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Environmental Factors Influencing the Distribution of the Lichens *Lobaria oregana* and *L. pulmonaria*

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Abstract. Lobaria oregana *(Tuck.) Müll. Arg. and* L. pulmonaria *(L.) Hoffm. are parapatric in western North America. However,* L. pulmonaria *is more widely distributed than* L. oregana; *in western Oregon,* L. pulmonaria *occurs in the Willamette Valley and forests of the Cascades and Coast Ranges, while* L. oregana *is largely restricted to the mountain forests. To determine whether distribution patterns are related to differential environmental tolerances, we examined responses to heat and desiccation and growth responses of transplanted thalli. Heat tolerances were tested by exposing thalli (air-dry or moist) to temperatures ranging from 24–40°C (3°C intervals) and 25–60°C (5°C intervals) for 1 hr. Sensitivity was assessed by measuring electrical conductivity of deionized water in which thalli were immersed, which reflects membrane damage. Heat tolerances of the two species did not differ.* Lobaria pulmonaria *from the Willamette Valley was apparently less desiccation tolerant than* L. oregana *from upper canopies in the Cascade Mountains. Intraspecific differences in desiccation tolerance depended on the environment from which thalli were collected and were as great as interspecific differences. Thus, differences in distribution between the two species do not appear to be due simply to differential heat or desiccation tolerances.* Lobaria oregana *from upper canopies in the Cascades grew more slowly than* L. pulmonaria *from lower tree trunks in the Willamette Valley when both were transplanted to the Willamette Valley for 18 weeks. However, survival of the two species did not differ 9 weeks after transplanting to the Willamette Valley.*

Lobaria oregana (Tuck.) Müll. Arg. and *L. pulmonaria* (L.) Hoffm. are parapatric in western North America (Jordan 1973). However, *L. pulmonaria* has a much broader distribution than *L. oregana. Lobaria pulmonaria* has a worldwide distribution, while *L. oregana* is endemic to the Pacific Northwest (Jordan 1973). In western Oregon, *L. pulmonaria* occurs in the Willamette Valley and in adjacent forests of diverse ages in the Cascades and Coast Ranges, while *L. oregana* is largely restricted to the forests and is more abundant in old-growth than in younger stands (Howe 1978; McCune 1993; Neitlich 1993; Pike et al. 1975).

The distributions of lichen species and communities are influenced by many environmental factors, including temperature, moisture (average humidity, rapidity and frequency of wetting and drying) light exposure, and availability of appropriate substrates, which often interact in influencing species distributions (Armstrong 1988; Kappen 1988; Kershaw 1985; Lesica et al. 1991; MacFarlane & Kershaw 1978). For example, heat tolerance in lichens is influenced strongly by moisture content of the thallus; measurements of the respiratory activity of saturated thalli of *L. pulmonaria* indicated a maximum heat tolerance of 36.5°C as compared with 78°C for air-dry thalli (Lange 1953).

Most lichens are extremely tolerant of desiccation and, depending on the species, the minimum water content of a living thallus can be 2 to 9% of the dry weight (Kappen 1973), with that water tightly bound in the protoplasm. Some lichen species can withstand desiccation for years (Thomas 1921). However, the extent to which desiccation tolerance influences ecological distribution is not known.

The objectives of this study are to compare the heat and desiccation tolerances of *Lobaria oregana* and *L. pulmonaria* and their growth rates when transplanted to the Willamette Valley, Oregon. These comparisons provide insights into whether their differential distribution patterns are related to differential tolerances. Elucidating causes of differences in geographic distribution is of basic interest, and also has increasing applied importance as the ecological indicator value of lichens is given greater emphasis. For example, "old growth associated" species including both *L. pulmonaria* and *L. oregana* are given particular attention in the new forest management plans being implemented on federal lands in the U.S. Pacific Northwest (U.S. Forest Service & U.S. Bureau of Land Management 1994). However, *L. oregana* is generally considered to be more strongly linked to old-growth forests than is *L. pulmonaria* (Howe 1978; McCune 1993; Neitlich 1993; Pike et al. 1975), with reasons for this linkage unclear. Perhaps *L. oregana* requires microclimatic features characteristic of older forests while *L. pulmonaria* has broader amplitudes of environmental tolerance. On the other hand, the distribution of *L.*

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TABLE 1. Collection sites for thalli used in heat and desiccation tolerance experiments and tests of growth and survival.

