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DISPERSAL LIMITATIONS OF EPIPHYTIC LICHENS RESULT IN SPECIES DEPENDENT ON OLD-GROWTH FORESTS

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Abstract. Epiphytic lichen biomass accumulates slowly in forest canopies. We evaluated three alternative hypotheses for the slow accumulation of epiphytic lichens, using two experiments in tree crowns from 15 Douglas-fir forest stands representing three age classes: old growth, young, and recent clearcuts. The first experiment evaluated whether forest age, bark roughness, or dispersal rate limits the establishment of the dominant old-growth-associated lichen, *Lobaria oregana*. Surface-sterilized branches with either rough or smooth bark were repeatedly inoculated with propagules and compared 1 yr after the last inoculation. Dispersal affected rates of establishment: inoculated branches had 27× more newly established thalli than controls. Establishment on smooth bark was highest in clearcuts, intermediate in young forests, and lowest in old growth. There was as much or more establishment of sown propagules on smooth-barked branches as on rough-barked branches in all age classes. In the second, transplant-performance experiment, *Lobaria oregana* grew as rapidly in young forests as in old growth but lost biomass and suffered more injuries in clearcuts. In contrast, *L. pulmonaria* performed at least as well in clearcuts as in young forests and old growth. Poor dispersal and establishment limit the development of *L. oregana* populations in Douglas-fir forests. Particular substrates and microenvironments found only in old growth are not essential for *Lobaria* establishment and growth. Maximizing the number and dispersion of remnant trees in cutting units should maximize the rate of accumulation of *L. oregana* biomass in the regenerating forest. The single most important action promoting the accumulation of old-growth-associated epiphytes will be the retention of propagule sources in and near all cutting units.

Key words: dispersal limitations; epiphyte; forest canopy; Hypogymnia inactiva; *lichen;* Lobaria oregana; Lobaria pulmonaria; *old growth; Oregon Cascades (USA);* Pseudotsuga menziesii.

INTRODUCTION

Epiphytic lichens are an integral component of many forest ecosystems. They provide food and habitat for animals (Carroll 1979, Hayward and Rosentreter 1994, Pettersson et al. 1995), contribute to nutrient cycles (Pike 1978), and represent a major part of species diversity (Lesica et al. 1991, Dettki and Esseen 1998). Comparisons between old growth and younger forests have consistently shown strong differences in species composition and abundance of epiphytic lichens (Lesica et al. 1991, McCune 1993, Selva 1994, Esseen et al. 1996, Kuusinen 1996, Dettki and Esseen 1998). In the *Pseudotsuga-Tsuga* forests of the Cascade Range, dozens of lichen species, especially nitrogen-fixing cyanolichens, are found predominantly in old forests (Rosentreter 1995). Old-growth (>400 yr old) Douglas-fir forest canopies commonly support megagrams of cyanolichens per hectare while nearby younger (<100 yr old) forests have only a trace of cyanolichens (McCune 1993, Sillett and Neitlich 1996). It is clear from these studies that a large biomass of old-growth associated lichens develops very slowly in forests. We have only speculation, however, as to the reasons for their slow rate of accumulation. The overused generalization that lichens grow slowly cannot account for such slow population and community development, since transplant experiments show that many epiphytic macrolichens are capable of 30% annual growth in a range of habitats (McCune et al. 1996, Muir et al. 1997, Sillett and McCune 1998). Furthermore, many green-algal foliose lichens, especially species of *Hypogymnia* and *Platismatia*, do rapidly colonize young conifer forests and peak in biomass in <150 yr (McCune 1993, Neitlich 1993).

We evaluated three alternative, but not mutually exclusive, hypotheses for the slow accumulation of epiphytic lichens in Douglas-fir forests: (1) epiphyte colonization is slow because of a shortage of suitable substrates (e.g., thick, rough bark) in young forests, (2) old-growth associated species are dispersal limited (i.e., suitable habitats are underused by epiphytes because of poor dispersal abilities), and (3) old-growth associated species demand particular microenvironments created by the structure of old forests. We tested these hypotheses with two experiments. In the dispersal experiment, we sowed lichen propagules onto both rough-barked and smooth-barked branches in contrasting environments. In the growth experiment, we trans-

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TABLE 1. Locations and characteristics of sites in a study of old-growth dependency in lichens in the Willamette National Forest in western Oregon.

