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Source: The Bryologist, 107(2):163-172. 2004.

Published By: The American Bryological and Lichenological Society, Inc.

DOI: [http://dx.doi.org/10.1639/0007-2745\(2004\)107\[0163:CFAREN\]2.0.CO;2](http://dx.doi.org/10.1639/0007-2745(2004)107[0163:CFAREN]2.0.CO;2)

URL: <http://www.bioone.org/doi/full/10.1639/0007-2745%282004%29107%5B0163%3ACFAREN%5D2.0.CO%3B2>

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Contrasting Fundamental and Realized Ecological Niches with Epiphytic Lichen Transplants in an Old-Growth *Pseudotsuga* Forest

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Abstract. *Three lichen transplant experiments examined the effect of height in the canopy on the growth rates of four lichen species, using the Wind River Canopy Crane in an old-growth Pseudotsuga-Tsuga forest in the Cascade Range of southern Washington. A total of 40 to 100 transplants were used for each species, and growth was measured over a one-year period. We then compared the vertical profiles of growth rates to the vertical profiles of natural abundance. The vertical pattern of abundance of Letharia vulpina more or less corresponded with the vertical pattern in growth rates. The other two species for which we had vertical profiles in both abundance (realized niche) and growth of transplants (fundamental niche) showed some potentially important discrepancies between the two niche spaces. Usnea peaked in abundance at the highest levels in the canopy, but appeared to reach a maximum growth rate at about 30 m. The treetop environment is evidently ideal for Usnea, and its capacity for rapid growth suggests that it is a vigorous competitor. Lobaria oregana peaked in abundance at 25–30 m, while its growth rates were maximal considerably higher in the canopy, at 40–45 m. We must conclude that some aspect of establishment or competition has a pronounced negative effect on L. oregana above about 35 m in the 65-m-high canopy. Further experiments are needed to test the hypotheses that these cyanolichens fail in the upper canopy because of competition, or that they fail by an inability to tolerate rare microclimatic extremes, such as low temperatures.*

Keywords. Competition, epiphytes, fundamental niche, *Letharia*, lichen, *Lobaria*, old-growth forests, transplants, *Usnea*.

Vertical stratification of epiphytes is well documented in forests around the world. Floristic surveys along vertical gradients from the understory to the upper canopy consistently reveal distinct distribution patterns and shifts in epiphyte communities (e.g., Arseneau et al. 1997; Bates 1992; Cornelissen & Ter Steege 1989; Ellyson & Sillett 2003; Kantvilas & Minchin 1989; Komposch & Hafellner 2000; McCune 1993; Pike et al. 1975; Rosso et al. 2000; Sillett 1995; Sillett & Rambo 2000). A number of studies have focused on describing the vertical distribution of the non-vascular epiphyte community in the old-growth forest surrounding the Wind River Canopy Crane in Washington (e.g., Clement & Shaw 1999; Lyons et al. 2000; McCune et al. 1997; McCune et al. 2000). In this particular forest, bryophytes dominate the understory and lower canopy, cyanolichens reach peak abundance in the mid canopy, and alectoroid and green algal foliose lichens dominate the upper canopy.

While it is relatively straightforward to describe

vertical patterns of epiphyte distribution, the underlying causes of these patterns are more elusive. Possible explanations include vertical gradients of light, moisture, and wind (Campbell & Coxson 2001; Coxson & Coyle 2003). A primary difficulty facing attempts to explain epiphyte distribution is that all environmental factors covary inextricably. Furthermore, quantifying the myriad light, moisture, and wind conditions that exist over spatial and temporal scales meaningful to forest epiphytes is daunting.

An alternative approach towards understanding the vertical distribution of epiphytes is to treat the vertical gradient as a complex suite of factors, and consider how epiphytes respond to this complexity. The vertical gradient is simplified to one variable (i.e., “canopy position”) and the research question becomes: how well do species perform in different canopy positions?

We can describe organismal responses to canopy position at three levels of integration: differences in growth rates, abundance, and individual physiological parameters. 1) By measuring growth rates with transplanted pendants, we exclude problems of establishment and competition. This allows us to as-

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sess the range of canopy positions that a species is physiologically capable of living in—its fundamental niche (Hutchinson 1957). 2) Differences in current abundance reflect a history of establishment, competition, and mortality in response to past environment and disturbance. Quantifying patterns of distribution and abundance allows us to assess the portion of the fundamental niche actually used by a species—its realized niche (Hutchinson 1957). 3) The physiological level (e.g., vertical patterns of photosynthesis, respiration, and nitrogen fixation) describes short-term organismal response in the absence of problems of establishment, competition, and fragmentation (or mortality). While we have physiological data on one of the species included here (*Lobaria oregana*; Antoine 2001, 2004), we have so far analyzed it in terms of individual environmental parameters (temperature, light, moisture, etc.) instead of canopy position.

In the current paper, we examine vertical canopy position as a single dimension of the niche. Any observed difference between the fundamental niche (as expressed in growth of transplants) and realized niches (distributional pattern) presumably expresses influences of the processes of establishment or competition.

