Understanding the Relationship Between Light Availability and Epiphytic Lichen Ecology: Canopy Openness, Photosynthetically Active Radiation, and the Role of the Host Tree Species

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Abstract

We investigated whether small-scale differences in light availability are correlated to ephiphytic lichen distribution in a hardwoods forest. We studied the relationship of canopy openness and photosynthetically active radiation (PAR) to the abundance, diversity, and community composition of epiphytic lichens on balsam firs (*Abies balsamea*) and sugar maples (*Acer saccharum*). Overall, sugar maples hosted significantly greater lichen cover than balsam firs, and their trunks were associated with significantly lower photosynthetically active radiation (PAR) exposures. However, no significant relationships were found between light availability and lichen community characteristics on sugar maples. We also found that canopy openness and PAR show dissimilar relationships to epiphytic lichen community characteristics. While canopy openness showed a significant positive correlation to lichen species diversity on balsam firs, we found no relationship between PAR and lichen diversity or abundance on either species. The differences in the impacts of the two measurements of light availability may be due to their distinct characteristics: canopy openness accounts for the spatial distribution access to sunlight without regard to its intensity, while PAR measured the instantaneous intensity of the light, integrated over the entire space measured in the immediate vicinity. Species containing the photoprotectant usnic acid were more likely to be found at higher levels of canopy openness and PAR on balsam firs. Because light is limited within a forest, we were unable to determine whether very high light availability diminishes lichen cover and diversity at very high intensities or degrees of openness.

Introduction

Lichens function as the dominant vegetation on about 8 percent of earth's terrestrial area, exerting key impacts on their environment and on the growth and development of other

organisms (Brodo et al. 2001). Lichens are major contributors to nitrogen budgets in North America (Forman 1977) because they fix nitrogen (Nash 1996), and in some ecosystems they contribute as much nitrogen to the soil as precipitation (Forman 1975). Because deforestation removes not only trees but also the lichens that inhabit them (Benavides and Gutierrez 2011) epiphytic lichens and the factors that influence their distribution are of particular interest.

The distribution of any forest-dwelling epiphyte is subject to both stand-level (forest age, soil moisture, and tree species) and substrate-level characteristics (tree age, bark pH, and nutrient content) (Strazdina 2010). Although lichens are generally ubiquitous in a northern hardwoods forest, their small-scale distribution and abundance depend on each species' compatibility with these substrates and atmospheric conditions as well as their biochemical response to those conditions. For example, on the stand level, stand age (Jüriado et al. 2009), incline (Hauck et al. 2007), and stand continuity (Selva 1994) all have been correlated to lichen abundance, species richness, and community composition. On the substrate level, tree species (Logsdon 2010, unpublished data; Uliczka and Agelstam 1999), tree age (Rainus et al. 2008; Johannson et al. 2007), bark pH (Jüriado et al. 2009) metal concentration in the bark (Hauck and Javkhlan 2009), moisture-holding capacity of the bark (Selva 1994), and branch versus trunk habitat (Lang et al. 1980) have important relationships with lichen abundance and diversity.

Light availability can be considered both a stand-level and substrate-level condition. Lichen species diversity has been shown to vary significantly among host tree species (Logsdon 2010, unpublished data; Uliczka and Agelstam 1999), and this could be due to light availability because tree species differ in their architecture and thus afford differ in the amounts of light to their epiphytes. Additionally, the age and species composition of the surrounding tree stand also influence how much light can reach a lichens residing on tree trunks (Selva 1994). Because

lichens are composed of not only a mycobiont (a fungus) but also a photosynthetic phycobiont (either green algae or cyanobacteria), they are in a position to respond in a significant ways to changes in light availability. Because small-scale natural disturbances and growth patterns can cause the understory light environment to vary both spatially and temporally (Gauslaa et al. 2006), they may be instrumental in maintaining the diversity, distribution, and relative abundance of epiphytic lichens.