Stand number	Age class	Latitude	Longitude	Elevation (m)	Aspect (°)	Slope position	VDSTR (m)	Tree basal area (m^2/ha)		Tree density (inds./ha)
								Conifers	Hardwoods	
1	old growth	44°22′40″	122°15′00″	490	20	mid-slope	60	109.0	4.0	2 410
2	old growth	44°13′40″	122°13′00″	520	18	lower slope	0	198.9	0.24	614
3	old growth	44°13′30″	122°11′05″	790	35	lower slope	12	107.2	6.4	1077
4	old growth	44°12′35″	122°15′00″	470	120	valley bottom	12	91.0	1.5	1348
5	old growth	44°05′05″	122°14′55″	700	0	valley bottom	3	183.0	1.2	1077
6	young	44°22′35″	122°14′55″	600	340	mid-slope	100	158.8	13.9	5 298
7	young	44°13′45″	122°12′55″	550	120	lower slope	15	84.0	5.4	11 012
8	young	44°13′30″	122°14′25″	500	220	valley bottom	15	118.9	5.1	11 309
9	young	44°13′25″	122°11′03″	650	340	mid-slope	25	138.7	22.1	10119
10	young	44°05′02″	122°14′55″	730	135	mid-slope	30	151.2	0.70	5 179
11	clearcut	44°25′00″	122°23′30″	400	120	lower slope	45	0.02	0.52	1317
12	clearcut	44°13′45″	122°12′35″	580	115	lower slope	50	5.4	0.17	614
13	clearcut	44°13′05″	122°11′25″	640	20	mid-slope	50	0.67	0.20	599
14	clearcut	44°12′32″	122°15′15″	490	0	valley bottom	0	<0.01	<0.01	105
15	clearcut	43°59′30″	122°10′45″	700	80	lower slope	120	0.42	<0.01	584

Notes: Stands are listed from north to south within each age class. The column heading VDSTR indicates vertical distance to the nearest stream or other permanent body of water.

planted lichen thalli into forests of different ages. Our experiments focused on the cyanolichen *Lobaria oregana*. This species is the dominant epiphytic lichen in humid Douglas-fir forests of the Cascade Range, accounting for 60–80% of all epiphytic lichen biomass in old growth (Pike et al. 1977, McCune 1994, Sillett 1995).

Our results have direct applications to forest management practices. Since the move away from clearcutting to "green tree retention" cutting (Swanson and Franklin 1992, FEMAT 1993), forest managers urgently need information from ecologists on the consequences of alternative densities and spatial arrangements of remnant trees. The alternative outcomes will influence epiphytes as well as all of the other ecosystem components that depend on epiphytes for food (small mammals, deer, and elk), mineral nutrition (input of fixed N), nesting materials (birds and small mammals), or habitat (invertebrates). There is particular hope that remnant trees will help maintain epiphytic lichens in managed forests. If slow dispersal limits lichen accumulation, then it will be important to leave an adequate local source of propagules (i.e., populations persisting in remnant tree crowns) for the inoculation of regenerating forests.

METHODS

Study area

Experiments on epiphytic lichen establishment and growth were conducted in fifteen stands (Table 1) from five areas of the Willamette National Forest in the Cascade Range of western Oregon: three watersheds of the H. J. Andrews Experimental Forest, the South Santiam River near House Rock Forest Camp, and the South Fork McKenzie River near Cougar Reservoir. One forest stand of each of three age classes (old growth, young, and clearcut) was selected from each area. The old-growth stands were between 450 and 500 yr of age, were dominated by *Pseudotsuga menziesii* and *Tsuga heterophylla,* and had canopies 60–85 m tall. The young stands were between 30 and 40 yr of age and had canopies 20–30 m tall. They originated from 10-30 ha clcarcuts that were replanted exclusively with *P. menziesii* and contained very little naturally regenerated *T. heterophylla.* None of the young stands had been thinned since replanting, and stem exclusion (Oliver and Larson 1990) was wcll underway. The clearcut stands (5 to 20 ha) contained scattered shrubs and young trees (mostly *P. menziesii)* ≤ 1.5 m in height and 10 yr of age. All stands were between 400 and 800 m elevation, <120 m vertical distance from a perennial stream or body of water, and within the *Tsuga heterophylla* zone (Franklin and Dyrness 1973).

