CEC California Ecology and Conservation Research

Natural Reserve System
UNIVERSITY OF CALIFORNIA

Lichen water retention: Vertical position in canopy as an indicator of desiccation tolerance across taxa

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ABSTRACT

Lichens play a crucial role in ecosystems, contributing to productivity, microhabitats, and nutrient cycling; they also serve as indicators of air quality. However, climate warming and increased sun exposure from logging are amplifying the risk of desiccation damages, though the effect may vary between lichen genera. Due to their vertical distribution, we predicted that lichens adapted to drier conditions higher in trees are less prone to drying than those in the shaded understory. This study explored lichen-microenvironment relationships and genus-specific responses to sun exposure and extreme dryness. Carried out at Angelo Coast Range Reserve, this research subjected lichens from various canopy levels to controlled drying conditions; in the shade, in direct sunlight, and in high-temperature conditions. Notably, this study revealed that while the high-canopy genus, *Usnea,* exhibited high desiccation tolerance, the low understory *Peltigera* was the most susceptible. The mid-level genera, *Lobaria* and *Hypogymnia,* demonstrated intermediate desiccation responses. Intriguingly, intense temperature did not impact lichen water uptake capacities. These findings may be used to inform forest management practices and bridge gaps in knowledge on lichen survival, community composition, and distribution amid climate change and risks posed by logging.

Keywords: lichen, water retention, sun exposure, logging, canopy position

INTRODUCTION

Excessive logging has presented a multifaceted list of complications for not only the species and habitats directly associated with regions disturbed by deforestation, but also globally, through the exacerbation of anthropogenic climate change. Unprecedented heat, unpredictable drought, and extreme weather patterns as a result now define the conditions where both flora and fauna are forced to survive (Strzepek et al. 2010). The adverse effects of logging are well documented in previous research. In one such project that studied the direct effect logging has on shade-dependent ferns, it was found that in clear-fell logging areas where sun exposure is dramatically increased, only 14% of ferns remained alive after two years (Ough and Murphy 1996). Forests provide moisture and sun protection for many species that inhabit the understory and are especially important for poikilohydric species, a non-vascular taxon, incapable of regulating their water uptake and are highly dependent on their surrounding microhabitats (He et al. 2016; Green et al. 2011).

Lichens are one of these poikilohydric organisms that are at the forefront of the adversities posed by logging and climate change. Logging has negatively impacted lichens by elevating desiccation risk due to heightened UV exposure, maximum air temperatures, wind speed, as well as reductions in humidity (Bunnell et al. 2008). Additionally, climate change continues to contribute to average temperature increases and decreases the frequency of days where dew-point is reached, causing water availability to become less predictable (Tomaszkiewicz et al. 2016). Consequently, the distribution, biodiversity, and abundance of lichen are often the first indications that something is amiss in their ecosystems (Rubio-Salcedo et al. 2017).

Lichens, a symbiosis between photosynthetic algae and fungi, play impactful roles in the many ecosystems they occupy. Not only do they provide primary productivity from habitats where few others can live, but they also contribute to water and nutrient cycling by intercepting them from the atmosphere (Bianchi et al. 2020). When their photobiont is a cyanobacterium, as seen in cyanolichens, they can also sequester nitrogen, further contributing to nutrient availability in a community (Henriksson and Simu 1971). Through nutrient cycling, they are important drivers of biogeochemistry, often playing a significant role in primary succession by the weathering of rocks (Cornelissen et al. 2007 and Bokhorst et al. 2015), solidifying their place as a key organism in an ecosystem.

Beyond lichens being essential members of their respective communities, they can be incredibly sensitive to changes in their environments (Rubio-Salcedo et al. 2017). Multiple studies have used lichens as an indicator of the effects of pollution as they cannot filter the air they absorb, leading to mortality when exposed to polluted air (Sharnoff 2015; LeBlanc and Rao 1973; Hawksworth and Rose 1979). Another property that makes lichens key indicators of environmental health is the fact that they are poikilohydric as previously mentioned, and acute to shifts in water regimes. When drought conditions lead to water scarcity in an ecosystem, they become naturally dormant and desiccated. When drought becomes prolonged, such as in conditions induced by climate change, there can be significant losses in lichen populations and therefore indicate a negative effect on the ecosystem they inhabit (Kranner et al. 2008). Consequently, humidity and dew are crucial sources of moisture for all lichens (Gauslaa 2014). For cyanolichens though, rainwater is often necessary to achieve full saturation. With the current shifts in climate and the increasing frequency and intensity of drought, we can expect hotter and drier periods with less dew yield therefore putting lichens at risk. (Feng et al. 2021).

