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Water relations in the soil crust lichen *Psora decipiens* are optimized via anatomical variability

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1 **Water relations in the soil crust lichen *Psora decipiens* are optimized via anatomical variability**2 **C. COLESIE, L. WILLIAMS, B. BÜDEL**3 **Abstract**

4 Biological soil crusts are communities composed of cryptogamic organisms such as lichens, mosses,
5 cyanobacteria and green algae that form a skin on soils in areas where vascular plants are excluded or
6 limited by water availability or temperature. The lichen *Psora decipiens* (Hedw.) Hoffm. is a
7 characteristic key organism in these communities in many different biomes. The species has a
8 generalistic ecology and high morphological variation, which contributes to the ability of the species
9 to withstand environmental changes. We investigated whether different populations, based on site and
10 associated morpho-anatomical differences, incorporate functional water relations and how/whether
11 this was mediated by changes in abiotic factors. Samples were collected from two climatically distinct
12 sites, one “dry” site in southern Spain, and one “wet” site in the Austrian Alps. Our results showed
13 that samples from the dry site had a significantly thicker epinecral layer, higher specific thallus area, a
14 faster water uptake and contained more water per dry weight, all of which contributed to a much
15 slower drying rate. Both populations showed a highly adjusted water gain that incorporates functional
16 water relations and diffusion properties as a result of local water availability. We show eco-
17 physiological and morphological mechanisms that underlie the high variability in *P. decipiens* and
18 draw conclusions around the ecological benefits for this generalistic lichen species such as optimized
19 water relations and light exploitation.

20

21 **Keywords**

22 Biological soil crusts, hydrological characteristics, epinecral layer, lichens, phenotypic plasticity,
23 drying rate

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Introduction

27 The concept of ecotypes, defined as distinct genotypes (or populations) within a species, resulting
28 from adaptation to local environmental conditions (Hufford & Mazer 2003), describes the geographic
29 variation within a species and the balance between local adaptation and intra-specific hybridization
30 (Begon et al. 2006). In lichenology, to distinguish between differentially exposed populations, the
31 concept of ecotypes can be used, for example to describe different altitudinal distributions (Nadyeina
32 et al. 2014). Another interpretation of structural changes in lichen thalli from different populations is
33 often described as phenotypic plasticity. For example, different rates of photosynthesis occur as a
34 result of differences in thallus hydration, due to structural changes, when comparisons are made
35 between north- and south facing populations of *Ramalina capitata* (Ach.) Nyl. (Pintado *et al.* 1997)
36 and vagrant compared with attached thalli of *Cetraria aculeata* (Schreber) Fr. (Pérez-Ortega *et al.*
37 2012). Increasing the amount of rhizinae is a modification that can improve thallus hydration and
38 therefore photosynthesis, when comparing epilithic versus epiphytic populations of *Parmelia*
39 *pastillifera* (Harm.) Hale (Tretiach & Brown 1995). Finally, *Catillaria corymbosa* (Hue) I. M. Lamb,
40 an Antarctic endemic species, showed an increased water retention capacity and therefore more
41 photosynthesis in shaded localities (Sojo *et al.* 1997).

42 In drylands, vascular plants are limited due to low water availability and therefore biological soil
43 crusts (BSC) become a dominant component of vegetation (Pointing & Belnap 2012; Büdel *et al.*
44 2014). BSCs also occur in high alpine areas above the tree-line, typically when the mean temperature
45 of the warmest month is below 10°C (Körner, 1998), seventy to eighty percent of the precipitation
46 falls as snow, and snow cover lasts 270 to 300 d (Auer et al., 2002). BSCs are small scale
47 poikilohydric lichen-bryophyte and microbial communities that are considered to be ecosystem
48 engineers (Pointing & Belnap, 2012) that stabilize soil (Belnap *et al.* 2003), and make significant
49 contributions to the carbon and nitrogen fixation budgets (Elbert *et al.* 2012). Lichens often form the
50 major proportion at the climax stage of these communities (Büdel *et al.* 2009). Studies on soil lichen
51 populations, including their functional aspects and morphological differences, are need to enable us to

52 predict climate change scenarios in these areas; these habitats are considered to be at high risk in
53 recent climate change projections (IPCC 2012).