Study organisms

Lobaria oregana (Tuck.) Mull. Arg. is well documented as an old-growth associated epiphyte (Spies 1991, McCune 1993, Neitlich 1993). It is a large foliose lichen with lobes often 5 cm wide and individual thalli reaching 30 cm long. It grows either loosely appressed to bark or draped over branches. It reproduces primarily by tiny, vegetative lobules that are borne on the margins and ridges of the thallus and are easily detached (Rhoades 1983). The fungal symbiont occasionally reproduces sexually via ascospores. The primary photobiont is a green alga, but the thallus also contains internal cephalodia with nitrogen-fixing, photosynthetic cyanobacteria. *Lobaria oregana* is endemic to the Pacific Northwest, ranging from Alaska to California, mostly west of the Cascade crest.

Lobaria pulmonaria (L.) Hoffm. is an old-growth associate in Europe, the northern Rocky Mountains,

and the eastern United States, but in Oregon and Washington it is also fairly common on deciduous trees in younger forests and at low elevations. It reproduces abundantly by vegetative propagules (soredia or isidia) that are 1–2 orders of magnitude smaller than the lobules of *L. oregana.* Like *L. oregana,* it is a large foliose lichen with a green algal primary photobiont and cyanobacteria in internal cephalodia. This species has proven durable and fast-growing in transplant studies (McCune et al. 1996, Muir et al. 1997).

Hypogymnia inactiva (Krog) Ohlsson is a green algal foliose lichen that is not at all restricted to old-growth forests. It is a ubiquitous colonist of exposed twigs in conifer forests of western Oregon and Washington and occurs along the Pacific Coast from Alaska to California inland to Montana. It often reaches its greatest abundance before stands are 150 yr old (McCune 1993, Neitlich 1993). Attached at only one point, its thallus grows in erect or drooping tufts up to 10 cm diameter. It reproduces entirely by sexually produced ascospores, having no known method of asexual reproduction.

Dispersal experiment

We sowed *Lobaria oregana* propagules (i.e., lobules and thallus fragments) onto 1 m long *Pseudotsuga menziesii* branch segments installed in the three forest age classes. Branch segments had bark of two types: rough, old and smooth, young. We collected rough-barked branch segments (5–10 cm diameter) in September 1995 from cut ~200-yr-old trees on Willamette Industries land east of Lebanon, Oregon in the foothills of the Cascade Range. We collected smooth-barked branch segments (2.5–5 cm diameter) in August 1995 from cut ~80-year-old trees from McDonald State Forest in the foothills of the Oregon Coast Range. Side branches and twigs were removed and macrolichens and bryophytes were rubbed off without damaging the underlying bark. Branch segments were kept in covered outdoor storage in a residential area of Corvallis, Oregon. To ensure that any lichens observed in the experiment were not regrowth of previously established thalli or propagules, we sterilized branch segments by fumigating them with a volatile oxidant. Branch segments were cross-stacked in large (1.5 x 2.5 m), double-wrapped plastic bags. Ninety-nine percent pure propylene oxide was poured into open glass dishes inside the bags through pipes that were then sealed. Each bag received a total of 0.25 L of propylene oxide in two installments over a 2-d period during which it vaporized and dispersed through the bags. Branch segments were then removed from the bags, allowed to air dry, and returned to covered outdoor storage.

We installed a total of eight rough-barked and eight smooth-barked branch segments in each forest stand. In the old-growth stands, we selected four trees (two dominant *Pseudotsuga menziesii,* one suppressed *P. menziesii,* and one codominant *Tsuga heterophylla).* Excessively leaning trees and trees with dead tops were avoided for the safety of tree climbers. We accessed tree crowns by shooting a monofilament over sturdy branches with a compound bow, hauling a nylon cord followed by a climbing rope over the branches, tying one end of the rope at ground level, and ascending the rope using vertical rope technique (Perry 1978). We used rope techniques developed by arborists (Dial and Tobin 1994) to access higher branches. A pulley secured to the trunk near the top of each tree was used to haul a climbing rope into place (via nylon cord) for subsequent ascents. Two pairs of branch segments were installed in each tree crown, one for experimental treatment and one for a control. Each pair consisted of a smooth-barked and a rough-barked branch segment oriented parallel to each other across a "V" formed by two living, horizontal branches. Branch segments were installed 1–2 m away from the main trunk and between 35 m and 60 m high in the tree crowns by lashing them to living branches with nylon cord. They were installed at the height of each tree's greatest estimated resident *L. oregana* abundance.