Lichen species differ in their in their tolerance to shade and light. While lack of light limits lichens' ability to photosynthesize (Gaio-Oliveira et al. 2004), light can also be an environmental stress. Some species are more susceptible to light stress than others (Gauslaa and Solhaug 1996). Certain species thrive in clearcuts and exhibit near zero growth in shaded areas, while other species exhibit relatively high gain in biomass under closed canopies and lose biomass in sun-exposed areas due to chlorophyll degradation (Gauslaa et al. 2006). Thus, the number and composition of species is likely subject to the amount of light available.

Such differential susceptibility to high light conditions between lichen species can depend on a lichen's biochemical and biophysical photoprotective mechanisms. For example, green algae phycobionts produce the photoprotective pigment zeanthanin via the xanthophyll cycle, but cyanobacteria lack this cycle (Demmig-Adams 1990a), and lichens with cyanobacteria phycobionts have been found to recover more slowly from exposure to high light (Demmig-Adams 1990b). Also, foliose (leaf-like) lichens may thrive in higher light conditions than fruticose (shrub-like) lichens because light-induced dessication induces leaf curling that protects the thallus from photoinhibition of photosynthesis (Bartak et al. 2006).

Lichens also differ in their ability to synthesize photoprotectants. These crystallized secondary metabolites absorb UV radiation (Bjerke et al. 2002) and protect the thallus from

photoinhibition (Solhaug and Gauslaa 1996). Lichens containing usnic acid, a widespread photoprotectant (Cocchietto et al. 2002), have shown to respond to ultraviolet irradiance and PAR by increasing synthesis of this chemical (Bjerke et al. 2002). Usnic acid-containing species have shown to dominate in a high-light geographic region (Hauck et al. 2007), yet whether the distribution of usnic-acid containing species is indeed related to light availability remains to be explored. Both usnic acid-containing lichens and non-usnic acid-containing lichens have been identified there, so we intend to investigate whether the likelihood of their presence increases with higher levels of light.

Because light is both required for lichen photosynthesis and can cause stress at high levels, we hypothesized that with an increase in PAR levels, lichen abundance would increase and then decrease in a unimodal fashion. Furthermore, because species vary in their sensitivity to light, we hypothesized that with an increase in PAR levels, lichen diversity would increase and then decrease in a unimodal fashion and that shifts will be observed in the relative proportions of individual lichen species. Finally, we hypothesize that the usnic-containing species are more likely to be found at sites exposed to higher levels of PAR.

Materials and methods

Study area

We conducted this study in June and July 2011 at the University of Notre Dame Environmental Research Center (UNDERC), a mixed deciduous and coniferous northern hardwoods forest in Vilas County, Wisconsin and Gogebic County, Michigan. Among other species, sugar maple (*Acer saccharum*) and balsam fir (*Abies balsamea*) are found with variable density and distribution.

Selecting the Unit of Replication

Because habitat conditions may influence the diversity, abundance, and species composition of supported lichens, only lichens growing on tree trunks were used in this study. Significant variation in lichen species diversity has been found among certain host tree species at UNDERC (*Acer saccharum>Batula papyrifera>Populus tremuloides*, Logsdon 2010), so samples were taken only from *Acer saccharum* (sugar maple) and *Abies balsamea* (balsam fir). The relationships between light availability, total lichen abundance, and lichen species diversity were analyzed separately for each tree species.

To assume that samples are independent, a grid was drawn on a map of UNDERC with gridlines every 125 meters, and a maximum of one sugar maple and one balsam fir were sampled per 125 x 125 m plot. To avoid areas susceptible to aeolien deposition, roads and early successional areas were avoided. Sample trees were selected by entering one of the 125 x 125 m plots adjacent to a road and then walking away from the road for at least 50 meters in a randomly chosen direction and choosing the first live, standing sugar maple and balsam fir greater than 15 cm in diameter were encountered. If either no sugar maples or no balsam firs were encountered in the plot, the next adjacent plot was investigated until the previously unencountered species was encountered. Selection proceeded this way in the next non-adjacent plot and until 22 trees of each species were sampled.