54 Here we studied the differences in morpho- anatomical and hydrological traits of two populations of
55 *Psora decipiens* (Hedw.) Hoffm., a typical lichen occurring in the climax stage of biological soil crusts
56 worldwide (Büdel 2003, Galun & Garty 2003, Rosentreter & Belnap 2003). Two contrasting areas
57 with distinct populations were selected: a high alpine environment (“Site Hochtör”, Fig. 1A) and arid
58 badlands (“Site Almeria”, Fig. 1B). Preliminary observations indicated (1) strong variance in overall
59 thallus structure and appearance and (2) higher vitality of the alpine population (based on mean thallus
60 size and vivid color). Based on this field observation we hypothesized, that local water availability is a
61 major driver for morpho-anatomical differences in lichens and thallus water relations can be optimized
62 to local necessities.

63 **Material and Methods**

64 **Study sites, organisms and sampling**

65 We chose two sampling sites that support natural BSC occurrence, but differ considerably in their
66 environmental conditions. The first, and humid “Site Hochtör”, was a high alpine area at an elevation
67 of 2500 to 2600 m asl. of the Großglockner massif, Austria. The second site was the dry site, “Site
68 Almeria”, located in South East Spain. This location was considered as one of the driest and sunniest
69 in Europe, and has been described in previous studies (Lázaro *et al.* 2001, Cantón *et al.* 2004).

70 *Psora decipiens* is a pale pink squamulose-crustose lichen with conspicuous white-pruinose, often
71 upturned margins. The lower cortex is white, poorly developed or absent and the attached hyphal net
72 penetrates into the substrate. It is a cosmopolitan lichen and is well known as indicator species for
73 intact BSC climax stages (Fig. 1C and D).

74 Samples (30) were randomly collected at each site in areas with homogenous BSC cover and no
75 shading from plants. Each sample unit was a 9.2 cm² section of an intact *P. decipiens* dominated BSC,
76 where several thalli were growing. Sampling at site Hochtör took place in August 2013 and at site
77 Almeria in June 2013. Samples were dried at room temperature within 3 d of collection, transported

78 and stored frozen. In the laboratory the surrounding soil crust was removed from the thalli, which were
79 then washed. The number of replicates used in each experiment is indicated below.

80 **Climate measurements**

81 Both investigation sites were equipped with similar climate stations, capable of monitoring air
82 temperature and humidity, solar radiation (Photosynthetically Active Radiation, PAR), $UV_{(A+B)}$ -
83 radiation and precipitation. Climate data were recorded from both sites over 2 y, from April 2012 -
84 March 2014 at site Almeria, and from August 2012 - July 2014 at site Hochtor. Air temperature and
85 relative humidity were measured 1.5 m above ground, and solar radiation at 2 m above ground. The
86 snow cover was estimated from the length of time the various sensors were inactive. Mean (\pm standard
87 deviation) values were calculated for summer and winter air temperature, humidity, PAR and UV_A and
88 UV_B combined radiation. Additionally maximum and minimum temperature, and maximum UV and
89 PAR radiation were extracted from the dataset.

90 **Thallus morphology and anatomy**

91 *Thickness.* The thicknesses of the lichen thalli, the epinecral layer, the photobiont layer and the
92 medulla were measured on freezing microtome sections, $n=400$ for the photobiont layer and medulla
93 measurements and $n=100$ for the epinecral layer measurements from each site, using the AxioVision
94 software (Carl Zeiss, Jena, Germany). To visualize thallus internal relationships between photo- and
95 mycobiont, the ratio between the photobiont layer and medulla was calculated.

96 *Specific thallus area.* To calculate the specific thallus area (STA, $\text{mm}^2 \text{mg}^{-1}$) thallus size was first
97 determined by binocular microscopy using the above mentioned software. A standard procedure was
98 used to delineate the extent of each lichen thallus. The lichen thalli were wetted to ensure maximum
99 surface area, placed on scale paper and photographed. The corresponding dry masses (DM) of these
100 thalli were determined by weighing after 3 d of oven drying at 60°C ($n=20$).