Experiment	Collection site and date	
	Lobaria pulmonaria	*Lobaria oregana*
Heat and desiccation tolerance; initial. Growth of desiccated and fresh thalli.	Willamette Valley, MacDonald State Forest 44°37′N, 123°15′W 106 m; Nov. & Dec., 1992 lower trunk, *Fraxinus latifolia*	Cascade Mts., Middle Santiam Wilderness Area 44°30′N, 122°12′W 650 m; Nov. & Dec., 1992 upper canopy, *Pseudotsuga menziesii*
Follow-up heat tolerance	As above; Cascade Mts., Fisherman's Bend Park 44°45′N, 122°31′W 260 m; Dec., 1993 lower trunk, *Acer macrophyllum*	Cascade Mts., Fisherman's Bend Park 44°45′N, 122°31′W 260 m; Dec., 1993 lower canopy, *Pseudotsuga menziesii*
Follow-up desiccation tolerance	Western Cascade Mts. 44°47′N, 122°12′W 933 m; Sept., 1994 lower canopy, *P. menziesii* Willamette Valley, MacDonald State Forest 106 m; Sept., 1994 lower trunk, *F. latifolia*	Western Cascade Mts. 44°47′N, 122°12′W 933 m; Sept., 1994 lower & upper canopy, *P. menziesii* Willamette Valley, MacDonald State Forest 106 m; Sept., 1994 lower trunk, *F. latifolia*
Transplant survival	Cascade Mts., H.J. Andrews Experimental Forest 44°10′N, 122°15′W 450 m; May, 1994 lower canopy, *P. menziesii*	Cascade Mts., H.J. Andrews Experimental Forest 44°10′N, 122°15′W 450 m; May, 1994 upper canopy, *P. menziesii*

oregana may be more strongly limited than that of *L. pulmonaria* by other factors such as dispersal or availability of appropriate substrates, with environmental tolerances being similar between the two species.

We used ion leakage measurements to assess injury to the lichens under various temperature and desiccation regimes. Ion leakage measurements have been used for assessing effects of desiccation on location of cations in lichens (Buck & Brown 1979) and damage to lichens subjected to air pollution (Pearson 1980). In some cases, such measures provide a more sensitive and faster indication of injury than methods focusing on rates of photosynthesis or respiration (Fields & St. Clair 1984). We also transplanted thalli of both species to a site in the Willamette Valley, Oregon, and monitored their growth and survival.

MATERIALS AND METHODS

Lichen material.—Lichens were collected from lower to mid-elevations in the Cascade Mountains of Oregon and from MacDonald State Forest in the Willamette Valley, Oregon (Table 1). The climate in both collection areas is maritime, with mild dry summers and cooler wet winters. The Cascades, however, receive more precipitation than does the Willamette Valley (approximately 230 versus 100 cm annual average for sites at 426 m in the Cascades and the northern Willamette Valley, respectively), and both winter and summer temperatures in the Cascades tend to be cooler than those in the Valley (annual averages of 8.5 and 12.6°C for sites at 426 m in the Cascades and the northern Willamette Valley, respectively; Bierlmaier & McKee 1989; Franklin & Dyrness 1973; Oregon Climate Service 1994).

Initial studies of heat and desiccation tolerance used thalli of *L. oregana* collected from upper canopies of *Pseudotsuga menziesii* in the Cascade Mts., while thalli of *L. pulmonaria* were collected from lower trunks of *Fraxinus latifolia* in MacDonald State Forest in the Willamette Valley (Table 1). A follow-up study of heat tolerance was designed to improve resolution on temperature responses over an ecologically realistic temperature range, and used thalli from lower canopies or trunks; *L. oregana* from *P. menziesii* in the Cascade Mts. and *L. pulmonaria* from *F. latifolia* in MacDonald State Forest (Table 1). A follow-up study of desiccation tolerance, designed to test the influence of collection location as well as of species on heat tolerance, included thalli of both species from lower canopies or trunks in both the Willamette Valley and the Cascade Mts. and *L. oregana* from upper canopies in the Cascades (Table 1). Finally, for studies of transplant survival, thalli of both species were collected from the Cascade Mts.; *L. oregana* from upper canopies and *L. pulmonaria* from lower canopy positions, both from *P. menziesii* (Table 1).