Are the three levels of integration of species performance likely to show the same patterns with canopy position? The answer can be “yes” only if each of the underlying components of life history shows similar patterns with canopy position. For example, if growth rates differ in vertical pattern from establishment rates, then the vertical pattern of growth rates is likely to differ from the vertical pattern in abundance. Similarly, if lichen fragmentation is an important component of lichen mortality, and fragmentation is highest in canopy positions with physiologically favorable conditions (e.g., see Coxson & Coyle 2003), then physiological responses alone cannot fully explain differences in abundance with canopy position.

This paper presents the results of three lichen pendant experiments designed to investigate the effect of canopy position (i.e., height in the canopy) on the performance of four lichen species [*Letharia vulpina* (L.) Hue, *Lobaria oregana* (Tuck.) Müll. Arg., *Lobaria pulmonaria* (L.) Hoffm., and *Usnea* spp.]. In each case, performance is defined as the growth rate of the pendants, which is the change in biomass over a one-year period.

METHODS

Site description.—We used the Wind River Canopy Crane (WRCC) near Carson, Washington to conduct the lichen pendant experiments. The crane site is located within the Wind River Experimental Forest (45°49' N, 121°55' W) in the Gifford Pinchot National Forest. The 4-ha crane

plot is centered on an 87-m-high Liebherr 550 HC construction crane. With its horizontal reach of 85 m, the crane provides access to 10⁵ m³ of old-growth forest canopy.

The dominant canopy trees at WRCC are Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco] and western hemlock [*Tsuga heterophylla* (Raf.) Sarg.]. Western red cedar (*Thuja plicata* Donn.) is also common but typically of smaller stature. Stand age is approximately 500 years, and the site displays old-growth characteristics such as the presence of western yew (*Taxus brevifolia* Nutt.) and an abundance of snags and fallen logs (Franklin & Spies 1991).

Study organisms.—*Lobaria oregana* is a foliose lichen whose yellow-green lobulate thalli drape over branches or grow loosely appressed to bark. In the moist, mid-elevation old-growth forests of the Pacific Northwest, *L. oregana* often accounts for 40–80% of the total epiphytic lichen biomass (McCune 1993; McCune et al. 1997; Pike et al. 1977; Sillett 1995). Nitrogen fixation by *L. oregana* can contribute over 16 kg N ha⁻¹ yr⁻¹ to the forest ecosystem (Antoine 2004). However, *L. oregana*'s sensitivity to air pollution and association with old-growth forests make it vulnerable to human impacts such as urban development and clear-cut logging.

Lobaria pulmonaria is the most widespread *Lobaria* species in the Pacific Northwest. Its greenish sorediate thalli can be found growing on conifers and hardwoods in old-growth forests, oak savannas, and even the large, old trees of municipal parks and college campuses of small towns. *Lobaria pulmonaria* and *L. oregana* are among the 3–4% of lichens representing a tripartite symbiosis among an ascomycete, green alga, and cyanobacterium (Honegger 1991). Although both are cephalodiate species, they are generally included in the “cyanolichen” functional group (McCune 1993).

Letharia vulpina is a fruticose lichen with vivid, charreuse, sorediate thalli. Although this lichen is common and widespread in western North America, west of the Cascade crest it is generally restricted to dry exposed microsites, such as fence posts, open forests on sunny slopes, and the upper canopy. It is particularly abundant on the bare wood of dead branches and snags (McCune et al. 2000).

The fruticose, pendulous, isidiate *Usnea scabrata* can be one of the dominant species in low to mid elevation Pacific Northwest forests. Its pendulous form puts it in the “alectoriid” functional group (McCune 1993). At WRCC it is most abundant in medium to dry bark microsites of the mid to upper canopy (McCune et al. 2000). Here it co-occurs with the similar *U. filipendula* Stirt. Because small individuals are difficult to assign to one of the two species, we combined them (as simply *Usnea*) for the purpose of this paper.

Lichen pendants.—The construction of pendants (McCune et al. 1996) and protocol for assessing lichen performance was identical for all three experiments. We constructed pendants by attaching pieces of lichen thalli to nylon monofilament loops using small amounts of clear silicone sealant. For the foliose species (i.e., *L. oregana* and *L. pulmonaria*), we used a single piece of thallus with an air-dried mass of around 0.2 g for each pendant. For the fruticose species (i.e., *L. vulpina* and *Usnea*), each pendant was comprised of several 10–15 cm strands, again with a total air-dried mass of around 0.2 g. We weighed the lichens before and after pendant construction in order to account for the mass of the non-lichen pendant materials. We used the “sacrificial” method ($n = 5$ for

each species) to correct all pendant masses to an oven-dried basis (McCune et al. 1996).

We placed the pendants in the old-growth forest canopy using the canopy crane. Crane coordinates were taken at each transplant site to facilitate retrieval of pendants the following year. The pendants were attached via plastic cable ties to branches within one m of the outside edge of foliage. The pendant design allowed our lichens to hang slightly beneath the attachment sites in order to eliminate the effects of competition from resident lichens. Experimental design varied among the three studies, and the details are described below. All experiments were conducted over the same one-year period.