101 *Specific thallus mass.* This parameter was emphasized by Kershaw (1985) as an important lichen
102 parameter for water loss and water uptake and is the inverse equivalent of STA (see above).

103 **Hydrological traits**

104 *Drying rate.* Photosynthetic activity was monitored by measuring the efficiency of PSII
105 photochemistry using an imaging-PAM chlorophyll fluorometer (Heinz Walz, GmbH, Effeltrich,
106 Germany). Specimens of roughly the same size ($\pm 10 \text{ mm}^2$), which had been submerged in water
107 overnight, were first weighed, then placed in a sealed plastic chamber on a wire net over a saturated
108 NaCl solution which maintained a level of humidity of 75% rH equivalent to a water potential of -37
109 MPa at room temperature (Pardow & Lakatos 2013). Initially the maximum quantum yield of PSII
110 F_v/F_m of the hydrated and dark adapted (30 min) samples was measured as a reference. Subsequently,
111 short saturation pulses were applied every 2 minutes to determine the fluorescence parameters for
112 calculating PSII yield ($Y = F_v/F_m$). The time was measured until a threshold of 0.2 PSII yield was
113 reached for $n=18$ replicates (3 thalli per chamber). To determine the absolute water loss during the
114 measurement, samples were weighed again, directly after the measurement. Drying rate was
115 calculated, and expressed as the time need for $1 \mu\text{l}$ of water to evaporate from one mm^2 of thallus
116 ($\text{min } \mu\text{l}^{-1} \text{ mm}^{-1}$).

117 *Water uptake.* To ensure full water saturation prior to weighing, the samples were submerged in
118 distilled water for 30 min. Excessive water and droplets were carefully shaken off before measurement
119 of maximum wet mass (WM_{max}). The corresponding dry mass (DM) of these thalli was determined by
120 weighing after 3 d at 60°C . The maximum water uptake relative to the thallus specific dry mass of the
121 samples ($n=36$) was calculated as $WM_{\text{max}} - DM / DM$ (Pérez 1997).

122 *Repellency.* To measure water repellency/hydrophobicity of individual lichen thalli, the water drop
123 penetration time (WDPT) was measured for $n= 30$ replicates. The WDPT test consists of placing a
124 drop of water on the surface of the epinecral layer and measuring the time until complete absorption
125 occurs. This is a commonly used test because of its simplicity (Letey *et al.* 2000) and the value of
126 information it provides, as it was considered to be the most indicative and sensitive way for the
127 hydrological consequences of water repellency to be investigated (Doerr 1998, Leelamanie *et al.*
128 2008).

129 *Optimum water content.* CO₂ gas exchange measurements were conducted under controlled laboratory
130 conditions using a portable mini cuvette system (GFS 3000, Walz Company, Effeltrich, Germany).
131 The response of net photosynthesis (NP) and dark respiration (DR) to thallus water content (WC) was
132 determined for three replicates (each replicate was composed of about 20 individual squamules) from
133 each of the sites. Complete drying-out cycles (from water saturated to air dry thalli) were measured at
134 750 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ (saturating light), ambient CO₂, at 17°C (which is within the optimal
135 temperature range for CO₂-gas exchange of this species). Samples were weighed between each
136 measurement and thallus water content (WC) was later calculated as a percentage of dry mass. Dry
137 mass was determined after five days in a desiccator over silica gel. Ninety percent of maximum net
138 photosynthesis was considered to be a reasonable estimate for optimal water content.

139 *Water holding capacity.* Water-holding capacity (WHC) was calculated by: saturated wet mass – dry
140 mass (mg) / thallus area (cm²) after shaking surplus water off the lichen thallus. The corresponding
141 dry mass (DM) of these thalli (n=20) were determined by weighing after drying for 3 d at 60°C.
142 Thallus area was measured as described above.

143 **Statistics**

144 To determine differences between the lichens anatomical features and the climate of the two sites
145 student's t-tests were used (Statistica 10, Stat soft). All data was normally distributed. Significance
146 level was defined at $P < 0.05$.

