several hundred years (Belnap & Warren 2002; Lalley & Viles in press). In many deserts, vehicle tracks and graded mining sites are common disturbances. These disturbances are difficult to remove because of soil compaction and destabilized soil surfaces that are easily eroded when rain channels along unprotected surfaces (Eldridge 1998). In hyper-arid coastal deserts, where dew or fog are the key moisture resources and rainfall is extremely rare, the rutted surfaces left by vehicles and mining machinery can, in

†Author to whom correspondence should be addressed.
E-mail: jennifer.lalley@ouce.ox.ac.uk

contrast, encourage the regrowth of lichens by trapping wind-blown thallus fragments, depending on the occurrence of fragmenting thalli in bordering communities (Lalley & Viles in press).

Presently it is unclear how long-standing alterations to soil surfaces will affect the productivity of recolonizing lichens. Given the extreme environment of hyper-arid deserts and the importance of thermoregulated micro-environments, any variation to the surface could alter microclimates, leading to changes in lichen productivity or community development. The microclimate of a habitat varies on a microtopographical scale, and the productivity of poikilohydric lower plants is intrinsically linked to these microconditions (Kershaw 1985). The temperatures of the laminar boundary layer at the soil surface can vary considerably according to the movement of air across the surface, which is dictated by the micro-relief of that surface and the surrounding microtopography (Kershaw 1985). Given the importance of water relations in desert lichen productivity, how do soil-crust lichens respond physiologically to human-altered microclimates on the soil surface, and could this affect the recovery of lichen communities and of future productivity?

We investigated the physiological response of lichens to the altered microtopographies and microclimates found in long-standing vehicle tracks in the hyper-arid Namib Desert of Namibia. Large areas of the Namib are dominated by ground-dwelling lichens that thrive on regularly occurring fog events. Vehicle tracks resulting from tourist activities and the development of mines are widespread throughout lichen-rich areas. We investigated the microclimates within vehicular disturbance sites and control sites, assessing differences in temperature, relative humidity, fog deposition and evaporation. We then examined the water relations and photosynthetic activities (as indicated by chlorophyll *a* fluorescence) of five soil-crust lichen species under natural conditions, and under conditions simulating those found in vehicle tracks.

STUDY AREA

The Namib Desert extends from South Africa, through Namibia, and into Angola in south-west Africa (Goudie 2002). It is characterized by large sand-dune systems, mountains and inselbergs, and extensive gravel plains dominated by lichen soil crusts. Lichen-dominated soil crusts occur primarily between the coast and 50 km inland, where fog is frequently deposited, and rainfall is too low for widespread vascular plant growth (Schiefer-stein & Loris 1992; Hachfeld 2000). Common lichen species occurring throughout the Namib Desert include *Ascoraspora schleicheri* (Almborn 1988); *Caloplaca elegantissima* (Poelt & Pelleter 1984); *C. namibensis* (Karnefelt 1988); *C. volkii* (Wirth & Vezda 1975); *Lecidella crystallina* (Wirth & Vezda 1975); *Neofuscelia namibensis* (Elix 1999); *Teloschistes capensis* (Almborn 1989); *Xanthoparmelia walteri* (Knox 1983); and *Xanthomac-ulina hottentotta* (Hale 1985).

Our field studies were carried out 20 km inland from the coast in the northern Namib Desert, where lichen-dominated soil crusts range from thin crusts (<10 mm) on sand sediments to thick crusts (>10 mm) on gypsum soil, where lichens vary in cover and species richness. The climate of the northern Namib Desert has not been described in detail because of a lack of meteorological stations, but is similar to that of the central Namib Desert where the mean annual temperature ranges from 19 to 30 °C on a coast-to-inland gradient, and average rainfall is between 0 and 19 mm per annum within the coastal fog zone studied here (Lancaster, Lancaster & Seely 1984). The mean annual deposition of fog is estimated at 37 mm per annum in the central Namib, and fog events occur on an average of 146 days a year at the coast (Lancaster *et al*. 1984; Olivier 1992).