Measuring light availability

PAR was measured on the selected trees using an L-100 DataLogger PAR meter (Li-Cor) and measured in µmol m^{-2} s^{-1}. The sensor was held horizontally 1 meter from the base of the tree on the north and south aspects. Measurements were taken during peak intensity (between 11:00 A. M. and 2:00 P. M.) on two separate clear days, and these measurements from these days were

averaged for analysis of variance and regression. We measured canopy openness with a spherical densiometer held against the north and south aspects of each tree sampled.

Lichen Sampling

Total lichen cover and individual lichen species cover was estimated via a grid system (see Stofer et al. 2003). A 10 x 54 cm frame containing five 10 x 10 cm quadrats separated by 1 cm was placed on the north and south sides of the with the bottom 10-cm side placed at 1 meter above the ground. Lichen cover within those quadrats was estimated with the aid of a 10 x 10 cm cellophane grid divided into 0.25 x 0.25 cm squares. A small sample of each lichen species was removed, without separating it from the bark to which it clung, and the samples will be allowed to dry overnight for identification using a light microscope and spot tests with 10% KOH and bleach.

Statistical analysis

Because this was an *in situ* field study in which sampling trees are subject to a host of microclimatic conditions that vary by site, we chose an alpha value of 0.08. To normalize data for regression analyses, percent canopy openness was log[log(arcsine)+2]-transformed and the averages of the two PAR measurements were log-square-root transformed and tested for normality with Lilliefors test. Although PAR and canopy cover values were not fully normally distributed, correlation analyses were conducted under the assumption that the test is robust enough to withstand somewhat nonnormal inputs. Total lichen cover values per sample were divided by the total area measured per sample (500 cm^2) to calculate percent cover for each site, and these values were log-arcsine-square-root-transformed for normal distribution as determined by a Lilliefors test.

We conducted a multivariate analysis of variance (MANOVA) to determine the relationship between tree species on canopy openness, lichen abundance, lichen species diversity, and each study site's averaged instantaneous PAR value.

Because lichen communities differ significantly with tree species (Uliczka and Angelstam 1999) correlation analyses were conducted separately for *Acer saccharum* and *Abies balsamea* to determine the effects of PAR and canopy openness on total lichen abundance and species diversity.

We employed binomial logarithmic regressions determine whether the presence or absence of usnic acid-containing was significantly related to species canopy openness and PAR.

Results

Epiphytic lichens grew on every tree encountered. In total, 31 species were identified. Among these were three usnic acid-containing species: *Flavoparmelia caperata*, *Lecanora thysanophora*, and *Lecanora symmitica*.

Total lichen abundance and PAR intensity at the trunk differed significantly between tree species (Table 1). In the 500 cm^2 plots measured *Acer saccharum* (*As*) hosted significantly greater cover of lichens (165.0 ± 12.78) than did *Abies balsamea* (*Ab*, 85.110 ± 22.720) ($F_{1,88}$=10.140, p =0.002, Fig. 1). The two tree species did not differ significantly in lichen species diversity (*As* 0.742 ± 0.072; *Ab* 0.819 ± 0.078; $F_{1,88}$=0.520, p=0.473; Fig. 2). *Abies balsamea* was subject to significantly higher PAR intensity than *Acer saccharum* (*Ab*, 11.210 ± 1.080; *As* 7.705 ± 0.607; $F_{1,88}$=3.384, p = 0.0692; Fig. 3), although the species did not differ significantly in canopy openness (*Ab*, 65.150 ± 21.40; *As*, 24.33 ± 7.299; $F_{1,88}$=0.223, p = 0.638; Fig. 4).

We found significant relationships between light availability and lichen community characteristics (total abundance, species diversity, and community composition) only on *Abies balsamea* (Table 2). No significant correlations were found between canopy openness and total lichen abundance for either *Acer saccharum* species (*As* p=0.081, r= 0.272) or *Abies balsamea* (*Ab* p=0.898, r= 0.019). There was a significant positive correlation on *A. balsamea* between canopy openness and lichen diversity (*Ab* p = 0.008, r = 0.386; *As* p = 0.951, r= 0.010). Total lichen cover showed no significant relationship to PAR intensity (*Ab* p = 0.469, r= 0.110; *As* p = 0.488, r= 0.107; Fig 12), nor did lichen species diversity (*Ab* p=0.119, r= 0.233; *As* p=0.111, r=0.243; Fig. 13).