In the young stands, we installed branch segments in the same manner as in the old-growth stands except that in the young stands all four trees were *P. menziesii* accessed by ladders and free climbing. These trees were selected on the basis of two additional criteria: (1) presence of branches < 10 m in height and (2) presence of resident populations of *L. oregana.* Installation height in the young trees ranged from 3 to 9 m, depending on the heights of the lowest living branches.

In the clearcuts, we used wooden racks instead of trees because the young trees could not support the cut branches. Racks were constructed by lashing crossbars between tripods at a height of 1.5 m above the ground. Tripods and crossbars were made from 5 cm by 5 cm by 2.5 m wooden poles. Rough- and smooth-barked branch segments were attached to the racks by lashing their ends to the crossbars with nylon cord. We placed racks side-by-side in relatively flat and open areas of the clearcuts such that they were not shaded by nearby vegetation.

We inoculated experimental branch segments in each tree or rack with *Lobaria oregana* propagules four times over the course of one year: once in each season beginning in September 1995. Propagules were derived from living *L. oregana* thalli collected from standing or freshly fallen *P. menziesii* tree crowns in old-growth forests within the study area. Thalli were air-dried (not cleaned), placed in a plastic bag, and manually crushed. This treatment freed natural propagules (lobules) and mechanically produced artificial propagules (thallus fragments). All propagules were passed through a 2 mm mesh screen to ensure semi-natural size. The resulting lobules and thallus fragments (along with small amounts of foliage and bark) were then thoroughly mixed. About 3.8 ± 0.4 g (mean $\pm$ 1 SD) of the propagule mixture was measured out as inoculum for each branch segment. Propagules were stored in an air-dried

state for no more than 1 mo before inoculation. In order to promote adhesion by propagules during inoculation, we first misted branch segments with deionized water. We then sprinkled propagules onto branch segments using a stainless steel spice shaker with 2–3 mm diameter holes. Although their total surface area varied, the upper surface of experimental branch segments was saturated with $> 10^3$ propagules/dm^2 after each inoculation.

We measured establishment rates in July 1997, 15 mo after the last inoculation (spring 1996). We misted branch segments with deionized water to help distinguish *L.* oregana, which appears bright yellow-green when wet due to the presence of usnic acid, from tiny thalli of other lichens (e.g., *Cladonia* and *Hypogymnia* spp.). A 5 dm long cylindrat (cylinder-shaped sample plot) was centered on each branch section. We counted the total number of newly established *L. oregana* thalli per cylindrat, including thalli growing on the upper and lower surfaces of the branch segments. We expressed establishment rate per cylindrat as the number of *L.* oregana thalli per square decimeter of bark. Bark surface area was estimated by multiplying branch diameter (in decimeters) by 5π.

Growth experiment

We transplanted lichen thalli into each forest age class. Biomass changes were measured after 1 yr. We used the old-growth associated species *L.* oregana as well as two species that are more abundant in younger forests, *Lobaria pulmonaria* and *Hypogymnia inactiva*. The general design of this experiment was similar to that of the dispersal experiment: three age classes (old growth, young, clearcut), five stands per age class, four trees per stand. Each tree received ten transplants per lichen species for a total of 1800 lichen transplants (600 transplants/species).

Material for transplants was gathered in two sets: one from more open, exposed environments ("sun forms") and one from more shaded, sheltered environments ("shade forms"). We thus attempted to maximize the match between source environment and target environment. We used this strategy because our objective was to evaluate the potential performance of these lichens in contrasting forests, not to evaluate whether individual lichens acclimated to one environment could survive transplanting into another environment. For example, we were not interested in whether a shade-form *Lobaria pulmonaria* could survive when transplanted into a clearcut, but rather whether that species could survive in the clearcut at all. Therefore, lichens transplanted into clearcuts were sun forms, and lichens transplanted into tree crowns were shade forms.

Sun forms and shade forms of *L. oregana* were gathered from the upper and lower crown, respectively, of an 80 m tall *P. menziesii* tree in the H. J. Andrews Experimental Forest (elevation 520 m, stand age ~450 yr). Sun forms of L. pulmonaria were gathered from young Fraxinus trees on an open floodplain meadow near the South Santiam River. Shade forms of L. pulmonaria were gathered nearby from a young, dense Pseudotsuga-dominated forest in lower Canyon Creek. Sun forms of *H. inactiva* were gathered from dead shrubs near a road cut adjacent to a young, thinned Pseudotsuga-dominated forest where the shade forms were gathered. This site was located near the South Santiam River old-growth stand. Lichen thalli were stored dry in a cool, shady environment for 2–3 wk prior to installing the growth experiment.