Heat treatments.—In the initial heat tolerance study, *L. oregana* and *L. pulmonaria* lobes (approximately 0.05 g air dry weight) were taken from freshly collected thalli (within 24 hr. of collection), rinsed briefly with deionized water to remove surface residue that may have confounded subsequent conductivity measurements, and air dried for 24 hr. at room temperature (23°/18° ± 3°C day/night) before heat treatment began. Air-dried samples (hereafter "dry samples") had means of 25 and 30% moisture content (by weight) for *L. oregana* and *L. pulmonaria*, respectively. Moist samples ($\bar{x}$ = 70% moisture content for both species) were generated by immersing the lobes in deionized water for 30 min. Dry or moist lobes (n = 5 lobes/species/temperature/moisture status) were weighed individually and

placed individually into polyethylene vials. The vials were sealed and immersed in a water bath at temperatures ranging from 25° to 60°C (5°C intervals) for 1 hr. Vial temperatures were monitored during treatments by placing a thermometer in an empty vial and immersing that in the water bath along with vials containing lichens. Lobe weights were remeasured after each treatment to determine whether moisture status had changed as a result of treatment. There were no changes for the dry samples, and moist samples lost weight at temperatures > 30°C.

The follow-up study of heat tolerance used moist (30 min. immersion in deionized water) thalli of both species. Thalli were treated as previously described at temperatures ranging from 25° to 40°C (3°C intervals) for 1 hr. at each temperature (n = 5 thalli/species-site combination/temperature).

Immediately after heat treatments, 15 ml deionized water was added to each vial, samples were shaken at 400 rpm and electrical conductivity of the water was measured after 2 hr. of shaking using a digital conductivity meter (Curtis Matheson Scientific Inc., Houston, TX). Electrical conductivity was expressed by dividing conductivity (μS) by dry weight (g) of each sample (Dexter, Tottingham & Graber 1932; Fields & St. Clair 1984; Pearson 1980).

Desiccation treatments.—For the initial study of desiccation tolerance, *Lobaria oregana* and *L. pulmonaria* lobes (approximately 0.05 g air dry weight) were taken from thalli within 24 hr. of sample collection (Table 1), rinsed with deionized water for a few seconds, blotted dry, and placed in an incubation room (23°/18°C day/night, 20–40% relative humidity, indirect light provided by laboratory window). Initial electrical conductivity of the samples was measured after 24 hr. air-dry incubation. Desiccation stress was assessed weekly for 14 weeks thereafter by measuring electrical conductivity of immersion solutions (n = 8 lobes/species/week) using methods described above.

The follow-up study of desiccation tolerance tested reproducibility of results from the initial desiccation study and also contrasted individuals of the same species collected from different sites (Table 1). This enabled us to assess whether an individual's desiccation tolerance appeared to be influenced both by its species and by the environment in which it grew (e.g., potential ecotypic differences or acclimation). Lichens were placed in the incubation room described above, however laboratory humidity was higher than during the initial desiccation tests (50–90% relative humidity). Desiccation stress was assessed after 24 hr. and after 1, 2, and 4 weeks by measuring electrical conductivity of immersion solutions (n = 8 lobes/species-site combination/week) using methods described above. Few specimens of *L. oregana* were found in the Willamette Valley site, hence this species was tested only following 24 hr. and after 4 weeks of desiccation.

Transplant treatments a: growth of desiccated thalli.—After 14 weeks of desiccation, desiccated and freshly collected *L. oregana* and *L. pulmonaria* lobes (n = 5/species; Table 1) were weighed and transplanted to an orchard site in the Willamette Valley near Corvallis, Oregon, (elevation 62 m) where they remained for 18 weeks (April 16–Aug. 25, 1993). *Lobaria pulmonaria* occurs sparsely in the orchard site, whereas *L. oregana* does not occur there. Transplanting methods are described fully in McCune et al. (1995), and involve attaching lobes to nylon monofilament with silicone, then hanging lobes from branches; this method is modified from Denison (1988). After 18 weeks in the field, samples were air-dried in the laboratory, reweighed, and growth (%) over the 18 weeks was calculated (McCune et al., 1995). Ion leakage of the samples was measured the day after samples were returned from the field, as previously described.