Canopy openness and PAR were significantly correlated with the presence of usnic acid-containing species on *A. balsamea* (canopy openness, p = 0.062, R^2= 0.103; PAR, p=0.059, R^2= 0.106) but not on *A. saccharum* (canopy openness, p = 0.952, R^2< 0.0001; PAR, p=0.758, R^2= 0.005; Table 3).

Discussion

The results of this study neither support nor reject our hypothesis that lichen abundance and diversity would respond to increases in light availability in a unimodal fashion. Due to limited availability overall within the forest, we were unable to determine whether the upward trends we observed for species diversity also had downward components at higher, photochemically-inhibitory values of PAR. Whereas some studies found that photosynthetic efficiency was lower when lichens were exposed to 1800 µmol m^{-2} s^{-1} than 600 µmol m^{-2} s^{-1} (Barták et al. 2008), the intraforest light measurements in this study only once exceeded 600 µmol m^{-2} s^{-1}; likewise, canopy openness at our study sites never exceeded 30%. To further probe our hypothesis, this study should be repeated in a forest with greater variability in light

availability. In future studies of light availability and lichen distribution, it might be appropriate to non-randomly choose sites based on light in order to achieve a greater distribution of sample plots at higher light distribution.

Despite lack of a significant difference in canopy cover, we found that significantly higher levels of PAR were available to epiphytes residing on balsam firs. This may be due to differences in the branch architecture or leaf structure (broad-leaf versus needle) between tree species. Despite lower PAR values overall, lichen abundance was significantly higher on sugar maples. Because sugar maple bark is much rougher than balsam fir bark, it provides a greater surface area for lichen attachment and a more stable substrate for growth (Uliczka and Angelstam 1999). This may account for the significantly higher lichen cover found on sugar maples than balsam firs, whose bark is fairly smooth. Regardless of whether trunk corrugation was key in determining lichen abundance, the lack of a significant increase in lichen cover and diversity with PAR on sugar maples affirms that the environmental factors that limit lichen abundance are separate from those that limit species diversity.

At the scales we studied, light availability was found to correlate with lichen diversity and community composition, but whether light significantly influenced lichen ecology was dependent upon host tree species. Specifically, lichen species diversity increased significantly with greater canopy openness on balsam firs, but not on sugar maples. Additionally, significant increases in the presence of usnic acid-containing of lichens increased with both PAR intensity and canopy openness, but these relationships too were only seen on balsam firs. These results suggest that on certain tree species, substrate-level characteristics (such as bark pH and micronutrient concentration) overpower stand-level characteristics (such as canopy cover and PAR intensity) in their ability to limit lichen species diversity and community composition.

Bark pH is one substrate-level characteristic that may make epiphyte diversity on balsam firs more susceptible to small-scale changes in light than sugar maples. Because photoprotective lichen substances have shown to be damaging to lichens when exposed to low pH (Hauck and Jürgens 2008) the notably acidic bark of a balsam fir tree (Schmull and Hauck 2003) may exclude a number of photoprotected lichen species. The remaining lichen species may be highly sensitive to light availability, and this may be to explain why lichens' light dependence was restricted to balsam firs. Our finding that balsam trunks are exposed to significantly higher intensities of PAR, compounded with balsam fir-bound lichens' potentially greater susceptibility to light, may suggest why significant trends differences in lichen diversity and community composition appeared at the scales of light variation we measured in this experiment.