We constructed transplants by attaching individual lichen thalli to a monofilament loop with a small dab of silicone sealant (McCune et al. 1996). Biomass changes were calculated based on the air-dried mass before and after transplanting and after subtracting the mass of the monofilament + silicone. Corrections to a standard moisture content were made by weighing standard reference thalli of each species, both the standards and the transplants having equilibrated for 24 h side by side in the laboratory. Standards were then oven dried and reweighed. The ratio of air-dried to oven-dried masses of the standards was used to estimate the oven-dried masses of the transplants. Initial oven-dried masses of thalli averaged 0.278, 0.132, and 0.052 g for *L. oregana*, *L. pulmonaria*, and *H. inactiva*, respectively.

We installed transplants in July 1996 by tying them to branches in the immediate vicinity of the dispersal experiment. On branches >4 cm diameter, transplants were tied individually using nylon cord. Ponytail holders (elastic hair ties) attached individual transplants to smaller branches. In all cases, transplanted thalli were attached to the upper surfaces of branches in a natural orientation. We retrieved transplants in July 1997. Their final oven-dried masses were calculated using the method described in the paragraph above. Annual biomass changes for individual thalli were expressed as a percentage of their initial oven-dried masses.

In addition to measuring annual biomass changes, we also visually inspected thalli for evidence of injury. Each thallus was scored for necrosis (percentage of thallus area discolored by death of the fungus) and bleaching (Percentage of thallus area whitened by death of the alga). These injury variables were each used to generate two dependent variables for a given lichen species. The first of these was simply a percentage of thalli per stand sustaining a particular type of injury. The second was a measure of the intensity of injury, calculated as the average percentage of thallus area injured for all thalli sustaining that injury per stand.

Obviously fragmented thalli (i.e., torn thalli missing pieces) were eliminated from the data set prior to analysis of growth data. However, fragmentation was not always obvious; a large proportion of thalli lost mass but appeared to be intact. We therefore removed from the data set thalli with biomass losses greater than two standard deviations below the mean for a given stand.

TABLE 2. ANOVA design for experimental field study of dispersal in the lichen *Lobaria oregana*.

Source of variation	Effect	Design	*F* ratio df†	
			Numerator	Denominator
Age	fixed	3 age classes (CC, Y, OG)	2	12
Stand(age)	random	5 stands per age	12	12
Dispersal	fixed	2 levels (+, −)	1	12
Substrate	fixed	2 types (smooth, rough)	1	12
Dispersal × substrate	fixed		1	12
Age × dispersal	fixed		2	12
Age × substrate	fixed		2	12
Age × dispersal × substrate	fixed		2	12
Dispersal × stand(age)	random		12	12
Substrate × stand(age)	random		12	12
Dispersal × substrate × stand(age)	random		12	180
Residual	random	4 trees per stand	180	
Total			239	

† For a balanced design with no missing data.

The remaining thalli (68%, 70%, and 63% of the *L. oregana, L. pulmonaria,* and *H. inactiva* thalli, respectively) were then assumed to be unfragmented. The average biomass change of unfragmented thalli per tree was used as a dependent variable (hereafter "average annual growth") for each lichen species.

Statistical analysis

We analyzed *L. oregana* establishment data by a four-way, mixed model ANOVA with one level of nesting using JMP 3.1 (SAS Institute 1995). This analysis tested for three fixed effects (age class, dispersal, and substrate), one random effect (stand nested within age class), and seven interactions (Table 2). The nesting was accommodated in the ANOVA by testing the main effects against the stand-to-stand variation within an age class rather than against the error term for the tree replicates within a stand. Since the distribution of residuals had high kurtosis, and variance among some groups (i.e., inoculated vs. control) was moderately heteroscedastic, we applied the Box-Cox transformation (Sokal and Rohlf 1995) to the establishment data. This transformation (i.e., $1.18[\text{number of propagules}]_{0.2} - 1$) succeeded in normalizing residuals and eliminating heteroscedasticity.