Materials and methods

ALTERED MICROCLIMATES

Field experiments were carried out between June and August 2003 to detect alterations of microclimates caused by vehicle-induced ruts in lichen-rich areas. Variables controlling the moisture relations of lichens, namely temperature, relative humidity and fog deposition, were measured in and out of vehicle tracks within a wide expanse of gravel plains north of the Hoarusib River. Using a portable thermocouple, the temperatures of the soil surface and boundary layer (within 20 mm of the soil surface) were measured hourly in 20 track and 20 control locations from 7 am to 5 pm. Measurements were carried out over five consecutive days in June 2003, using a different track on each day. Only tracks on flat gravel plains were used to avoid the effects of slope, and all tracks ran in a north to south direction. Track depths were 10–15 cm, as measured from the edge of the track to the lowest point in the middle of the track. Hourly sampling of each track included five measurements in four different locations within the track, and five measurements in four control locations adjacent to the track, 1 m from the track edge. Each measurement set was sampled in a different location along each track to reduce the effects of surface disturbance by continual measurement activity in one area. The order of measurements alternated between track and control to reduce the effects of ambient temperature change during the measurement period. Each measurement set in each sampling location was averaged to produce one sample value. Therefore the total number of samples gathered on the five sample days was 20 in track and 20 in control locations for each hour. Relative humidity just above the soil surface was sampled in the same manner using a hand-held humidity gauge. Both temperature and relative humidity were tested for differences between track and controls, using *t*-tests in SPSS ver. 11·5 (Kinnear & Gray 2000).

To compare fog deposition and postfog evaporation in and out of tracks, five fog events were measured in

five different track locations. Ten fog collectors were placed inside tracks and 10 control fog collectors were placed 1 m from the tracks. Fog collectors were designed after the cloth–plate method used by Kidron, Herrnstadt & Barzilay (2002), where absorbent pieces of cloth are clipped to glass plates and weighed before and after a fog or dew event. Mass measurements of the fog cloths were made at hourly intervals immediately following sunrise (7 am) to 11 am, using a portable electronic precision balance (0·000 g). This measurement period was chosen because most winter fog events in the Namib Desert take place predawn, and lift in the early morning. At the time of this study, fog lifted completely by 8 am every sampling day. Calculations of the relative moisture content (RMC) of each cloth were carried out at the end of the experiment using the differences between saturated fog cloth masses and their previously determined dry masses. Final RMC values were calculated as a percentage using equation 1. Values were plotted on line graphs illustrating the comparison of control and track desiccation rates. The significance of differences was tested using standard *t*-tests in SPSS.

$$\%\text{RMC} = [(sm - dm) \times 100]/dm \qquad \text{eqn 1}$$

where *sm* = saturated mass (g) and *dm* = dry mass (g).

WATER-USE EFFICIENCY AND PHOTOSYNTHESIS OF LICHENS

Five lichen species were assessed for differences in water-use efficiency under natural conditions during morning fog events. The following five chloro-lichen species were chosen based on their morphology and abundance in the study area: the crustose species *C. elegantissima* and *L. crystallina*; two foliose species, *X. walteri* and *N. namibensis*; and one fruticose species, *T. capensis*.

saturation and desiccation rates in situ

To assess the naturally occurring moisture regimes of the five lichen species, we measured *in situ* saturation and desiccation during 10 fog events from June to August 2003. During each fog event, 10 specimens of each species, measuring 2–5 cm, were weighed repeatedly at hourly intervals from immediately following sunrise (7 am) to 11 am, using a portable precision electronic balance (0·000 g). The first hours of morning are a critical time for lichen productivity, as this is the period when lichens are still fully saturated from a fog event and are exposed to UV light. Fog lifted by 8 am on every sample day.

Following the above *in situ* saturation and desiccation measurements, the RMC of each specimen was calculated, as for the fog cloths, using equation 1. Lichen dry masses were measured in a laboratory after drying specimens for 48 h at 30 °C. Additionally, gravel-attached

lichens were soaked in water until lichen material could be removed with a scalpel. The gravel was then oven-dried and its mass subtracted from the overall dry mass of the original specimen. Mean RMC values for each species were plotted against the measurement period of 0–4 h following sunrise, illustrating rates of desiccation. Differences among species' RMC values at each hour following sunrise were calculated using ANOVA.

lichen photosynthesis at varying relative moisture contents

As an indicator of lichen productivity at varying RMCs, chlorophyll *a* fluorescence measurements were used, representing the potential quantum efficiency of PSII in photosynthesis. Photosynthetic activity can vary considerably between species depending on the photobiont and on various properties of the mycobiont (ergesterol or chitin concentrations) (Sundberg *et al.* 1999). All species studied here have green algal photobionts, but even so, photosynthetic potentials are expected to vary between species. Chlorophyll *a* fluorescence is an efficient means of deciphering these differences and of detecting the physiological response of a species to desiccation or to an altered environment. Field fluorometers enable rapid *in situ* measurements of chlorophyll *a* fluorescence, which is more realistic than field gas analysers (H_2O/CO_2 porometers) that confine specimens to a measurement chamber.