Though lichens are all poikilohydric, they can vastly differ in their abilities to resist and survive desiccation (Green et al. 2011) and differences in rehydration and recovery rates from desiccation vary between species. Prolonged desiccation decreased chlorophyll-a counts by 45% and 40% in *Lobaria pulmonaria* and *Peltigera polydactyla,* respectively, but the effects of shorter-term extreme desiccation are not as well researched (Kranner et al. 2003). As previously mentioned, the use of lichen as an indicator species has also been widely studied in terms of how they react to environmental stressors, but how the same stressor, such as direct sun exposure may impact different genera of lichen is little understood.

In this study, we observe water uptake and retention in four genera of lichen at distinct positions along a vertical gradient in the canopy. We tested the water-retentive ability of these lichens when exposed to direct sunlight to imitate the loss of canopy cover and compared it to how they perform in shaded regions. Additionally, we imposed extreme temperature conditions and observed how this impacted water uptake. Our hypotheses were informed based on where we observed the genera naturally occurring. We expected *Usnea* to have the highest water retention rate as it typically can be found higher in the canopy, where it is naturally exposed to more direct sunlight and therefore might be better adapted to desiccation. *Peltigera* on the other hand, would be more sensitive to sun exposure, as they are typically found at the base of trees and on the forest floor, shaded and closely associated with moisture-retaining bryophytes. The genera *Hypogymnia* and *Lobaria* were expected to be intermediate in terms of water retention, as they usually occur in the mid-canopy where they receive less direct sunlight than *Usnea* but more than *Peltigera*. When exposed to extreme temperatures and sunlight, we predict that all four genera would have a reduction in their ability to uptake water due to damage caused by such conditions.

METHODS

2.1 Study Site

We collected our data at Angelo Coast Range Reserve in Mendocino County, California (GPS: 39.7409031, -123.6312794) where the main habitats are old-growth mixed conifer-deciduous forests, meadows, and riparian areas. The elevation of our study area is 421 meters and has an average annual precipitation of 203 centimeters. Despite being less than 15 kilometers east of the Pacific Ocean, Angelo does not get the Pacific marine fog typical of nearby areas due to blocking from the Coast Range. The average August high temperature is 31°C, but summer peak temperatures can exceed 38°C. Our study was carried out for 5 days, from August 2-6th, 2023. During our study the maximum average air temperature was 31.1°C. The relative humidity was 54% on average but during the day in the sun, the relative humidity dropped to 19%. Climate data was obtained from the Western Regional Climate Center (WRCC).

Four genera of lichen within the old-growth forest were chosen for our study: *Usnea spp., Peltigera sp., Lobaria sp.,* and *Hypogymnia spp*. While we were unable to identify all samples to the species level, we ensured that samples within the genera had similar morphology. These particular taxa were chosen for their overall abundance as well as the variability in their vertical distribution within the environment. *Usnea* are commonly found high in the upper branches of trees (Sharnoff 2014). *Peltigera* is most common in moist environments, at the base of trees, or on soil-cut banks and mossy rocks (Sharnoff 2014). *Lobaria* are typically found in well-lit sites of Coast Range forests (Sharnoff 2014) and *Hypogymnia* are commonly found on conifer bark (Sharnoff 2014). *Usnea* was found high in the canopy and collected from fallen branches, *Peltigera* low in the understory and carefully scraped off of rocks and buildings, and *Lobaria* and *Hypogymnia* were found and collected in the middle trunks and lower-hanging or fallen branches.