Upon retrieval, we held a paper bag underneath each pendant as it was removed to catch any fragments that might otherwise have been lost. The pendants were taken back to the laboratory, air-dried for 24 h, and then weighed with their monofilaments still attached. Once again, a set of five "sacrificial" thalli per species was used to correct the air-dried masses to oven-dried masses. Finally, biomass growth rates were calculated as the percent difference between the initial (i.e., pre-transplant) oven-dried mass and the final (i.e., post-transplant) oven-dried mass. Pendants that were obviously torn or damaged or that were more than two standard deviations below the mean biomass change were not considered in subsequent analyses. Three *Usnea* pendants that had apparently intercepted falling alectorioid lichen fragments were also removed from the dataset.

Experiment 1.—This experiment was designed to test the effect of height in the canopy on the biomass growth of *Lobaria oregana* and *Usnea*. Fifty *L. oregana* and 50 *Usnea* pendants were placed in the canopy. The gondola was lowered into a gap from above, and stops were made at predetermined heights of 43, 33, 23, and 13 m. The lowest height was three m and these transplant sites were accessible from the ground. At each height five transplant sites were arbitrarily chosen based on accessibility and evenness of spacing around the 360° gap opening. Two pendants of each species were hung on the same branch at each site, with a total of 20 pendants per height. The pendants placed from the gondola were all on western hemlock and those placed from the ground were on vine maple (*Acer circinatum*) or western yew.

Experiment 2.—This experiment was designed to test the effect of height in the canopy on the biomass growth of *Lobaria oregana* and *Letharia vulpina*. Fifty *L. oregana* and 50 *L. vulpina* pendants were installed in the crown of a single large Douglas-fir. This tree was chosen because it was accessible on all sides via the crane gondola. There were eight sites in the upper crown (height class 3, 49–56 m), eight in the middle crown (height class 2, 39–48 m), four in the lower crown (height class 1, 29–38 m), and three in the understory (height class U, <3 m). Two thalli of each species were hung at every site. The understory sites were accessible from the ground, and pendants were placed on western yew and western hemlock.

Experiment 3.—This experiment was designed to test the effect of height in the canopy on the biomass growth of *Lobaria pulmonaria*. A total of 108 pendants were installed in three western hemlock trees. In each tree, there were two transplant sites in the upper crown (height class 3, 47–52 m), two in the middle crown (height class 2, 29–37 m), and two in the lower crown (height class 1, 17–24 m). Transplant sites were evenly distributed between the north and south sides of the trees, and six pendants were hung at every site.

Abundance.—Abundance was scored from the crane

gondola at sites throughout the canopy (sampling details in McCune et al. 2000). At each of 72 sites we recorded percent cover of individual species in 50 × 20 cm flexible quadrats, using a 4-step logarithmic scale (0, <1, 1–10, 10–100%). Only those species for which we had transplant results were analyzed further here.

Statistical analyses.—We used two approaches to summarize the data: ANOVA contrasting mean growth rates at various transplant sites (JMP 4.0; SAS Institute 2001) and nonlinear regression based on kernel analysis (Bowman & Azzalini 1997) to describe for each species the relationships of growth rates and abundance to height in the canopy (canopy position was a continuous variable). The chief advantage of nonparametric regression is avoiding distributional assumptions and not needing to specify the form of the relationship. Instead, the form of the relationship is derived directly from the data. *Lobaria oregana* was involved in two experiments, so we ran a separate regression for each experiment.

For the first two experiments, we used one-way ANOVA of lichen growth rate against canopy position. We used two-way ANOVA to analyze the pendant growth rate data from experiment three. The dependent variable was the average lichen growth rate and the independent variables were canopy position and tree. Multiple comparisons of group means were made using the standard least squares procedure for single degree of freedom orthogonal contrasts. To control experimentwise error rates in these comparisons, the contrasts were made in a stepwise manner. Results of all analyses were considered statistically significant if p (Type I error) < 0.05.

For nonparametric regression we used the add-in NPMR version 1.01 (nonparametric multiplicative regression; McCune 2003) for PC-ORD version 4 (McCune & Mefford 1999). NPMR is available for free download from <www.pcord.com>. We analyzed growth rates and abundance as continuous responses to height in the canopy, using a local mean with Gaussian weighting for the kernel function. A standard deviation of four m in height was used for all response variables, this smoothing parameter being broad enough not to overfit our data, yet narrow enough to allow a wide variety of response shapes. Because abundance was scored on a logarithmic scale, we did no further transformation of abundance. Degree of fit was expressed as a cross-validated R^2 value ("cross R^2 "), calculated as follows:

$$\text{cross } R^2 = 1 - \frac{\text{RSS}}{\text{TSS}} = 1 - \frac{\sum_{i=1}^n (y_i - \hat{y}_i)^2}{\sum_{i=1}^n (y_i - \bar{y})^2}$$

RSS is the residual sum of squares, TSS is the total sum of squares, y_i is the individual observation for the response variable in sample unit i and \hat{y}_i is the estimated value for that sample unit. The cross R^2 is more conservative than the traditional R^2 in that the estimate for point i is based on the data excluding point i . With a weak model, it is not uncommon for RSS > TSS and cross R^2 < 0, while a true R^2 is always non-negative.