The finding that total lichen abundance and diversity do not increase with higher levels of PAR underscores the validity of the finding lichens containing usnic acid are significantly more likely to be found in higher-light environments. These lichens' relationship to PAR worth noting because whether usnic acid is sensitive to PAR in addition to UV has been debated (Rikkenen 1995; Hauck 2011). Laboratory studies suggest that these lichens respond to PAR by upregulating usnic acid synthesis (Bjerke et al. 2002), but whether this biochemical ability is manifested ecologically by limiting certain species' distribution was previously unexplored. Our results suggest that PAR levels are correlated to the distribution of lichens containing usnic acid; however, we must be cautious in suggesting a causal relationship, because higher levels of PAR in a natural environment may be accompanied by higher levels of ultraviolet radiation. Further investigations of this chemical's ecological significance should take both UV radiation and PAR measurements into account to distinguish their relationships to lichen distribution. In general, further research on whether abundance and diversity of usnic acid-containing species, as well as

species containing other photoprotective secondary metabolites, would contribute to the understanding of the ecological role that these compounds play.

The difference in the influence of canopy cover and PAR on epiphytic lichen abundance and diversity emphasize that light availability is a multifaceted concept with intensity, duration, spatial patchiness components at all wavelengths. In this study, canopy openness represented the spatial patchiness aspect, while PAR measurements represented the intensity component. These components were distinct in their effects on the abundance and diversity of forest-dwelling epiphytic lichens, again confirming that abundance and species diversity are limited by separate factors.

Conclusions

This study emphasizes the impact that the intimate biotic relationship with tree bark may have on an epiphyte's susceptibility to other environmental factors. Just as substrate-related variables such as host tree age and bark pH do not affect the abundance and community composition of lichen species uniformly for all tree species (Juriado et al. 2009), neither do stand-related effects such as PAR exposure and canopy cover.

Because lichens contribute to forest biogeochemical cycles through nitrogen fixation (Nash 1996), the dependence of light's impact on tree species may help determine which forest types have biogeochemical cycles susceptible to light availability. Further investigation is needed to test the hypothesis that a forest's tree species composition determines whether light availability has a significant impact on nitrogen inputs from lichens.

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Tables and Figures

Table 1. Relationship between host tree species and characteristics of resident lichen communities. *Note:* levels of significance: ***P<0.08**, ****P<0.008**; abbreviations: *Ab=Abies balsamea, As=Acer saccharum.*

	P-value	F-ratio
Abundance	**0.002****	$F_{1,88}$=10.140
Diversity	0.473	$F_{1,88}$=0.520
PAR	**0.0692***	$F_{1,88}$=3.384
Canopy openness	0.638	$F_{1,88}$=0.223

Table 2. Relationship between light availability and lichen community characterisitics; ***p<0.08**.

Canopy Openness	*Abies balsamea*		*Acer saccharum*	
	P-value	r	P-value	r
Abundance	0.898	0.019	0.0811	0.272
Diversity	**0.008***	0.386	0.951	0.0097

PAR	*Abies balsamea*		*Acer saccharum*	
	P-value	r	P-value	r
Abundance	0.469	0.11	0.488	0.107
Diversity	0.119	0.233	0.111	0.243

Table 3. Likelihood of increased presence of usnic acid-containing lichens at higher levels of light; ***p<0.08**.

	Abies balsamea		*Acer saccharum*	
	P-value	R^2	P-value	R^2
Canopy openness	**0.062***	0.103	0.952	<0.0001
PAR	**0.059***	0.106	0.758	0.005

Figures

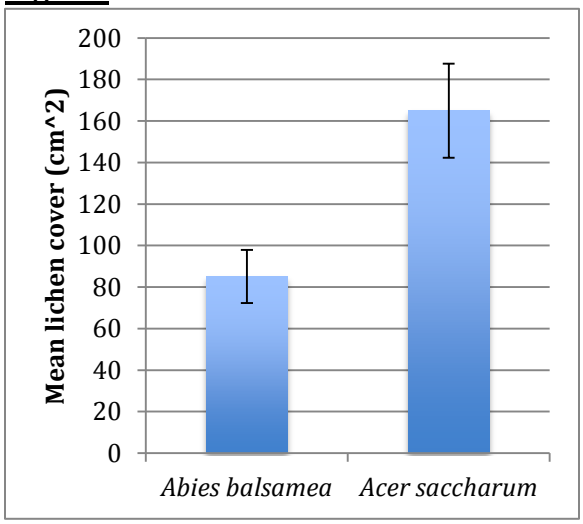

Figure 1. Comparison of lichen cover between *Abies balsamea* and *Acer saccharum*. *Acer saccharum* hosted significantly greater cover of lichens (165.0 ± 12.78) than did *Abies balsamea* (*Ab*, 85.110 ± 22.720) ($F_{1,88}$=10.140, p = 0.002)