Transplant treatments b: survival of freshly collected thalli.—Freshly collected lobes of both species (Table 1) were attached to a number of sites in the orchard used in regrowth tests, to monitor their fate. Lobes (n = 110 per species across all sites within the orchard; 10 per species at each of 11 sites) were attached to substrates using silicone. Substrates included hardwood tree trunks and branches (*F. latifolia, Salix* sp., and *Prunus avium*) and wooden roofs and sides of farm buildings (*Thuja, Pseudotsuga* or other conifer woods), on all aspects. Lobes were transplanted to the site on May 30, 1994 and survivorship and condition was assessed on August 8, 1994. Condition classes were 1) apparently healthy, thalli green, 2) partly necrotic or bleached (10–90% surface area necrotic or bleached), 3) bleached or dead (> 90% surface area necrotic or bleached), and 4) missing.

Statistical analysis.—Data were analyzed using one-way analysis of variance (SPSS PC+; Norusis 1988), comparing responses of the species (or species-site combinations) at each temperature or week of desiccation.

Results

Heat tolerance.—Ion leakage from moist *Lobaria oregana* (from upper canopies, Cascade Mts.) and *L. pulmonaria* (from lower trunks, MacDonald State Forest) was high at 40°C and above (Fig. 1). There were no statistically significant differences ($p \leq 0.05$) in ion leakage between moist thalli of the two species at any temperature. Similarity in ion leakage between the two species from these sites, particularly for the controls, suggests that initial quantities and cellular location of cations were similar between the two species. Subsequent tests of heat tolerance using smaller temperature steps within the ecologically-realistic 25°–40°C range, indicated that the species' heat tolerances did not differ across this range (minimum $p = 0.31$ from ANOVA, $F = 1.29$; data not shown). Both species were more heat tolerant when dry, as ion leakage did not increase until temperatures were greater than 50° and 55°C for *L. pulmonaria* and *L. oregana,* respectively (Fig. 1).

Desiccation tolerance.—Ion leakage from *L. oregana* (from upper canopies, Cascade Mts.) began to increase after 2 weeks of dry storage and increased markedly after only one week for *L. pulmonaria* (from lower trunks, MacDonald State Forest) (Fig. 2). *Lobaria pulmonaria* was apparently less tolerant to drying than *L. oregana,* as electrical conductivities of solutions with *L. pulmonaria* were higher than those with *L. oregana* on all but the initial measurement of the 14 week period of incubation in the laboratory. Differences were statistically significant (maximum $p = 0.03$) on eight of the sampling dates. As for thalli used in assessing heat tolerance, initial conductivities did not differ between the two species, lending credence to the hypothesis that later differences between the species can be related to desiccation sensitivity (Buck & Brown 1979).

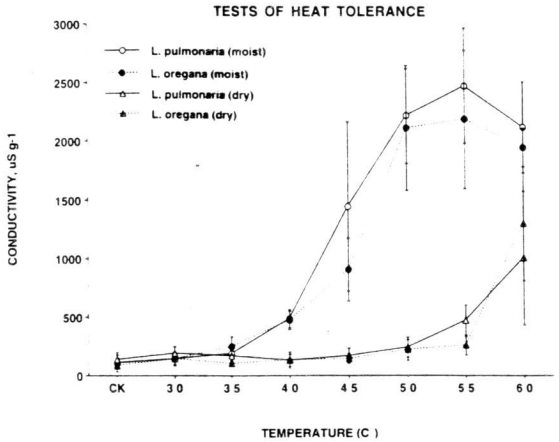

FIGURE 1. Tests of heat tolerance. Electrical conductivity (μS g^{-1} dry weight) of solutions containing moist or dry *Lobaria oregana* and *L. pulmonaria* treated at 25°–60°C (5°C intervals). Data are means and 95% confidence intervals (n = 5 lobes/species/temperature/moisture status).