RESULTS

Experiment 1.—Biomass growth of *Usnea* was affected by canopy position ($p < 0.0001$). Pendant growth rates increased with increasing height in the canopy (Fig. 1). Average growth rates for *Usnea* at 43 m, 33 m, 23 m, 13 m, and 3 m were 61%, 61%,

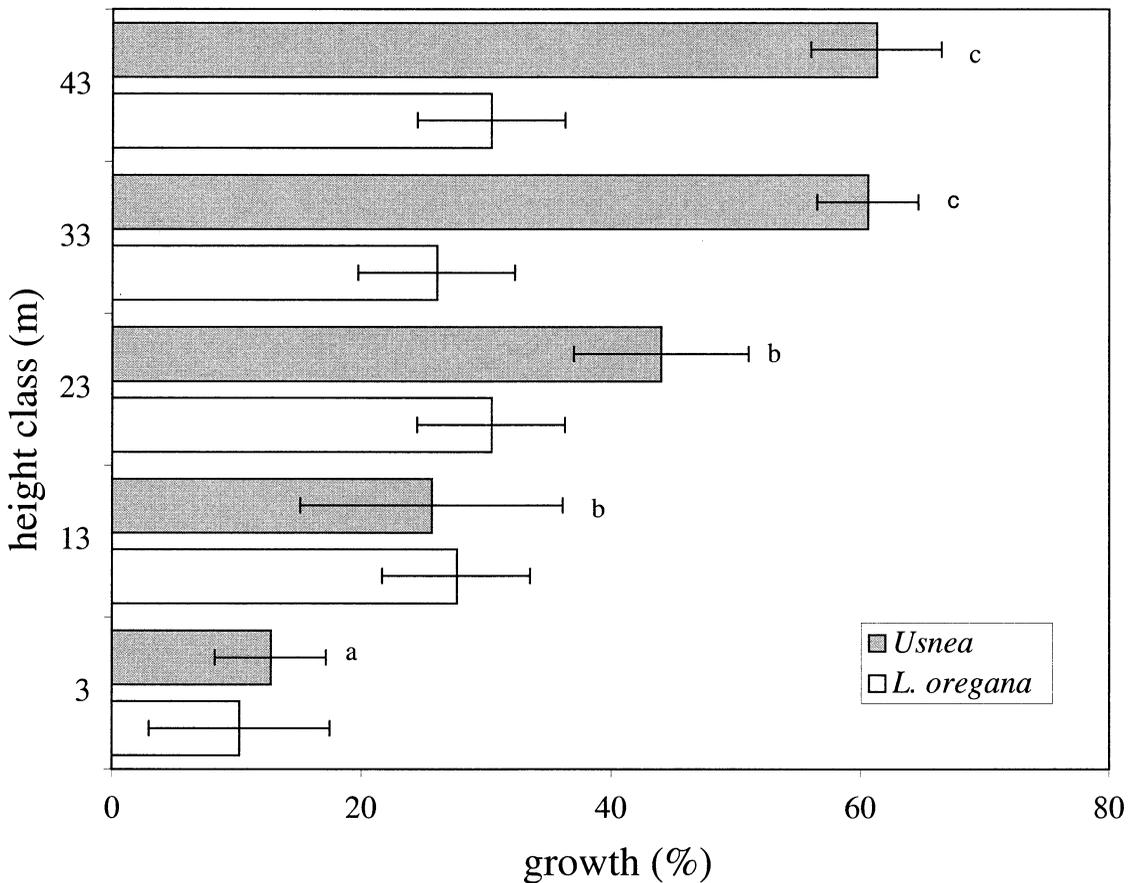


FIGURE 1. Growth rates of *Usnea* and *Lobaria oregana* pendants transplanted to five height classes in the old-growth forest canopy at WRCC. Letters (a, b, and c) next to the *Usnea* data indicate mean growth rates that are significantly different from one another ($p < 0.05$). Mean growth rates of *L. oregana* are not significantly affected by height. Data are shown as the least square means of $n = 10 \pm 1$ SE.

44%, 25%, and 13%, respectively. Pendants placed in the understory grew less than those in the 13 m and 23 m transplant sites ($p < 0.05$). Pendants placed in the two highest canopy positions (i.e., 43 m and 33 m) grew more than those in any of the lower sites ($p < 0.05$).

The performance of *Lobaria oregana* was not significantly affected by canopy position ($p = 0.2301$). Average growth rates for *L. oregana* at 43 m, 33 m, 23 m, 13 m, and 3 m were 30%, 26%, 30%, 28%, and 10%, respectively. The understory appeared to be the least favorable canopy position for growth of *L. oregana* (Fig. 1), but the growth rates were so variable within heights that this difference was rendered nonsignificant.

Experiment 2.—The performance of *Letharia vulpina* was affected by canopy position ($p = 0.0201$). Pendant growth rates increased with increasing height in the tree (Fig. 2). Average growth rates for *L. vulpina* in height classes 1, 2, and 3 were 24%, 29%, and 36%, respectively. Pendants placed in the understory lost an average of 5% of

their biomass, and they grew less than in any other crown position ($p < 0.05$).

The performance of *Lobaria oregana* was affected by canopy position ($p = 0.0003$). Pendants placed in the understory lost an average of 8% of their biomass, and their performance was lower than the growth rates in any other crown position ($p < 0.05$). Average growth rates for *L. oregana* in height classes 1, 2, and 3 were 29%, 39%, and 35%, respectively (Fig. 2).