147 **Results**

148 **Climate measurements**

149 The data (Table 1) demonstrate the pronounced differences in temperature, humidity and precipitation
150 between the sites, and also within the sites based on seasonality. In Almeria it was significantly
151 warmer, drier and brighter than at the alpine site Hochtor. However in site Hochtor the growing season
152 only lasted about 3 months in a year, due to the persistent snow cover.

153 **Thallus morphology and anatomy**

154 Thalli from Almeria had thicker epinecral layers, but only half the medulla thickness compared to
155 samples from Hochtor (Fig. 1E and F; Table 2). The photobiont layer showed no difference between
156 the sites, therefore, the photobiont layer to the medulla-ratio of the thalli from site Almeria was twice
157 as high. This indicates significant differences in the internal structure of the thalli between the
158 populations. STA was also higher for samples from site Almeria (Table 2), indicating that these thalli
159 can support relatively large areas despite their reduced thallus matter. Corresponding to this finding,
160 STM was significantly higher for samples from site Hochtor, indicating that these samples are thicker
161 than those from site Almeria.

162 **Hydrological traits**

163 Both populations had similar water holding capacities per area (Table 2) and showed some common
164 drying characteristics, independent of sampling site and thallus size (Fig. 2). For example, the initial
165 activity of PS II was similar, with high yields of PSII at ca. 0.6 (blue color, Fig. 2). Additionally, these
166 levels of activity remained relatively stable for certain amounts of time independent of thallus size
167 (around 0.6). As soon as a threshold of desiccation was reached, the actual drying event occurred
168 quickly, and no fluorescence signal could be detected shortly after this. In contrast to these common
169 features, the actual drying rate was different between the two populations. Thalli from site Almeria
170 dried six-times slower than those from site Hochtor (Table 3, Fig. 2). Additionally, *P. decipiens*
171 specimens from site Almeria took up water faster (1.2 ± 0.27 sec compared to 168.4 ± 15.8 sec for
172 samples from site Hochtor) and contained more water per dry mass than those from site Hochtor
173 (Table 2). The optimum WC for CO₂ exchange extended over a significantly narrower range, (109-156
174 % DM) for samples from site Almeria than for samples from site Hochtor (131-195 % DM).

175

Discussion

176 In the present study we have demonstrated distinct differences between two populations of the lichen
177 species *P. decipiens*, derived from climatically contrasting habitats. Morpho-anatomical differences
178 appear to be reflected in differences in functional water relations and diffusion properties as a result of
179 local water availability. We have identified eco-physiological and morphological mechanisms that
180 underlie the high variability in *P. decipiens* that determine its ecological fitness in a particular habitat.

181 The most striking difference between the two populations is water gain. Considering the differing STA
182 and the maximum water uptake relative to the thallus specific dry mass, thalli from both sites have the
183 same water holding capacity on an area basis (WHC in Table 2). This indicates that, not only surface
184 area, but also thallus internal structure must be studied to understanding the drying processes in
185 lichens. During the actual drying process we need to consider the amount of water in the thallus, based
186 on thallus area. The resulting calculation shows that drying from optimal water content to completely
187 desiccated lichen thalli takes 2.5 minutes mm^{-2} for thalli from Hochtor, but 15 minutes mm^{-2} for
188 Almeria thalli. This conclusion is supported by the chlorophyll fluorescence results, which show a
189 much slower rate of decrease in activity in Almeria thalli (Fig. 2).