Hansatech's Handy PEA fluorometer (Hansatech Instruments, Norfolk, U.K.) was used to measure continuous excitation fluorescence after dark-adaptation. The fluorometer calculates F_m, the maximum fluorescence level reached within 500 ms of measurement; F_o, fluorescence when fully oxidized; F_v, the product of $F_m - F_o$, which is thought to represent emission by excited chlorophyll *a* molecules; and F_v/F_m, which is believed to be representative of PSII photosynthesis. This indicator value is sensitive to changes in PSII efficiency, and hence changes to the photosynthetic performance of the plant or lichen under investigation. These systems have been designed for assessing higher plants, but have been used effectively for the assessment of lichens (Palmqvist & Sundberg 2000; Schlenslog & Schroeter 2001).

Fluorometers can be adjusted to the optimal photon flux density (PFD; μmol m^{-2} s^{-1}) for detecting the optimum performance of a specimen (Rascher, Lieberg & Luttge 2000). Therefore the light-response curves for all species were measured prior to the experimental work by testing F_v/F_m values at increasing PFD. Specimens were chosen according to the thickness of their substrate, opting for thin encrusted soil bases or gravel so that the fluorometer leaf clips could be secured, fully preventing light penetration during dark-adaptations. Specimens were artificially misted with distilled water over several hours until the weights of the specimens no longer increased. Specimens were then dark-adapted

for a period of 25 min prior to each measurement. This dark-adaptation period was pretested on each species to ensure optimal responses during measurements. A PFD setting of 2500 μmol m^{-2} s^{-1} was chosen for all subsequent measurements, based on the highest PFD where all measured specimens had ceased to increase in photosynthetic activity.

To detect the photosynthetic performance of the five lichen species at decreasing moisture contents, chlorophyll *a* fluorescence measurements were made continuously on 10 specimens of each lichen species during *in situ* desiccation. As with the preliminary measurements, lichens were saturated artificially to maximum RMC and dark-adapted for 25 min before each measurement. Specimens were reweighed immediately following each measurement and then dark-adapted for another 25 min before the next measurement. Measurements were achieved until the fluorometer no longer produced a value for F_v/F_m, indicating arrested photosynthetic activity. Given the low range of F_v/F_m values found for most lichen species, particularly those in extreme environments, specimens were considered active until values fell below the instrument's viability threshold of 0·150, under which specimens could confidently be considered inactive. Chlorophyll *a* fluorescence measurements were averaged to produce a mean value of F_v/F_m at each level of RMC. The RMC of each specimen at each chlorophyll *a* measurement was calculated using equation 1, once lichens were oven-dried and gravel-attached thalli were removed from stones as described previously. The RMC values were then matched to those found for lichens under natural conditions during morning fog events, and corresponding F_v/F_m values were plotted along the 0–4-h time span following sunrise.

lichen photosynthesis in the altered microclimates of tracks

To estimate the physiological response of each species in an altered microclimate, we examined how the desiccation rates of each species might change if growing in a vehicle track, and how this change would affect durations of photosynthesis. Measuring the desiccation of each species in existing tracks as fog lifted was logistically difficult due to the distance of open plain tracks from the research base that was positioned according to National Park restrictions, and due to the time-consuming procedure of measuring ample sample sizes of each species every hour with no protection for recording materials. Therefore we used the fog cloths as surrogates, quantifying the increase in evaporation that can occur in tracks, as previously described, and applying this condition to the drying behaviour of the different species, as measured under natural conditions. By predicting the change in a lichen species' RMC if growing in a track, we could then estimate how the duration of photosynthesis would change based on previously

measured chlorophyll a measurements (Fv/Fm) at decreasing RMC.

First, the evaporation rates, or gradients of decreasing RMC, of the fog cloths in track and control sites were calculated as percentages of decrease using equation 2. Because RMC values are a ratio between dry and wet masses of the material measured, it was important to calculate rates of decreasing RMC as percentages rather than ratios, so that the resulting values could be applied to any values of *y* (RMC). This was important because the arithmetic difference between these percentages of decrease in track and control sites was then added to the desiccation gradient (percentage of decreasing RMC) previously measured for each lichen species under natural conditions. New desiccation gradients and RMC values were produced for each species, giving an indication of how track conditions could affect the moisture regimes of lichens.

$$\text{Decrease in RMC}(\%) = [(y_2 - y_3)/y_2] \times 100 \qquad \text{eqn 2}$$

where y_2 is the mean value of *y* at $x = 2$ (x = hours following sunrise) and y_3 is the mean value of *y* at $x = 3$.