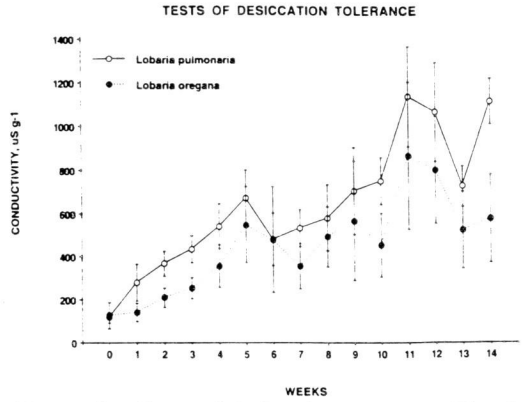

FIGURE 2. Tests of desiccation tolerance. Electrical conductivity (μS g^{-1} dry weight) of solutions containing *Lobaria oregana* or *L. pulmonaria* following various periods of desiccation. Data are means and 95% confidence intervals (n = 8 lobes/species/week).

The occasional decreases in conductivities, which were often synchronous between the two species (Fig. 2), are unexplained.

We found differences among species-collection site combinations in the follow-up desiccation study (Fig. 3, maximum p from the ANOVA of species-site combinations within weeks = 0.07 [week 2]; all other $p < 0.05$). As in the initial study, *L. pulmonaria* from the Willamette Valley appeared less desiccation-tolerant than *L. oregana* from upper canopies in the Cascade Mts. after all desiccation periods. However, interpreting these differences is complicated by the fact that differences among species-site combinations existed within 24 hours of initial collection ($p = 0.03$), unlike earlier results in which initial differences between *L. oregana* and *L. pulmonaria* were not apparent (Fig. 2). The relative order of electrolyte leakage from the various species-site combinations after one and 2 weeks desiccation was the same as their order within 24 hours of collection; *L. pulmonaria* from the Willamette Valley > *L. oregana* from lower trunks in the Cascades > *L. pulmonaria* from lower trunks in the Cascades > *L. oregana* from upper canopies in the Cascades. This ordering suggests that differences in leakage among species-site combinations after one and 2 weeks desiccation may reflect initial species-site differences in electrolyte quantities or cellular locations rather than reflecting differences in desiccation tolerances (Buck & Brown 1979). (Leakage from *L. oregana* from the Willamette Valley 24 hours after collection was comparable to that from upper canopy individuals from that species from the Cascades, but was not assessed at weeks one or 2.) However, by the fourth week of desiccation, electrolyte leakage from all species-site combinations had increased markedly and relative orders had changed from initial orders (Fig. 3). Apparently, most desiccation resistant was *L. oregana* from upper canopies, followed closely by *L. pulmonaria* from lower trunks in the Cascades. Least resistant were Valley samples of both species (*L. oregana* less resistant than *L. pulmonaria*) and lower trunk samples of *L. oregana* from the Cascades (*L. oregana* less resistant than *L. pulmonaria*).

Transplant treatments a: growth of desiccated thalli.—Both species lost weight over 18 weeks in the field following 14 weeks desiccation in the laboratory (−8 and −14% change in weight for *L. oregana* and *L. pulmonaria*, respectively; Table 2), suggesting that both species were probably killed by the prolonged desiccation stress. Death of these desiccated lobes was also suggested by high rates of ion leakage following the 18 weeks in the field (Table 2). Fresh (non-desiccated) *L. oregana* grew more slowly than fresh *L. pulmonaria* at the Willamette Valley transplant site (6 and 24% increases in weight for the two species, respectively, over 18 weeks; Table 2). Late spring and summer are not the optimum times for *Lobaria* growth in the Willamette Valley (Muir and Shirazi, unpublished data) at least in part because summers are usually warm and dry in this semi-Mediterranean climate. However, April though July, 1993 were unusually moist and cool by comparison with the 30 yr means (1961–1990, Oregon Climate Service 1994), and these relatively cool, moist conditions may have favored growth of both species. Similarly, fresh *L. pulmonaria* had lower ion leakage than fresh *L. oregana* following the 18 weeks in the field (Table 2), indicating that *L. pulmonaria* was less stressed by the Willamette Valley habitat than *L. oregana*.