190 Samples from the dry site Almeria show both improved water uptake and reduced water loss. A
191 reduction of water loss in lichens seems remarkable, because lichens, as poikilohydric organisms are
192 known for their passive water control and unregulated loss of water over the whole thallus surface.
193 Nevertheless, Beckett (1995) showed that lichens from dry habitats seem to make better use of their
194 water, by maintaining turgor down to low relative water contents. The reduced rates of water loss
195 found here, may be the result of increased diffusive resistance caused by the thicker epinecral layer.
196 This layer is often described as amorphous, and is composed of decomposing hyphae with indistinct
197 cell lumina; it forms a very dense layer that can act as a barrier to water loss, more so than the upper
198 cortex. In the revised generic concept of Parmelioid lichens (Crespo et al. 2010) a pored epicortex is
199 an important diagnostic feature beside molecular, morphological and chemical evidence. The
200 epicortex probably provides an extra layer of protection against evaporation. A thick epinecral layer,
201 as present in the samples from the dry site Almeria may therefore account for such a reduction in
202 water loss. Nevertheless, developing a thick epinecral layer also seems contradictory to improved
203 water gain, because it is also reported to have hydrophobic properties (Lakatos *et al.* 2006). The
204 occurrence of hydrophobins, proteins unique to mycelial fungi, has been suggested to be important for
205 the survival of lichens (Wessels 2000). According to Honegger (1991), a hydrophobic lining of gas
206 spaces allows efficient apoplastic transport of water and solutes between the symbionts, and permits
207 optimal gas exchange during wet periods. Therefore, very low water repellency of the samples from
208 site Almeria is unsurprising. The suggested explanation for this result derives from the structure of the

209 epinecral layer itself and how this influences the lichen surface (Fig. 1C and D). In dried thalli, the
210 epinecral layer has open cracks (Fig. 1E), thus increasing the surface area and facilitating water uptake
211 by cohesion and adhesion, leading liquid water towards the photobiont layer (Fig. 1E and F). With
212 WHC_{shaking} being close to $50 \text{ mg H}_2\text{O cm}^{-2}$ (Table 2, $10 \text{ mg H}_2\text{O cm}^{-2}$ equates to 0.1 mm dew or rain)
213 these lichens use the rare rain events more often than dewfall (Gauslaa et al. 2014). Both findings
214 support the explanation that a functional role of the epinecral layer is to influence the lichen
215 hydrology. To our knowledge, this has not been previously described. The function of the epinecral
216 layer is usually suggested to be protection against high light stress (Büdel & Lange 1994, Büdel *et al.*
217 1997, Rikkinen 1995, Kappen *et al.* 1998, Dietz *et al.* 2000). For chlorolichens, drying combined with
218 light exposure can be particularly harmful (Gauslaa *et al.* 2012) and it was suggested that the ability to
219 recover, correlates positively with increasing species-specific water holding capacities (WHC). In
220 Almeria, light intensities and UV-radiation are much higher throughout the year (Table 1), and in this
221 population the thicker epinecral layer is therefore necessary to prevent light damage. In the Hochtor
222 site, where light intensity is less and exposure time to both PAR and UV are shortened due to snow
223 cover, such protection would not be required or beneficial to the lichen.

224 In the wet site of Hochtor, the lichens experience a different set of stresses. Water saturation for many
225 hours a day may result in negative carbon gain for two reasons. First high respiration rates during the
226 night and under the snow cover can influence carbon balance negatively, and second CO_2 diffusion
227 resistance is high in water supra-saturated thalli, thus reducing the substrate for photosynthesis
228 (Cowan *et al.* 1992). The high WHC_{shaking} values indicate that these lichens are more often exposed to
229 rain events of about 40 mm precipitation (Gauslaa et al. 2014), which underlines their frequent water
230 saturation. For lichens, it is essential to minimize periods of water supra-saturation. Indeed, the
231 functional aspects that we report here for the lichens from the wet site Hochtor are fast desiccation
232 times, high hydrophobicity, low maximum water uptake relative to the thallus specific dry weight and
233 a broad range of thallus water contents for optimal photosynthesis. All of these may be explained by
234 specific thallus anatomy, which includes a very thick medulla layer and is best quantified by the high
235 STM values (Table 2). The medulla is the fungal zone in the lichen thallus, composed of hyphae, with
236 cell walls often incrustated with crystalline secondary metabolites. It was shown that lichen substances