2.2 Experimental Design

All lichen samples were separated from bryophytes and substrates, cleared of debris, and then stored in paper bags as recommended by the U.S. Forest Service to prevent deterioration until they were used. Each trial had one sample from each genus to ensure the consistency of environmental conditions throughout testing periods. We studied a diverse sample set as *Usnea spp.* ranged from 0.34 g to 1.69 g in weight, *Peltigera sp.* 0.1 g to 2.3 g, *Hypogymnia spp.* 0.13 g to 2.13g, and *Lobaria sp.* 0.26 g to 1.35 g. Most samples were broken apart from larger collected individuals to fit the size of our weight scale (100 g). We ran three experiments to test the water retention ability of the lichen: ambient conditions overnight, sun and shade in the day, and manipulated extreme temperature in the sun.

To explore the natural absorption of non-rainfall water, such as dew and atmospheric water vapor, for each genus, mass was recorded (in grams) before individuals were left outside overnight (N = 13). Their mass was then reweighed the following morning to record the amount of water gain.

To test the effects of sun exposure on drying for each species, we conducted a sun versus shade experiment in natural conditions (trials: $N_{sun} = 13$, $N_{shade} = 13$) and a separate sun experiment under intense temperature (N=13). All samples were soaked for 5 minutes, which we determined to be the time they stopped gaining water weight. They were then manually shaken until no water droplets fell. Mass in grams was recorded immediately after saturation (0 minutes) and samples were placed on separate aluminum trays in one of three treatment locations: in full shade with 100% canopy cover, in direct sunlight with 0% canopy cover, or on a high-temperature surface. For our natural condition experiment, we continued to weigh them at chosen time increments (2, 5, 8, 10, 15, 20, 40, 60, 90, and 120 minutes) as the time the lichen had been drying since saturation. The samples in our extreme experiment were left in direct sunlight where the surface temperatures ranged between 48°C to 65°C throughout the day. After 9 hours, we resoaked, dried, and weighed the lichen to see if there were changes in their absorption ability following extreme temperature exposure.

2.3 Data Analysis

For our ambient absorption treatment, a one-way ANOVA was used to evaluate the relationship between genus and water weight each sample gained overnight. A two-way ANOVA was used to test the effect of sun exposure, genus, and the interaction of sun exposure and genus on water retention at all chosen time increments (2, 5, 8, 10, 15, 20, 40, 60, 90, 120 minutes). A Tukey pairwise comparison test was then used to examine differences between genera. For the extreme sun experiment, we ran a one-way ANOVA to test for the effect of genus on percent water retention before and after desiccation. All statistical analysis was conducted using the software program JMP v16 (SAS Institute Inc, 2021).

RESULTS

Overnight, all genera absorbed more water in the morning compared to their weight the night before (N = 13, F ratio = 1.397, p = 0.2549). Between genera, there was no difference in the amount of water they absorbed. After saturation for the sun and shade trials, *Hypogymnia.* absorbed an average 244% of its weight, *Lobaria* 251%, *Peltigera* 290%, and *Usnea* 196%.

We found there was an effect of sun and shade on the ability of the lichens to absorb and retain water from 2 to 90 minutes (Table 1, see "Treatment"). At 120 minutes, there was no longer an effect of sun and shade on water retention. All genera lost more water at a faster rate in the sun than in the shade (Fig. 1). For some genera, however, sun exposure had more of an effect than others (Table 1, see "Genus, Test Effect"). *Usnea* retained the highest percentage of its max weight over time while *Peltigera* retained the lowest percentage. *Hypogymnia* and *Lobaria* held onto their water at similar rates in the sun and the shade (Fig. 1).

There was no effect of extreme temperature on the ability of each lichen genus to absorb water (Fig. 2). Anecdotally, however, we did observe visual bleaching symptoms on some samples of *Lobaria.* These were observed as bright discolored areas on the samples. We also noticed minor lobe curling in some *Peltigera* samples and more obvious curling across all *Lobaria* samples.