Experiment 3.—The performance of *Lobaria pulmonaria* was affected by canopy position ($p = 0.0037$) and was not affected by tree ($p = 0.07$). There was no interaction between canopy position and tree ($p = 0.16$). Pendant growth rates increased with increasing height in the canopy (Fig. 3). Average growth rates for *L. pulmonaria* in height classes 1, 2, and 3 were 4%, 10%, and 13%, respectively. Pendants placed in the lowest height class grew less than those in the other canopy positions ($p < 0.05$).

Fundamental vs. realized niche.—For some spe-

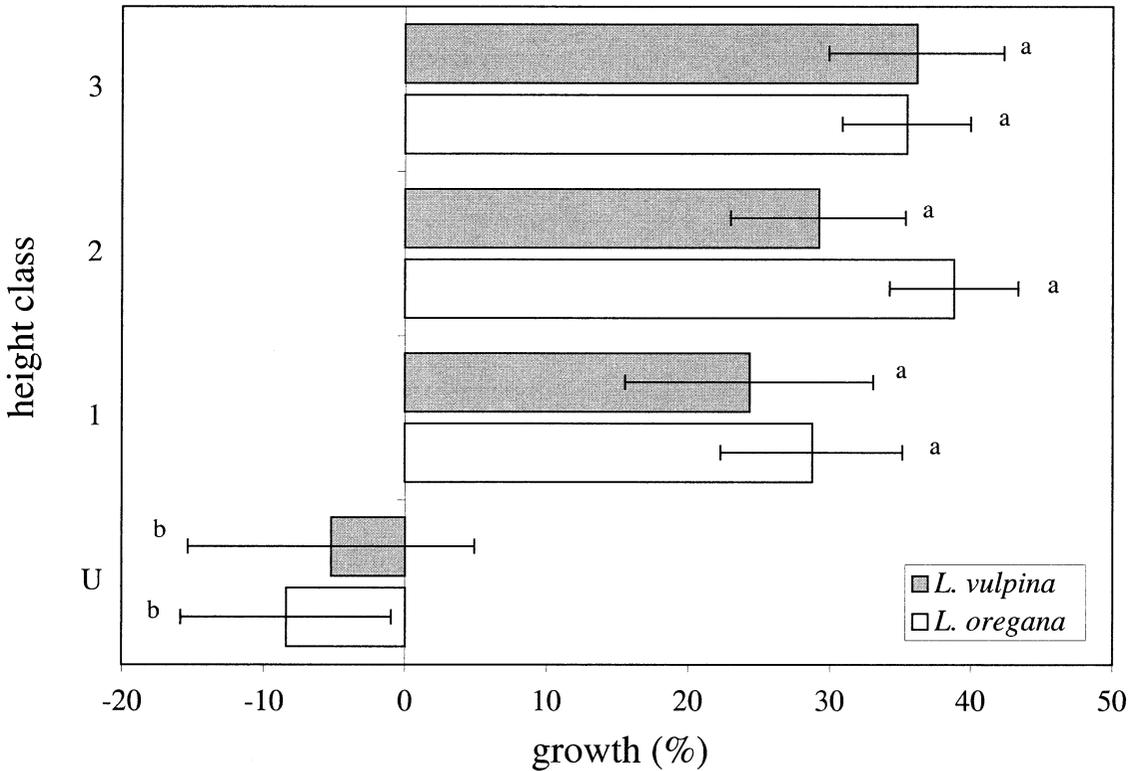


FIGURE 2. Growth rates of *Letharia vulpina* and *Lobaria oregana* pendants transplanted to four height classes in the crown of a Douglas-fir at WRCC. Data are shown as the least square means of $n = 8$ for height class 3 (49–56 m), $n = 8$ for height class 2 (39–48 m), $n = 4$ for height class 1 (29–38 m), and $n = 3$ for height class U (below 3 m). Error bars are ± 1 SE. Letters (a and b) indicate mean growth rates that are significantly different from one another ($p < 0.05$).

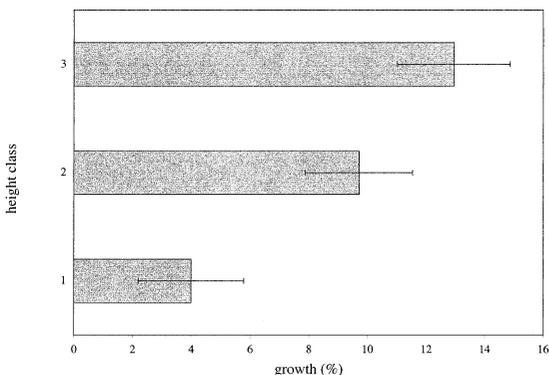


FIGURE 3. Growth rates of *Lobaria pulmonaria* pendants transplanted to three height classes in the old-growth forest canopy at WRCC. Pendants were placed in three replicate western hemlock trees. Data are shown as the least square means of $n = 12$ for height class 3 (47–52 m), height class 2 (29–37 m), and height class 1 (17–24 m). Letters (a and b) indicate mean growth rates that are significantly different from each other ($p < 0.05$). Error bars are ± 1 SE.

cies, biomass growth rates of transplants had qualitatively different relationships to canopy height than did cover of natural populations (Fig. 4). Growth rates of individual transplants were quite variable, yielding low cross R^2 values in some cases (Table 1). Nevertheless, some trends emerged. *Usnea* increased in abundance with height in the canopy, showing a pronounced peak at the highest levels. Growth rates of *Usnea* transplants appeared to stabilize above 30 m, but no data were available above 40 m.