As an indicator of how the duration of a lichen's metabolic activities might change in the altered environments of tracks, the photosynthetic activities of each species were estimated, represented by chlorophyll *a* fluorescence measurements (F_v/F_m). The F_v/F_m values were attained previously for each species on a continuum of decreasing RMC. From these values, the potential F_v/F_m for each species was extrapolated according to the RMC values estimated for track-recolonizing lichens. The in-track F_v/F_m values were plotted by hours following sunrise to illustrate the changes in duration of lichen activity.

lichen photosynthesis under extreme temperatures

To ascertain whether certain lichen species are more tolerant than others of extreme temperatures, the photosynthetic activity of the five species was measured at increasing temperatures (40, 45, 50 and 55 °C). Species subsisting in altered microenvironments may experience extreme temperatures more often than usual. Even under natural conditions in the Namib Desert, it is possible for soil surface temperatures to exceed 40 °C after lichen imbibition and photosynthesis are activated by summer precipitation or high humidity. Chlorophyll *a* fluorescence measurements were taken in a laboratory environment. Specimens were first artificially saturated and dark-adapted for 25 min, 20 min at room temperature and the final 5 min in a temperature-controlled oven. Following measurements, specimens were weighed and their RMC values were calculated. The RMC calculations ensured that specimens were optimally water-saturated for maximum photosynthesis at the time of measurement, so that the effect of temperature could be isolated.

Results

ALTERED MICROCLIMATES

Temperatures in tracks were significantly warmer than those in control sites between 7 am and 3 pm (Table 1). The greatest mean difference of 2·05 °C occurred at 1 pm. There were no significant differences between the relative humidity found in track and control locations (*t*-tests, $P > 0.05$).

Significant differences were found in fog deposition and fog-cloth evaporation between track and control locations (Fig. 1). At 7 am there was significantly more fog collected in the controls than in the tracks ($t = -3.925$; $P < 0.01$). Two hours after sunrise (9 am) there was a much steeper gradient of evaporative moisture loss in the track than in the control. Following this initial rapid rate of moisture loss, the evaporation rates in the track slowed considerably and eventually converged with the control, almost coming to a plateau. This may

illustrate different phases of evaporation, controlled surface air movement, or a number of external factors. Regardless, this study is only interested in the phase in which rates of decreasing RMC values diverged between 2 and 3 h following sunrise. The gradient of evaporation, or changes in RMC values, between 2 and 3 h following sunrise were calculated as percentages of change. In the control sites, RMC values between 2 and 3 h following sunrise decreased by an average of −17·47, which was converted to −24·27% using equation 2. In the track sites, RMC values between 2 and 3 h following sunrise decreased by an average of −42·62, converted to −60·90% using equation 2. The arithmetic difference between these percentages of decrease is −36·63%, meaning that an additional 36·63% of moisture evaporated between 2 and 3 h following sunrise when fog cloths were placed inside a track.

WATER-USE EFFICIENCY AND PHOTOSYNTHESIS OF LICHENS

saturation and desiccation rates in situ

The mean RMC of each lichen species was calculated at hourly intervals after sunrise (Fig. 2a). At each hour there were highly significant differences between the mean RMC values of the different species (ANOVA, $P < 0.001$). The highest *F* values were found at 7 am ($F = 23.03$); 8 am ($F = 22.15$); and 11 am ($F = 20.34$). Figure 2(a) illustrates the higher saturation levels of

Table 1. Significance of differences in temperature (*t*-test) between track and control sites

Time of day	Mean temperature (°C)		
	Control	Difference†	*t*
7 : 00	18·33 (SE = 0·12)	+0·21	5·640***
8 : 00	18·00 (SE = 0·12)	+0·38	3·383**
9 : 00	17·66 (SE = 0·11)	+0·65	3·556**
10 : 00	20·45 (SE = 0·26)	+0·53	2·213*
11 : 00	25·92 (SE = 0·30)	+0·18	4·808***
12 : 00	31·78 (SE = 0·39)	+0·60	6·213***
13 : 00	29·10 (SE = 0·34)	+2·05	5·309***
14 : 00	25·94 (SE = 0·26)	+1·35	6·841***
15 : 00	22·4 (SE = 0·11)	+0·30	4·204***
16 : 00	20·98 (SE = 0·33)	+0·33	1·506
17 : 00	18·40 (SE = 0·34)	−0·02	0·065

Significance: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.
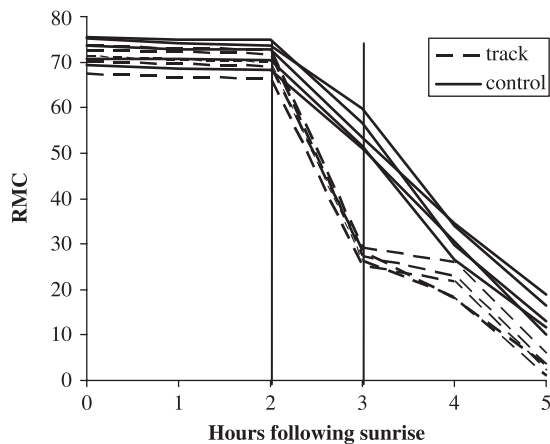†Amount by which mean track temperature differs from control.