237 did not maintain the water-free diffusion pathways (Lange *et al.* 1997) and the authors suggested that
238 these pathways are rather maintained by structural changes. Together with numerous hydrophobic air
239 spaces in the medulla, supra-saturation with water is minimized or even avoided (Lange *et al.* 1993).
240 The morpho-anatomical adjustments leading to water repellency of the upper layers involve reduced
241 STA for the samples from site Hochtor. The parameter of STA is analogous to specific leaf area
242 (SLA), in higher plants, which can yield information about life strategies. Species with low SLA
243 conserve acquired resources, due to their large dry matter content, high concentration of cell walls and
244 secondary metabolites, and high leaf and root longevity (Marron *et al.* 2003). By applying these
245 features to lichens, the lower the STA, the lower the fitness and the more lichen material is needed to
246 support the same surface area. Our results show higher STA values for lichens from the dry site
247 Almeria, which means that these lichens have a higher fitness. One conclusion from this result might
248 be that anatomical and functional adjustments within *P. decipiens* are more easily made towards
249 dryness and high light stresses than towards water supra-saturation, a common phenomenon in the wet
250 site Hochtor. This conclusion may be of general interest towards regions with climate change
251 predictions that include increased flood and heavy rain risks (IPCC 2012), as the conditions are
252 expected to occur in the future in many areas that sustain natural BSCs covers. Accumulations of such
253 events may influence the natural BSC more severely than increasing drought.

254 This study suggests that two populations show variations in morpho-anatomical traits that result from
255 their native environments climatic differences. These differences could result from ecotypic variation
256 or phenotypic plasticity. Increasingly, recent studies on plant plasticity describe not only growth rates
257 documentation and morphological parameters, but also functional aspects of plasticity. The plasticity
258 of functional traits (both long- and short term) can contribute to the ability of species to occupy
259 diverse and variable habitats in nature (Sultan *et al.* 1998). Phenotypic plasticity plays an important
260 role in community ecology because it contributes to the ability of species to withstand environmental
261 changes, such as those caused by human disturbance. The timescale of such changes is often too short
262 for an evolutionary response, thus species that lack sufficient plasticity might be at risk of altered
263 reproduction, degradation or extinction (Sultan 2000). On the other hand, ecotypic variation would
264 result in the two populations also being different on a genetic level. This would suggest that the

265 observed differences are not due to the species plasticity and could therefore be at risk to climate
266 change and habitat loss. This study has focused on purely morphological and physiological
267 characteristics of the lichen *P. decipiens*. In order to reveal a complete picture of the variation of this
268 important soil crust lichen molecular analysis has to be included. The next step is to investigate the
269 genetic diversity and acclimation potential of both the algal and fungal partners of *P. decipiens* from
270 the two populations at the climatically distinct sites.