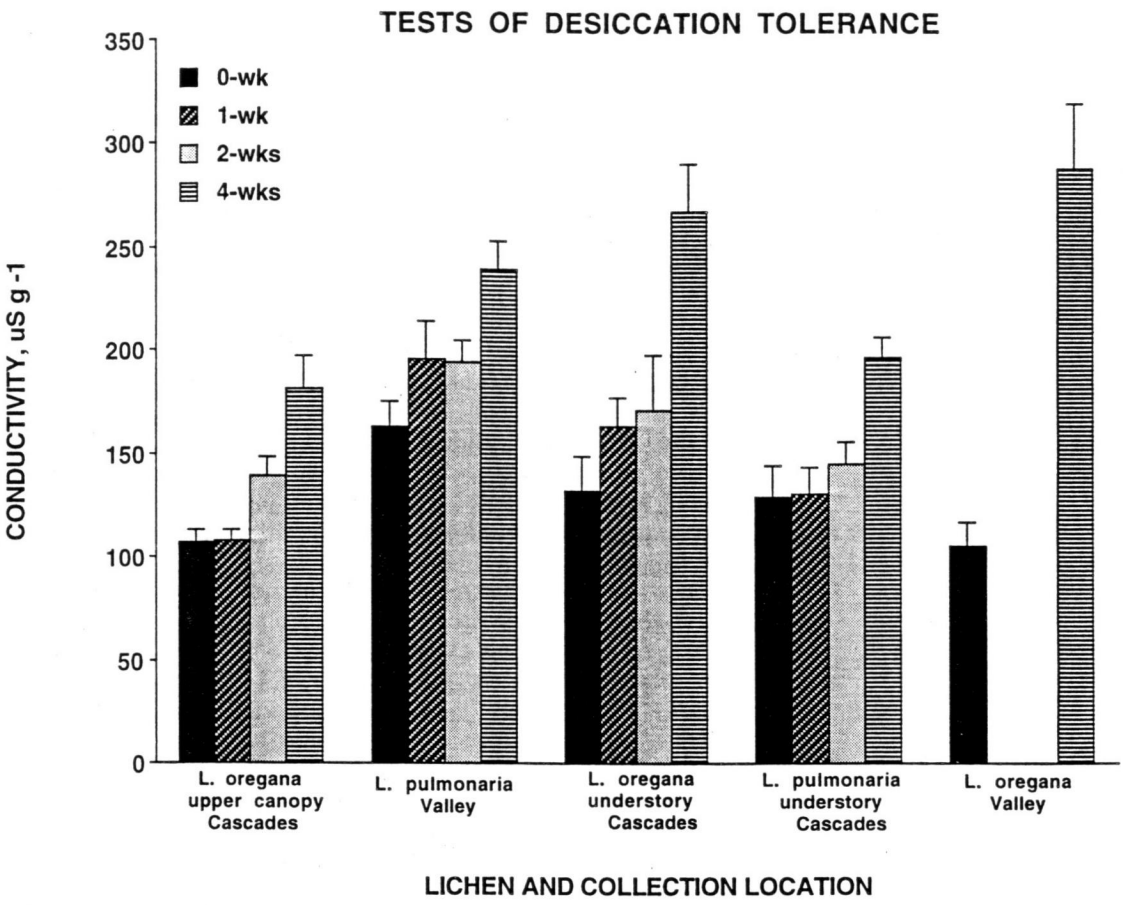

FIGURE 3. Tests of desiccation tolerance. Electrical conductivity ($\mu S\ g^{-1}$ dry weight) of solutions containing *Lobaria pulmonaria* or *L. oregana* from various collection sites; conductivity assessed initially and after 1, 2, and 4 weeks of desiccation. Data are means and 95% confidence intervals (n = 8 lobes/species-collection site combination/week).

Transplant treatments b: survival of freshly collected thalli.—Survivorship and condition of transplants grown May 30–Aug. 8, 1994 at the orchard site did not differ strongly between the two species across all transplanting sites. For both species, 17% of transplants died over the two month period. A slightly higher percentage of *L. pulmonaria* transplants were apparently healthy (57% and 52% for *L. pulmonaria* and *L. oregana,* respectively), while 25% and 30% (*L. pulmonaria* and *L. oregana,* respectively) of transplants were slightly bleached. For both species, individuals in shaded positions had almost no apparent injury or mortality, while transplants in exposed sites (receiving direct sunlight for more than 2–3 hr./day) suffered high mortality rates, presumably from heat and/or moisture stress.

DISCUSSION

Many environmental factors influence the distribution of lichen species. Our results indicate that, under laboratory conditions, heat and desiccation stress were not necessarily more limiting for *Lobaria oregana* than for *L. pulmonaria.* The two species apparently did not differ in heat tolerance (Fig. 1). *Lobaria pulmonaria* from the Willamette Valley appeared more sensitive to desiccation than *L. oregana* from upper canopies in the Cascade Mts. (Fig. 2), a result opposite to expectations.