Fig. 1. Desiccation of fog cloths in track and control sites based on mean values of relative moisture content (RMC) at 1-h intervals following sunrise. Vertical lines delineate diverging gradients of evaporation on which analyses are focused.
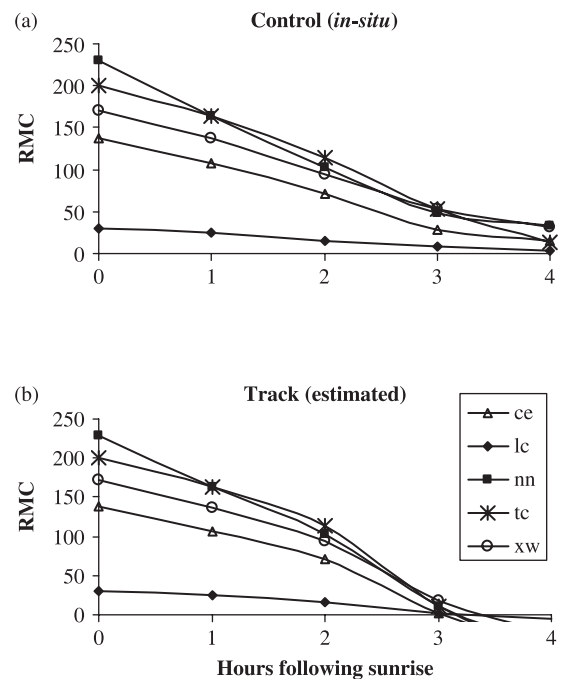

Fig. 2. Mean relative moisture content (RMC) of each lichen species at 1-h intervals following a fog event in (a) natural conditions; (b) as estimated in the altered microclimate of a track. ce, *Caloplaca elegantissima*; lc, *Lecidella crystallina*; nn, *Neofuscelia namibensis*; tc, *Teloschistes capensis*; xw, *Xanthoparmelia walteri*.
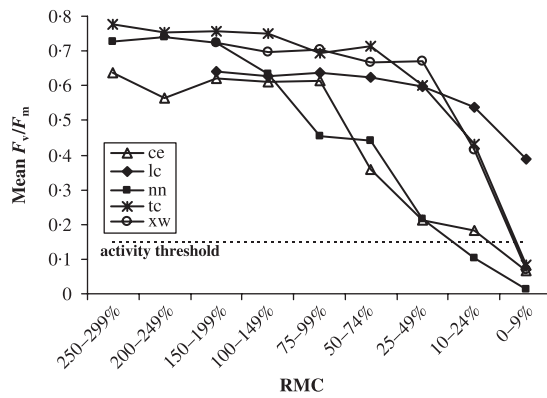
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Functional Ecology,
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Fig. 3. Chlorophyll *a* fluorescence (mean F_v/F_m values) of five lichen species at decreasing relative moisture content (RMC). Dotted line, F_v/F_m threshold under which specimens are considered inactive. ce, *Caloplaca elegantissima*; lc, *Lecidella crystallina*; nn, *Neofuscelia namibensis*; tc, *Teloschistes capensis*; xw, *Xanthoparmelia walteri*.

the foliose species *X. walteri* and *N. namibensis*, and the fruticose species *T. capensis*, immediately following sunrise. This relationship shifted 4 h into desiccation (11 am) where *T. capensis* dropped to a lower RMC comparable with the crustose species *C. elegantissima*, while the two foliose species continued to have the highest RMC of the five species.