Lobaria oregana peaked in abundance in the mid canopy, yet this peak occurred at a height sub-optimal for its growth. *Lobaria oregana* transplants grew almost twice as fast on average at the upper end of the species' natural height range.

Letharia vulpina occurred from mid canopy to the treetops, peaking in abundance at about 60 m. Similarly, its growth pattern showed increases to 50+ m, the maximum height of its transplants.

DISCUSSION

Overall growth rates.—A number of studies have measured performance of epiphytic lichens,

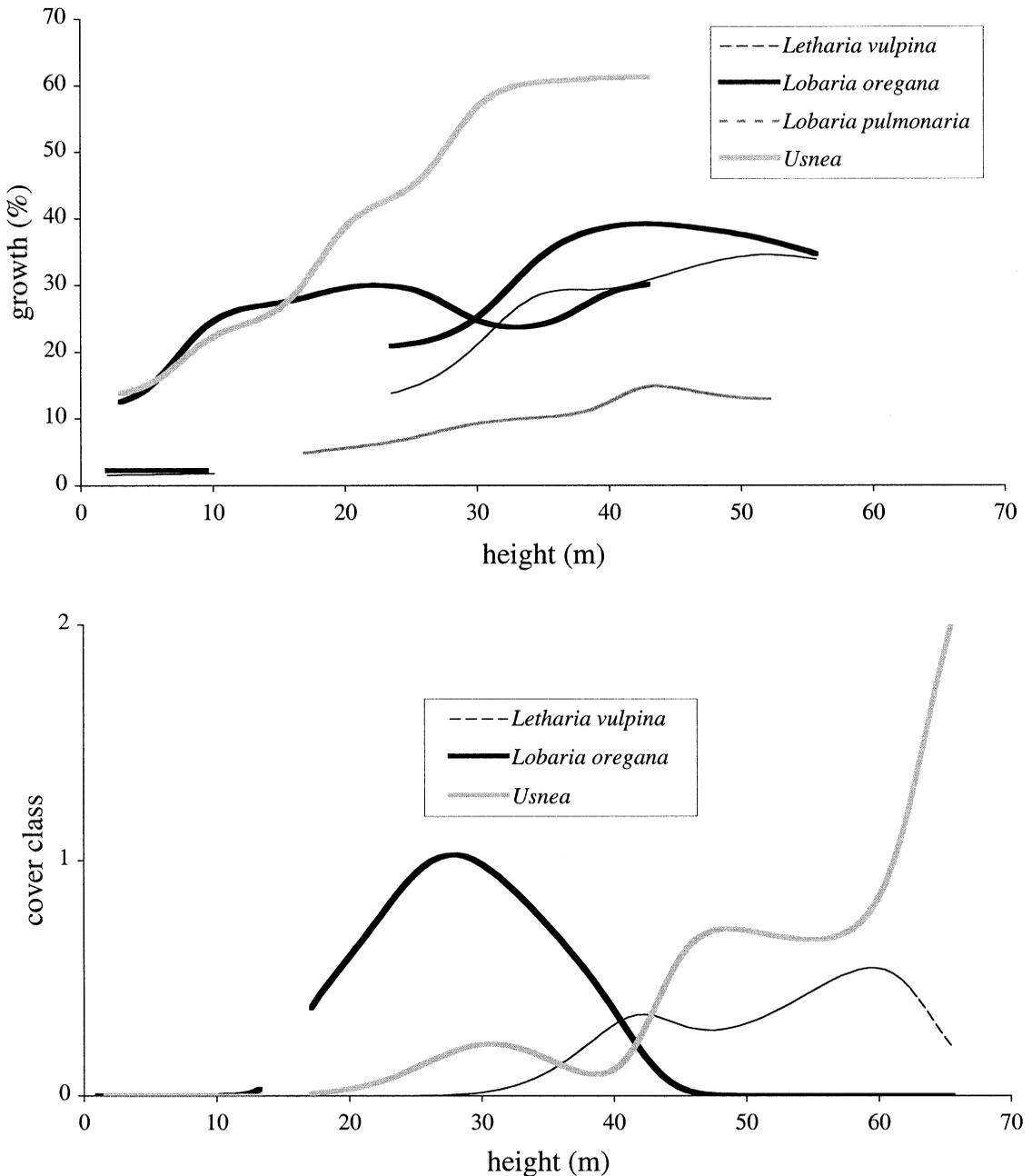


FIGURE 4. Biomass growth of transplants (upper) and natural abundance (lower) in relationship to height. Smoothed curves were generated from scatterplots using a locally weighted mean and Gaussian weights with a standard deviation of four m in height. The two growth curves for *Lobaria oregana* represent results from two different transplant experiments. Curves are broken in areas with insufficient data. Biomass growth data were obtained for *Lobaria pulmonaria*, but this species was uncommon in the forest canopy at WRCC and not encountered in the cover class data.