Differences in desiccation tolerance were not strictly a function of the species, but were also influenced by the environment from which thalli were collected. For example, upper canopy thalli of *L. oregana* were apparently more tolerant of desiccation than were lower canopy thalli of that species from both the Willamette Valley and the Cascade Mts. (Fig. 3). Similarly, lower canopy thalli of both species from the Cascades were apparently more desiccation tolerant than those from the Willamette Valley, with lower canopy *L. pulmonaria* being more tolerant than *L. oregana* in both environments. These intraspecific differences in desiccation tolerance between collection locations may have several sources 1) ecotypic differentiation within species, 2)

TABLE 2. Responses of transplanted lichens. Percent growth and electrical conductivity ($\mu S\ g^{-1}$) of desiccated (14 weeks) or fresh *Lobaria oregana* and *L. pulmonaria* transplanted to the Willamette Valley for 18 weeks.

Lichen species	Treatment	*n*	% Growth (St. dev.)	Conductivity, $\mu S\ g^{-1}$ (St. dev.)
L. oregana	Fresh	5	6.82 (0.03)	85.43 (13.95)
	Desiccated	5	−8.18 (0.04)	151.66 (64.75)
L. pulmonaria	Fresh	5	24.52 (0.01)	107.69 (18.05)
	Desiccated	5	−14.12 (0.02)	153.39 (82.83)

different capacities of individuals to acclimate to alternative environments, and 3) different levels of pre-collection stress in the various habitats. Further study would be required to test whether the observed intra-species differences in desiccation tolerance result from genetic differences among subpopulations, or from non-genetic sources.

The Willamette Valley during spring and summer (seasons of relatively high temperature and low precipitation) was apparently not as suitable for growth of upper canopy *L. oregana* as for growth of *L. pulmonaria* from the Valley (Table 2). Despite differences in growth rates, upper canopy *L. oregana* did survive in the Valley nearly as well as *L. pulmonaria* from lower canopies in the Cascade Mts., and visible injury and mortality of *L. oregana* transplants was not significantly greater than that of *L. pulmonaria*.

Results suggest that factors other than simple heat or desiccation tolerance (as measured in the laboratory) must underlie the apparent inability of *L. oregana* to establish and grow well in the Willamette Valley. Its occurrence here may be limited by a lack of readily dispersed propagules such as soredia (Armstrong 1988). The lobules that function as propagules in *L. oregana* (Jordan 1973) are more than an order of magnitude larger than the soredia of *L. pulmonaria* and are, presumably less mobile. In addition, propagule sources for *L. oregana* are lacking in the central Willamette Valley. Species with limited dispersal abilities may have been excluded from the Willamette Valley by relatively high disturbance frequencies compared to the surrounding forests (e.g., high presettlement fire frequencies in the Valley).

Alternatively, perhaps propagules are dispersed from the adjoining forests into the Valley, but individuals are not able to establish due to lack of adequate substrate or to some aspect of microhabitat other than those tested here. Appropriate substrates are important for lichen establishment (e.g., Barkman 1958) and *L. oregana* is found most commonly on conifers, which are less abundant in the Valley than in nearby forests. However, *L. oregana* is not obligately associated with conifers; for example it occurs sporadically on the Valley margins on *Fraxinus latifolia* and *Alnus rubra*. In addition, transplant tests argue against the importance of substrate limitations, in that survivorship and condition of transplants affixed to various substrates in the Valley did not differ in a substrate-dependent fashion. Finally, limiting factors other than substrate are suggested in that substrate-independent transplants (dangling from monofilament line) of *L. oregana* grew more slowly than those of *L. pulmonaria* in the Valley.

In summary, causes for the scarcity of *L. oregana* in the Willamette Valley do not appear related to simple inter-specific differences in heat or desiccation tolerance, and require further investigation. In particular, reciprocal transplants of *L. oregana* and *L. pulmonaria* between the forests and the Willamette Valley would be informative. The slower growth rates of *L. oregana* in the Valley than *L. pulmonaria* suggest that other habitat features, such as air quality, should be studied, and that dispersal limitations are unlikely to be the sole factor creating the distributional differences between the two species.

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