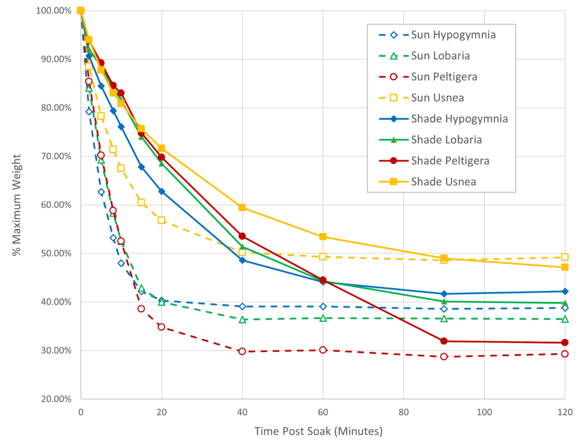

Figure 1. The effect of sun or shade treatment on the drying rates across lichen genera Percent mean maximum weight of each lichen genus over time following soak was plotted for two drying treatments: in the shade vs in the sun. All genera dried out faster in the sun but *Usnea*, the high canopy genus, was able to dry out at a far slower rate than the other genera. *Peltigera*, the understory genus, was the most affected by the sun treatment and lost mass far quicker than it did in the shade. *Lobaria* and *Hypogymnia*, the mid-level genera, had intermediate effects of sun exposure on drying rate.

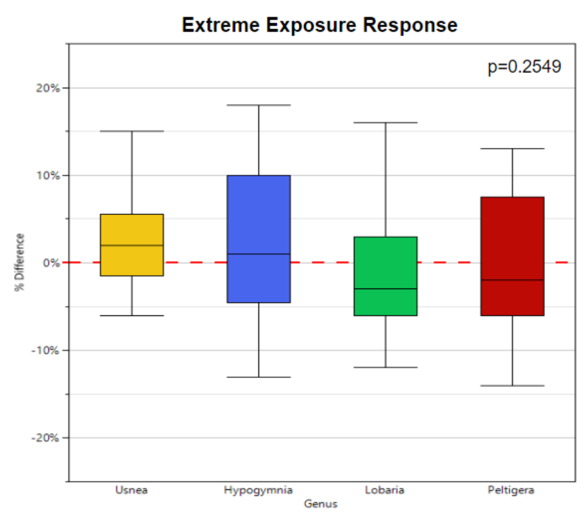

Figure 2. Difference in water absorption before and after exposure to extreme temperatures The percent difference in water absorbed by each genera before and after exposure to extreme temperature was plotted to test the effects of extended drought on the ability to obtain water. There was not an effect across all genera.

Table 1. Effect of genus, sun, and shade on lichen water retention Statistical values of the 2-way ANOVA tests run for the effect of genus, treatment (Sun=Sun, Shade=Sh), and the interaction of genus and treatment against % of water absorbed at each time increment. *Notes:* Each treatment type (Sun=Sun, Sh=Shade) had the same sample size unless specified. The test effect summarizes how each genus compares to each other (U=*Usnea,* P=*Peltigera,* H=*Hypogymnia,* and L=*Lobaria).*

Time (min)	Variable	Sample Size	F Ratio	p-value	Test Effect
2	Genus	26	4.61	**0.0046**	U,P > H; L = U,P,H
	Treatment	13	44.05	**<0.0001**	Sun > Sh
	Genus*Treatment	26	0.96	0.4158	
5	Genus	26	5.93	**0.0009**	U,P > H; L = U,P,H
	Treatment	13	17.60	**<0.0001**	Sun > Sh
	Genus*Treatment	26	2.85	**0.0413**	
8	Genus	25	6.15	**0.0007**	U > H; U = P, L; H = P, L
	Treatment	N_{shade} =12; N_{sun} =13	154.31	**<0.0001**	Sun > Sh
	Genus*Treatment	25	3.91	**0.0112**	
10	Genus	25	8.99	**<0.0001**	U > P, L, H; P = L, H
	Treatment	N_{shade} =12; N_{sun} =13	230.53	**<0.0001**	Sun > Sh
	Genus*Treatment	25	5.76	**0.0012**	
15	Genus	26	9.84	**<0.0001**	U > P, L, H; P = L, H
	Treatment	13	208.01	**<0.0001**	Sun > Sh
	Genus*Treatment	26	5.73	**0.0012**	
20	Genus	26	11.82	**<0.0001**	U > P, L, H; P = L, H
	Treatment	13	219.08	**<0.0001**	Sun > Sh
	Genus*Treatment	26	6.44	**0.0005**	
40	Genus	26	13.81	**<0.0001**	U > P, L, H; P = L, H
	Treatment	13	80.98	**<0.0001**	Sun > Sh
	Genus*Treatment	26	4.59	**0.0048**	
60	Genus	26	19.85	**<0.0001**	U > P, L, H; P = L, H
	Treatment	13	32.69	**<0.0001**	Sun > Sh
	Genus*Treatment	26	2.85	**0.0412**	
90	Genus	22	93.88	**<0.0001**	U > H, L, P; H, L > P
	Treatment	N_{shade} =10; N_{sun} =12	10.31	**0.0019**	Sun > Sh
	Genus*Treatment	22	0.83	0.4839	
120	Genus	19	64.07	**<0.0001**	U > H, L, P; H, L > P
	Treatment	N_{shade} =9; N_{sun} =10	3.68	0.0591	
	Genus*Treatment	19	1.99	0.1233	