and published growth rates exist for *Lobaria oregana*, *Lobaria pulmonaria*, and *Usnea* (Table 2). Our *Usnea* pendants were constructed using two different species (*U. scabrata* and *U. filipendula*), which confounds direct comparison of our growth rates to others. However, our average *Usnea* growth rates are considerably higher than those previously

observed in this genus (e.g., Renhorn & Esseen 1995). In their study, *U. filipendula* thalli were transplanted into sub-optimal microsites (i.e., lower crown and close to the trunk) so their observed growth rates may have underestimated the species' growth potential. Some of the discrepancy may also be a result of the effect of latitude—the other study

TABLE 1. Cross-validated R^2 values for nonparametric regression of transplant growth rates and natural cover against height in the canopy. n is the sample size. Insufficient data were available for a regression of natural cover on height for *Lobaria pulmonaria*.

Species	Transplant growth		Natural cover	
	n	cross R^2	n	cross R^2
<i>Letharia vulpina</i>	43	0.10	72	0.10
<i>Lobaria oregana</i> , Expt. 1	42	-0.07	72	0.14
<i>Lobaria oregana</i> , Expt. 2	41	0.32	72	0.14
<i>Lobaria pulmonaria</i>	90	0.04	—	—
<i>Usnea</i>	48	0.44	72	0.21

was carried out in a European boreal forest almost 20° farther north than the WRCC site. Therefore, much of the variation between the two sets of *Usnea* growth rates may be due to differences in climate between the study sites in addition to intrinsic differences between *Usnea* species.

The growth rates of our *L. oregana* pendants are also somewhat higher than we would have predicted given the results of other transplant studies (Denison 1988; McCune et al. 1996; Sillett 1994; Sillett & McCune 1998). However, *L. oregana* has long been considered a species capable of high productivity rates (Rhoades 1977). Unfortunately, a different technique for estimating growth (i.e., sequential photographs) and a small sample size (i.e., $n = 4$) makes it difficult to directly compare Rhoad-

es' results to ours. Our *L. pulmonaria* growth rates correspond to the low end of the range previously observed for this species (Denison 1988; McCune et al. 1996). This implies that the forest at WRCC may not be an optimal location for *L. pulmonaria*, and indeed it is not naturally abundant at the site (McCune et al. 2000).

Fundamental vs. realized niches.—We conducted these transplant experiments to test the effect of canopy position on the performance of different lichens. By comparing the vertical profile of transplant growth to the vertical profiles in abundance, we contrast one aspect of the fundamental niche to the corresponding realized niche. This separates the effects of basic physiological performance of the species from non-physiological processes such as competition and establishment.

The vertical pattern of abundance of *Letharia vulpina* more or less corresponded with the vertical pattern in growth rates. The other two species for which we had vertical profiles in both abundance (realized niche) and growth of transplants (fundamental niche) showed some potentially important discrepancies between the two niche spaces.

Letharia vulpina is an upper canopy species at WRCC, and when transplanted into the crown of a single Douglas-fir it showed a steady increase in growth rates with increasing height. Our transplant sites (i.e., live branches surrounded by foliage) might have been sub-optimal for *L. vulpina* because

TABLE 2. Mean growth rates of various epiphytic lichen species. All growth rates were calculated using variations of pendant experiments and repeated weighing techniques, except Rhoades (1977) used sequential photographs.

Lichen species	Mean growth rate	Reference
<i>Alectoria sarmentosa</i>	12%	Renhorn & Esseen 1995
<i>Bryoria</i> spp.	6–9%	Renhorn & Esseen 1995
<i>Evernia prunastri</i>	31%	McCune et al. 1996
<i>Letharia vulpina</i>	25–36%	this paper
<i>Lobaria oregana</i>	10–40%	this paper
<i>L. oregana</i>	4–7%	McCune et al. 1996
<i>L. oregana</i>	14–22%	Denison 1988
<i>L. oregana</i>	10%	Sillett 1994
<i>L. oregana</i>	15–18%	Sillett & McCune 1998
<i>L. oregana</i>	50%	Rhoades 1977
<i>L. oregana</i>	7%	Shirazi et al. 1996
<i>L. pulmonaria</i>	10–13%	this paper
<i>L. pulmonaria</i>	13–44%	McCune et al. 1996
<i>L. pulmonaria</i>	6–12%	Denison 1988
<i>L. pulmonaria</i>	25%	Shirazi et al. 1996
<i>L. pulmonaria</i>	28%	Muir et al. 1998
<i>L. scrobiculata</i>	20%	Hilmo 2002
<i>Platismatia</i> spp.	20–38%	Hilmo 2002
<i>Pseudocyphellaria rainierensis</i>	4–8%	McCune et al. 1996
<i>P. rainierensis</i>	6%	Sillett 1994
<i>P. rainierensis</i>	14–20%	Sillett & McCune 1998
<i>Usnea filipendula</i>	16%	Renhorn & Esseen 1995
<i>U. longissima</i>	6–30%	McCune et al. 1996
<i>U. longissima</i>	9%	Renhorn & Esseen 1995
<i>U. scabrata/filipendula</i>	40–60%	this paper

this species is typically epixylic in dry, exposed microsities. If this is the case, we may have underestimated its growth rates. On the other hand, *L. vulpina*'s substrate selectivity may result purely from the establishment phase, and it might grow equally well on bark or wood.