The mean F_v/F_m values for each species at naturally decreasing RMC illustrated how *L. crystallina* requires lower saturation than other species to trigger photosynthetic activity (Fig. 3). *Neofuscelia namibensis* and *C. elegantissima* required the highest saturation levels for photosynthetic activity. The foliose lichen *X. walteri* and the fruticose species *T. capensis* required greater RMC for photosynthetic activity than did *L. crystallina*; however, they were productive for the longest period following a fog event (Fig. 4a) due to their extended periods of saturation under natural conditions (Fig. 2a). Photosynthetic activity at dawn also varied between lichens, as shown by the light-response curves produced for each species (Fig. 5). At low PFD (50 µmol m^{-2} s^{-1}), only one species, *T. capensis*, was capable of optimal photosynthesis (Fig. 4). Three of the lichen species started with low photosynthetic rates, and *L. crystallina* commenced activity only at a much higher PFD (200–250 µmol m^{-2} s^{-1}) than the rest of the species.

lichen productivity in altered microclimates

To estimate the change in desiccation of each lichen species within a track indentation, the percentage by which fog-cloth evaporation increased in tracks was applied to the known natural desiccation rates of the five lichen species. The increase in fog-cloth evaporation was calculated as 36·63% inside tracks, which occurred 2–3 h after sunrise (Fig. 1). For each lichen species, the gradient of decreasing RMC found under natural conditions between 2 and 3 h following sunrise (Fig. 2a) was calculated as a percentage using equation 2. By
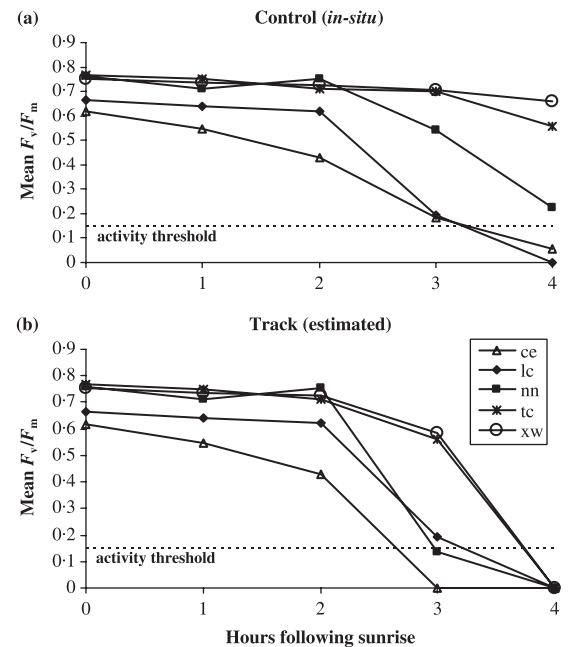
Fig. 4. Chlorophyll *a* fluorescence (mean F_v/F_m values) of five lichen species following fog events as measured under natural conditions (a, control) and estimated under altered conditions of a vehicle track (b, track). Dotted line, F_v/F_m threshold under which specimens are considered inactive. ce, *Caloplaca elegantissima*; lc, *Lecidella crystallina*; nn, *Neofuscelia namibensis*; tc, *Teloschistes capensis*; xw, *Xanthoparmelia walteri*.
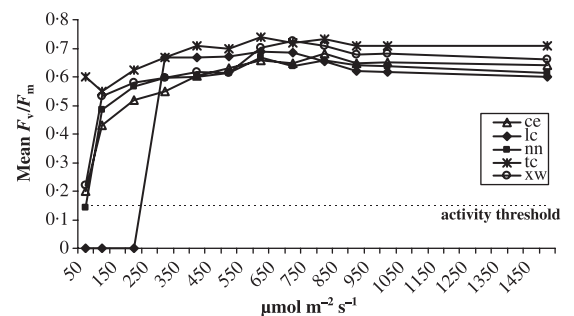

Fig. 5. Chlorophyll *a* fluorescence (mean F_v/F_m values) of five lichen species at increasing photon flux density (PFD; µmol m^{-2} s^{-1}). Dotted line, F_v/F_m threshold under which specimens are considered inactive. ce, *Caloplaca elegantissima*; lc, *Lecidella crystallina*; nn, *Neofuscelia namibensis*; tc, *Teloschistes capensis*; xw, *Xanthoparmelia walteri*.

increasing this percentage gradient by an additional −36·63%, new RMC values were calculated at $x = 3$ (Fig. 2b). Calculations of RMC at $x = 4$ were made using the original gradients found under natural conditions between 3 and 4 h following sunrise.