DISCUSSION

Body text. For our overnight experiment, we found that all genera had about equal proportions of water gained despite them being very different morphologically and being located at different vertical positions in the canopy. Despite this, they did differ in how much water they absorbed when soaking, such as in our sun vs. shade experiment. This is interesting because it seems that water vapor is collected in a similar manner across the genera, however, how they absorb liquid water is likely different.

In the Sun vs. Shade experiment, we did find that there was an effect of genus on water retention and that the effects fell in line with our predictions that the higher canopy genus *Usnea* would have the highest water retention, the lower understory genus *Peltigera* would have the lowest, and that mid-level canopy genera *Hypogymnia* and *Lobaria* would have intermediate water retentive abilities. Canopy position, however, may not be the only variable at play. Perhaps these differences can also be explained by their morphology or community composition across the gradient. *Usnea* and *Hypogymnia* are lichens with narrow branching limbs while *Peltigera* and *Lobaria* are characterized by large flat lobes. Additionally, bryophytes were more commonly noticed at the base and trunks of trees in association with *Peltigera*, and also at times with *Lobaria*. The presence of bryophytes may increase relative humidity directly around these genera, possibly reducing their need to hold water since it is more often readily available. Further research may look into the effects of surface area or morphological characteristics on water retention across lichen taxa and community composition differences along the vertical gradient.

From our findings, we did not see an effect of extreme sun exposure on the water uptake ability across lichen genera. This is likely explained by the fact that our samples may not have been exposed to direct sunlight long enough to observe an effect. Previous findings suggest that irreversible damage accumulates with time (Gauslaa and Solhaug 1996 and 1999) and a longer study may be needed to confirm the effect. We did observe, however, notable signs of bleaching on some samples of *Lobaria.* Despite water uptake not being a concern, it became evident in this genus that prolonged sun exposure had damaging effects. Moreover, the curling behavior of *Lobaria* lobes has been previously investigated as a means of mitigating foliar damage. This phenomenon was observed in all examined *Lobaria* samples and in some *Peltigera* samples. To delve deeper, future research could investigate potential bleaching effects and other associated morphological changes. By closely observing these transformations, researchers could gain insights into the resilience of different taxa. Studying lichen protective mechanisms may offer a deeper understanding of lichen composition changes across the environment.

Our study's findings may help frame predictions as to how lichen will respond to deforestation and current climate trends of drought and rising temperatures. The response of the high-growing genus *Usnea* to these conditions can imply that other genera in high canopy positions may fare better in long periods of drought and when exposed to more sun. We might also begin to observe a shift in lichen distribution and community composition to *Usnea* and other sun-tolerating species dominated as the habitats become more hot, dry, and low-shade. On the contrary, shaded, low-growing genera such as *Hypogymnia*, *Lobaria, and Peltigera* are at a higher risk of the effects of sun exposure. With the current trends of logging, the canopy cover that they depend on is declining. With this, we can expect a similar decline in their populations. The suggested negative effects resulting from deforestation can offer insights for forest management strategies, encouraging a shift towards prioritizing forest thinning over complete clear-cutting. This approach aims to safeguard against the total loss of canopy cover.

ACKNOWLEDGMENTS

We want to acknowledge Tim Miller, Renske Kirchholtes and Lydia Dean for their guidance and input throughout this project as well as the course assistants Hannah McCafferty and Sophia Puliatti all of their hard work.

This work was performed at the Angleo Coast Range Reserve, doi:10.21973/N3R94R This reserve is part of the University of California Natural Reserve System.

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