Usnea peaked in abundance at the highest levels in the canopy, but it appeared to reach a maximum growth rate at about 30 m. Unfortunately, we had no *Usnea* transplants above 43 m. The fact that *Usnea* pendants thrived in the upper canopy is not surprising—it is one of the most abundant lichens in the upper canopy epiphyte community at WRCC. The microclimate of the treetops is evidently ideal for *Usnea*, and its capacity for rapid growth suggests that it is a vigorous competitor.

Lobaria oregana peaked in abundance at 25–30 m, while its growth rates were maximal considerably higher in the canopy, at 40–45 m. We must conclude that some aspect of establishment or competition has a pronounced negative effect on *L. oregana* above about 35 m in the 65-m-high canopy. We return to this problem below, but first some comments on the variability in results observed for *L. oregana*.

The two sets of *L. oregana* pendants placed in the understory sites showed distinctly different responses. In one case some of the pendants grew reasonably well (i.e., around 10%) but with a high variance, while in the other case they fared abysmally (i.e., around –8%). The reason for this discrepancy is probably due to the fact that one set of transplant sites was around the edge of a canopy gap, while the other was beneath the crown of a large Douglas-fir. The large variance in growth rates around the canopy gap resulted in nonsignificant differences between heights for experiment one (Fig. 1) and a negative cross R^2 (Table 1). Although *L. oregana* is not a light-demanding species (Antoine 2001), it requires a certain minimum level of photosynthetically active radiation, and conditions under dense crowns were probably just too dark for sufficient net photosynthesis.

Both *L. oregana* and *L. pulmonaria* reach peak abundance in the “light transition zone” of the mid canopy at WRCC (McCune et al. 1997). But our transplants showed that *L. oregana* is capable of growing equally well, if not slightly better, far above where it is actually most abundant. Similarly, growth rates of *L. pulmonaria* pendants peaked in the upper canopy transplant sites. Although *L. pulmonaria* is not a dominant species at WRCC, when it is present it is confined to the mid-canopy. *Lobaria pulmonaria* may be susceptible to damage by high light (Gauslaa & Solhaug 2000, 2001). Extensive melanization (i.e., darkening of thalli through production of brown, UV-absorbing compounds)

was observed in most *L. pulmonaria* pendants after one year in the upper canopy. On the other hand, the melanized transplants increased in biomass, so there is no reason to believe that high light levels in the upper canopy are responsible for the absence of *Lobaria*.

These results from the cyanolichen pendants pose an intriguing paradox. When transplanted, these species grow fastest at canopy heights where they are virtually absent in the naturally occurring community. Why do *L. oregana* and *L. pulmonaria* fail in the treetops at WRCC? One possible explanation is competitive exclusion by other upper canopy dominants. The high growth rates of *Usnea* pendants in the upper canopy positions may allow it to be an aggressive colonizer and defender of substrate surface area. This hypothesis could be tested by transplanting *Lobaria* thalli and propagules directly onto upper canopy substrates (i.e., not using the pendant technique), with resident lichens either removed or intact.

The explanation for the absence of *Lobaria* in the upper canopy may also lie in rare microclimatic extremes of the upper canopy. Moving down from the treetops, microclimates are increasingly buffered by the canopy. In the treetops wetting/drying cycles are more rapid, temperature oscillations are more pronounced, and exposure to wind and radiation is more acute than in middle or lower canopy positions (Campbell & Coxson 2001; Coxson & Coyle 2003; Parker 1995); the studies by Parker and by Campbell & Coxson were in a more open forest with less pronounced vertical differences. *Lobaria oregana* is sensitive to temperature fluctuations when it is hydrated: temperatures below 5°C inhibit nitrogen fixation, while temperatures above 15°C promote unsustainably high respiration rates (Antoine 2001). The abundance of *L. oregana* decreases sharply at elevations above about 1,000 m in western Oregon (McCune et al. 2003), suggesting a temperature sensitivity that may occasionally come into action in the upper canopy. Long-term pendant experiments could be used to test the hypothesis that these cyanolichens are confined to the mid canopy by an inability to tolerate rare low-temperature extremes, or other microclimatic extremes.

ACKNOWLEDGMENTS

We thank D. Fischer, K. Fujimura, C. A. Grenz, R. Hamill, P. Helm, S. Holmes, D. Holmgren, S. Kovacs, T. Lamphear, E. Muench, C. Nelson, S. Nelson, T. Rodenkirk, M. Russell, T. Sechler, and D. Woodruff for their roles in designing and implementing the lichen transplant experiments; arborists Dave Shaw and Buzz Baker and crane operator Mark Creighton for transportation into the forest canopy; Steve Sillett for assistance with statistic analyses and manuscript review; and Jeanne Ponzetti for

manuscript review. We thank the WRCCRF (<http://depts.washington.edu/wrccrf/index.html>) and the Department of Botany and Plant Pathology, Oregon State University for funds for use of the crane.

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- ms. received Sept. 16, 2003; accepted Dec. 5, 2003.