Based on the estimated in-track desiccation gradient, the potential photosynthesis (F_v/F_m) of each species was extracted from known F_v/F_m values calculated previously at decreasing RMC (Fig. 3). The estimated F_v/F_m values for track-growing lichens are plotted along the 0–4-h time-scale following sunrise (Fig. 4b), illustrating considerable decreases in the durations of productivity when compared with durations occurring under natural
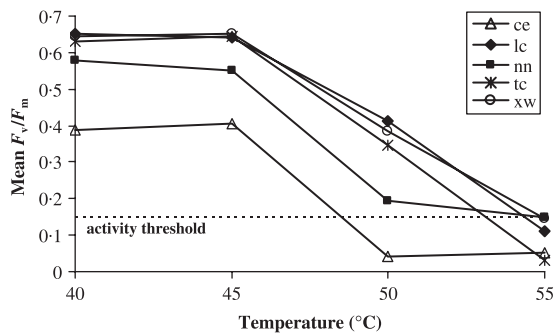
Fig. 6. Chlorophyll *a* fluorescence (mean F_v/F_m values) of five lichen species at extreme temperatures. Dotted line, F_v/F_m threshold under which specimens are considered inactive. ce, *Caloplaca elegantissima*; lc, *Lecidella crystallina*; nn, *Neofuscelia namibensis*; tc, *Teloschistes capensis*; xw, *Xanthoparmelia walteri*.

conditions (Fig. 4a). Of the five species, *L. crystallina* was the least affected by higher desiccation rates, due to its already low water-saturation levels. Three hours into desiccation, when desiccation rates are projected to increase for all species, photosynthesis was reduced by 100% in *C. elegantissima*; 74·6% in *N. namibensis*; 20·1% in *T. capensis*; and 17·37% in *X. walteri*. *Lecidella crystallina* experienced no reduction in performance (Fig. 4).

Additionally, lichen productivity under extreme temperatures was tested, and all species were unchanged at 40 and 45 °C (Fig. 6). At 50 °C, all species showed a marked decline in photosynthesis. At 55 °C *T. capensis* showed zero activity, and low levels of activity were detected in the four other species. The foliose species *N. namibensis* and *X. walteri* showed the highest photosynthetic activity at 55 °C.

Discussion

WATER-USE MECHANISMS AND PHOTOSYNTHESIS

The performance of soil-crust lichens proved to be dependent on the delicate balance of moisture and temperature on the soil surface immediately following a precipitation event. As shown in this study, the disturbance of this balance in track ruts and trenches, a common disturbance in deserts, resulted in higher temperatures and hence higher desiccation rates, leading to negative impacts on PSII. This study used fog cloths as surrogates, which commenced desiccation later than lichens in natural conditions. But once desiccation began, the significant increase in the track desiccation rate was unmistakable. By focusing only on this critical phase of evaporative increase in tracks, it was possible to estimate a similar effect on lichens. In relation to track and control temperatures, this evaporative increase coincides with the first significant increase in temperature, which occurred in both track and control sites. The higher temperatures in tracks magnify this daily microclimatic shift. In summer months tracks could

reach extreme temperatures, which would further inhibit physiological activity in some species (Fig. 6).

These results follow previously studied trends of lichen activity in other environments, where changes to moisture, light regimes and temperature altered physiological performances significantly (Sundberg *et al.* 1999; Gaio-Oliveira *et al.* 2004). Nevertheless, some caution is needed in extrapolating from the findings of this study, as they are based on the photosynthetic activity of healthy lichen specimens. Any lichens or lichen fragments that remain in a disturbed site might have even lower productivity due to damaged thallus surfaces, and could respond more severely to altered microclimates. This study also used fog cloths as a surrogate in order to ensure consistent measurements of fog saturation and evaporation in and out of tracks, and to avoid the influence of unknown lichen variables such as the varying mechanisms for osmosis, water retention or resistance to imbibition and oversaturation (Nash 1996). By doing so, it was necessary to take a conservative approach in applying surrogate results to the desiccation and productivity of lichens. Hence the analysis focused only on the evaporation period in which highly significant differences occurred between track and control sites.

This study also demonstrates how the physiological adaptations of lichens to the environment are species-specific, as seen with higher water-use efficiency in *T. capensis* and *X. walteri*; optimal use of low PFD in *T. capensis*; and a tolerance of extreme temperatures by *L. crystallina*, *N. namibensis* and *X. walteri*. These findings confirm the species variations found in desert lichen activity by Nash & Moser (1982); Palmer & Friedman (1990); Lange *et al.* (1994).

Interestingly, the species found to have one of the lowest levels of PSII, *C. elegantissima*, is the most widespread species in the Namib Desert (Jurgens & Niebel-Lohmann 1995; Lalley & Viles 2005), which is testament to the importance of its phenotypic plasticity. Another example of a seemingly disadvantaged species was *L. crystallina*, which not only showed low water-absorbing capacity, but commenced photosynthetic activity at a much higher PFD than the other species. Lange *et al.* (1994) studied the light-compensation points of different Namib Desert species, including *L. crystallina*, and also showed this species to have a high light-compensation point. Such slow reactions to light have been seen in other species, and may indicate a high resistance to intense light or other unknown mechanisms (Kershaw 1985). So, while the duration of photosynthetic activity is key to the functioning of each species, it is not inherent to its success within the variety of microhabitats found in deserts. Within an altered microclimate, however, the importance of water-use efficiency in a species may supersede other adaptations.