271

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281

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392 **Figure captions:**

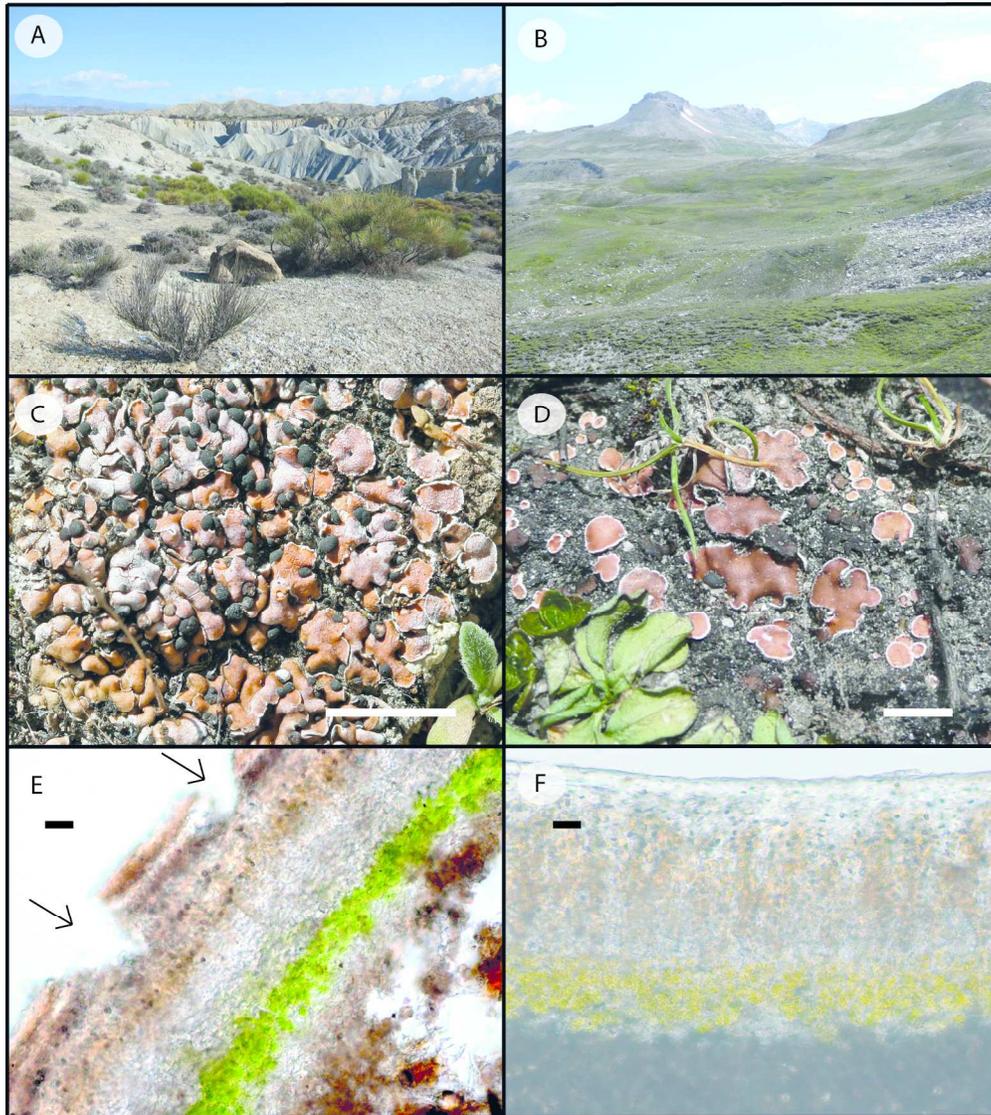
393 Figure 1: Characteristics of *Psora decipiens*. A) Study site Almeria overview, B) study site Hochtor
394 overview; C) natural appearance at study site Almeria (photo: Martin Westberg); D) natural
395 appearance at the study site Hochtor; E) cross section from site Almeria with the thick cracked
396 (arrows) epinecral layer; F) cross section from site Hochtor with a continuous epinecral layer and a
397 thick medulla including a thick photobiont layer. White scale bars indicate 1 cm, black bars indicate
398 20µm.

399 Figure 2: Dehydration kinetics of *Psora decipiens*. False color chlorophyll fluorescence images of the
400 effective quantum yield (Y) of photosystem II distribution over three thalli from site Almeria (upper

401 row) and site Hochtort (lower row), obtained using an Imaging PAM (Walz GmbH, Effeltrich,
402 Germany). Yield intensity is color coded covering a range from 1-0 with red indicating very high
403 values and violet low values. Red flags indicate exact Yield values at a chosen area of interest in the
404 picture. Pictures were taken every 2 minutes.

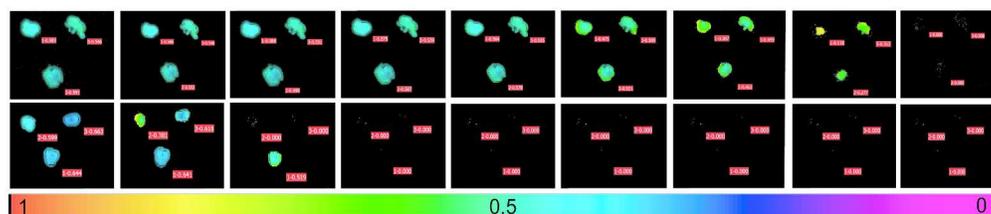
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Characteristics of *Psora decipiens*. A) Study site Almeria overview, B) study site Hochtor overview; C) natural appearance at study site Almeria (photo: Martin Westberg); D) natural appearance at the study site Hochtor; E) cross section from site Almeria with the thick cracked (arrows) epinecral layer; F) cross section from site Hochtor with a continuous epinecral layer and a thick medulla including a thick photobiont layer. White scale bars indicate 1 cm, black bars indicate 20 μ m.