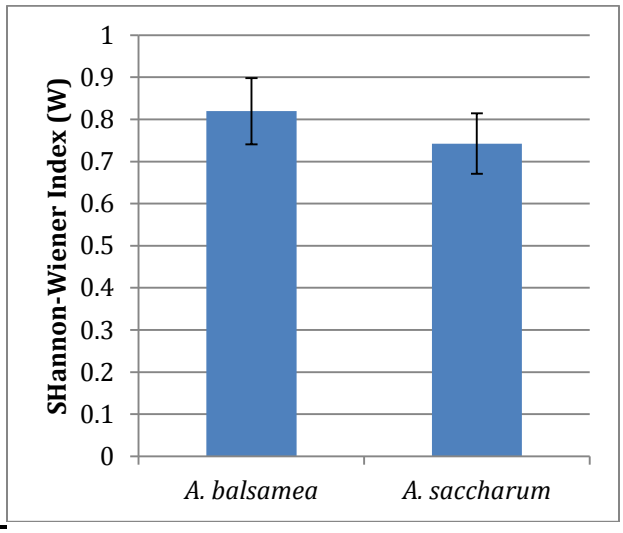

Figure 2. Comparison of species diversity between *Abies balsamea* (0.819 ± 0.078) and *Acer saccharum* (0.742 ± 0.072) ($F_{1,88}$=0.520, p=0.473).

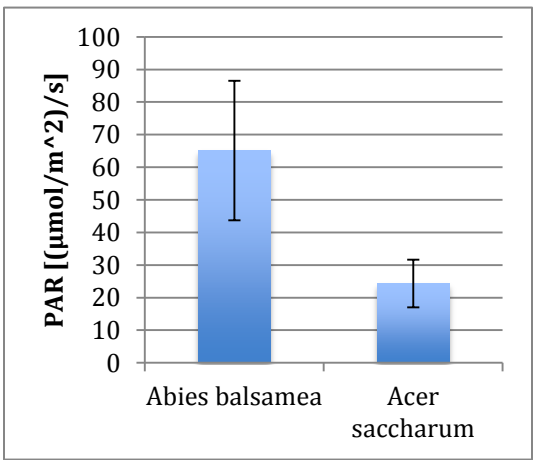

Figure 3. Comparison of PAR exposure between *Abies balsamea* (11.210 ± 1.080) and *Acer saccharum* (7.705 ± 0.607) ($F_{1,88}$=3.384, p = 0.069).

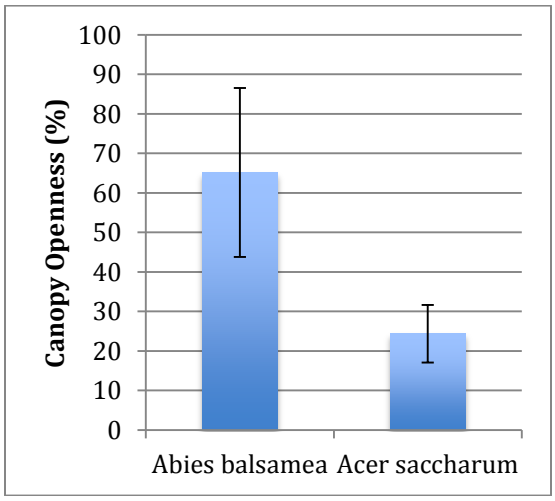

Figure 4. Comparison of canopy openness between *Abies balsamea* (65.15 ± 21.40) and *Acer saccharum*. (24.33 ± 7.299) ($F_{1,88}$=0.223, p = 0.638).