On a long-term basis it may be possible for species to adjust their water-use efficiency in new environments. The high absorption of fog and long durations of PSII seen in *T. capensis* and *X. walteri* may be partially attributed to morphology (Rundel 1982), but there may

be other mechanisms allowing for longer periods of activity at low RMCs. Lange *et al.* (1990) reported the rapid uptake of moisture by *T. capensis*, and Beckett (1998) describes possible mechanisms in the Namib species *X. hottentotta* that control osmosis and delay desiccation. It is possible that such mechanisms could be enhanced if these species were to subsist for long periods in altered microclimates. Certain lichen species with intercontinental distributions have adapted to extreme climate variations, which may be a result of adjusted mycobiont (fungal) and photobiont (algal) ratios (Sun & Friedman 2005). Most species have narrow thermal ranges, but can still display photosynthetic acclimation during different seasons. If evidence of thermal adaptations can be applied to the species studied here, responses to extreme temperatures could be a result of using species that have acclimated to the winter season. Regardless, thermal-related acclimation may not necessarily counteract decreased water-use efficiency in altered microclimates, especially in an already water-limited environment. Cross-seasonal measurements would help to isolate possible adaptive mechanisms.

ECOLOGICAL IMPLICATIONS

Decreased photosynthetic activity in soil-crust lichens may affect carbon cycling, nitrogen fixation, growth rates, soil stabilization and all related ecosystem functions (Evans & Johansen 1999). The extent to which these ecosystem functions change depends on the lichen species in the recovering community, given the variations between species' physiological activities. For example, *L. crystallina* showed little change in photosynthetic performance in the altered microclimate studied here, while optimally fog-adapted species such as *T. capensis* and *X. walteri* showed a marked decrease.

The ecosystem functions that will be directly affected by any alteration of lichen species' metabolic activities are nitrogen fixation and carbon cycling (Beymer & Klopatek 1991; Evans & Johansen 1999; Belnap 2002). The results of this study shed some light on how the water-use efficiency and photosynthetic potential of a lichen species can be affected by an altered microclimate, which indicates how the overall productivity of a recovering lichen community may respond. A resulting shift in spatial patterns of growth, due to the altered microtopography and lichen activity, will also affect overall primary production, as demonstrated in a spatial pattern analysis by Maestre *et al.* (2005).

Secondary impacts from lowered productivity levels include not only all ecosystem links to soil mineralization, but also lichen-dependent organisms (secondary producers that depend on specific community types; Zaady & Bouskila 2002; Lalley *et al.* in press). Altered microenvironments could lead to the exclusion of certain lichen species and a domination of others, causing a shift in lichen community compositions and associated organisms. The microtopographic changes studied here have been shown to accelerate lichen colonization by trapping lichen fragments, but community compositions are significantly different regardless of recovery periods (Lalley & Viles in press). Given the addition of microclimatic changes and the variations in species' responses found in this study, there may be unknown physiological variables contributing to this lack of successional convergence.

The slow growth of lichens and the reactive nature of these organisms are obstacles to standard recovery monitoring and rehabilitation strategies. Therefore predicting the future productivity of a disturbed lichen soil crust, and how its ecosystem roles will be affected, is extremely challenging and leaves many unanswered questions. Further impacts on the microenvironment, not considered here, are soil compaction and erosion, which would alter soil surface-moisture retention and substrate stability, respectively. More extreme impacts on microclimates from the regional effects of global climate change also have the potential to cause significant shifts in the composition and productivity of lichen communities in the future. With the predicted increase in temperature and less frequent, more intense rainfall for southern Africa (Hadley Centre for Climate Prediction and Research 2003), only certain lichen species would remain unaffected, while others could fail to subsist in extreme temperatures. Even if less frequent, more intense rain episodes would erode tracks and trenches, possibly before any lichen growth could establish. There are numerous other scenarios, not considered here, that could have an impact on the functioning of lichen soil crusts. Further research into species' responses to microenvironmental changes will provide insights into the future challenges of lichen soil-crust management. While we are still in the infancy of predicting biological productivity in deserts of the world, especially in relation to biological soil crusts, our knowledge of current systems and immediate impacts allows for some quantification of desertification processes in need of conservation attention.

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