188x211mm (300 x 300 DPI)



Dehydration kinetics of *Psora decipiens*. False color chlorophyll fluorescence images of the effective quantum yield (Y) of photosystem II distribution over three thalli from site Almeria (upper row) and site Hochtort (lower row), obtained using an Imaging PAM (Walz GmbH, Effeltrich, Germany). Yield intensity is color coded covering a range from 1-0 with red indicating very high values and violet low values. Red flags indicate exact Yield values at a chosen area of interest in the picture. Pictures were taken every 2 minutes.

297x67mm (300 x 300 DPI)

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Table 1: Climate data at the study sites. Climate data are differentiated by summer and winter for both investigation sites. Summer: April-September, Winter: October-March, Almeria: April 2012-March 2014, Hochtor: August 2012-July 2014. Shown are mean values with standard deviation where appropriate, maximum and minimum values recorded across the measuring period, average rainfall per season and snow cover duration. PAR and UV are based on daily average and maximum values. a: values are significantly different within the sites (summer vs. winter), b: values are significantly different between sites (eg. Site Almeria summer vs. site Hochtor summer).

Parameter		Site Almeria		Site Hochtor	
		Summer	Winter	Summer	Winter
Air temp. (°C)	Average	23.0 ± 6.6 ^{ab}	13.6 ± 5.8 ^{ab}	2.0 ± 4.6 ^{ab}	-3.7 ± 3.0 ^{ab}
	Max	43.8	34.8	19.86	14.6
	Min	2.8	0.0	-7.5	-18.6
Humidity. (%)	Average	51.4 ± 20.5 ^b	60.6 ± 19.7 ^b	92.4 ± 12.3 ^b	93.1 ± 9.5 ^b
PAR (μmol m ⁻² s ⁻¹)	Average	962.5 ^{ab}	619.8 ^{ab}	441.8 ^{ab}	152.8 ^{ab}
	Max	2650	2406	2680	1862
UV _{A+B} (μmol m ⁻² s ⁻¹)	Average	89.69 ^{ab}	60.6 ^{ab}	77.8 ^{ab}	33.8 ^{ab}
	Max	346.9	266.8	384.2	244.6
Rain (mm)	Average	25.5 ^{ab}	91.8 ^{ab}	558.3 ^{ab}	75.45 ^{ab}
Snow cover	Year	None	None	3 months	6 months

Table 2: Comparison of anatomical and hydrological characteristics of lichen thalli deriving from the wet exposed site Hochtor and the dry site Almeria. Shown are mean values with standard deviation and significance levels from t-tests.

parameter	Thallus morphology		Significance of difference between dry and wet exposed thalli		
	Site Almeria	Site Hochtor	t	df	p
Epinecral layer thickness (μm)	92.2 \pm 18.8	70.1 \pm 9.8	7.3	98	0.000
Photobiont layer thickness (μm)	91.5 \pm 16.2	93.0 \pm 20.2	-0.7	398	0.4
Medulla thickness (μm)	102.4 \pm 38.6	224.6 \pm 59.4	-24.4	398	0.000
Photobiont/Medulla ratio	0.89	0.41			
Specific thallus area ($\text{mm}^2 \text{ mg}^{-1}$)	4.7 \pm 0.9	2.9 \pm 0.3	5.6	19	0.005
Specific thallus mass (mg cm^{-2})	22.3 \pm 3.8	36.7 \pm 7.6	5.6	19	0.005
Thallus hydrology					
Maximum water uptake relative to the thallus specific dry weight ($\text{mg H}_2\text{O}/\text{mg dry weight}$)	2.1 \pm 0.7	1.4 \pm 0.1	-4.1	34	0.000
WC opt (%)	109.7 -156.1	131.8 – 195.4		2	0.03
WHC ($\text{mg H}_2\text{O cm}^{-2}$)	46.4 \pm 12.8	51.6 \pm 9.9	-2.5	19	0.1
WDPT (sec)	1.2 \pm 0.3	168.4 \pm 15.8	-4.1	28	0.000
Drying rate ($\text{min } \mu\text{l}^{-1} \text{ mm}^{-2}$)	34.1 \pm 28.8	5.3 \pm 4.3	-4.2	34	0.000