We also compared lichen growth and injury between age classes using ANOVA models. Lichen growth data were analyzed by a two-way, mixed model ANOVA with one level of nesting. This analysis tested for one fixed effect (age class) and one random effect (stand nested within age class). The nesting was accommodated in the ANOVA by testing the age class effect against the stand-to-stand variation within an age class rather than against the error term for the tree replicates within a stand. We analyzed lichen injury data by one-way ANOVA. This analysis tested for an age class effect with stands as the unit of replication. Untransformed data satisfied ANOVA assumptions for both models.

A few trees or stands failed to yield data suitable for statistical analysis. The upper crown of one *P. menziesii* tree in stand 1 snapped in a January 1996 windstorm, eliminating the experimental units from this tree. Data from one of the trees in stand 6 were discarded because the controls were accidentally inoculated. All transplants died or were severely injured in stand 8 (see Table 1). Although *Lobaria oregana* transplants had gained biomass (average growth 6–23%) and remained healthy in this stand during a previous year (Sillett and McCune 1998), average annual growth rates for all three lichen species in this stand were sufficiently deviant from observed growth rates in the other young stands to justify deletion of stand 8 from the growth experiment as an outlier (Dixon's test, $a < 0.05$, Sokal and Rohlf [19951). Unequal sample sizes resulting from these missing data were accommodated in ANOVA by applying Satterthwaite's approximation (SAS Institute 1995).

We used single degree of freedom orthogonal contrasts to make multiple comparisons of group means for significant factors with the standard least squares procedures in JMP 3.1 (SAS Institute 1995). Experimentwise error rates were controlled in these comparisons by employing the contrasts in a stepwise manner. Results were considered statistically significant if P (Type I error) < 0.05. We performed retrospective power analyses using JMP 3.1 to determine the minimum effect sizes necessary for statistical powers >80%. Finally, growth and injury data for *L. oregana, L. pulmonaria,* and *H. inactiva* were analyzed separately.

RESULTS

Dispersal experiment

Since ANOVA on both untransformed and Box-Cox transformed establishment data identified the same main effects and interactions as statistically significant (Table 3), we present untransformed group means for simplicity. Establishment of *Lobaria oregana* was 27X higher on inoculated branch segments than on controls (Table 4). Age class and substrate type did not have significant overall effects on *L. oregana* establishment,

TABLE 3. ANOVA summary for field study of dispersal in the lichen *Lobaria oregana*. Original data were expressed as number of thalli per square decimeter of bark.

Source of variation	df	Untransformed			Box-Cox transformed		
		MS	*F*	*P*	MS	*F*	*P*
Age	2	185.71	1.31	0.306	0.39	0.41	0.675
Stand(age)	12	142.95	1.08	0.453	0.97	1.35	0.312
Dispersal	1	3453.27	26.21	<0.001	49.11	67.79	<0.0001
Substrate	1	123.55	4.17	0.063	0.15	1.93	0.190
Dispersal × substrate	1	137.53	4.60	0.053	0.03	0.38	0.548
Age × dispersal	2	208.64	1.58	0.245	1.42	1.96	0.184
Age × substrate	2	126.81	4.28	0.039	0.38	4.84	0.028
Age × dispersal × substrate	2	119.76	4.01	0.046	0.47	5.34	0.021
Dispersal × stand(age)	12	132.53	4.43	0.008	0.73	8.32	<0.001
Substrate × stand(age)	12	29.62	0.99	0.506	0.08	0.88	0.582
Dispersal × substrate × stand(age)	12	29.89	0.97	0.483	0.09	0.59	0.846
Residual	172	30.93			0.15		

but there were three significant interactions (Table 3). First, the effect of substrate type was inconsistent across age classes. Specifically, establishment was higher on inoculated smooth bark than on inoculated rough bark in clearcuts, establishment on smooth bark was lower in old growth than in either clearcuts or young stands, and establishment on smooth bark in clearcuts was higher than establishment on smooth or rough bark in old growth (Table 4). Second, the effect of added propagules was inconsistent across different combinations of age and substrate. Specifically, establishment on inoculated smooth bark was highest in clearcuts, intermediate in young stands, and lowest in old growth. Establishment on inoculated smooth bark in clearcuts and young stands was also higher than establishment on inoculated smooth or rough bark in

TABLE 4. Separation of group means in a field study of dispersal in the lichen *Lobaria oregana*.

Source of variation	Experimental contrast	Least-squares mean (1 SE)	δ
Dispersal?	treatment (T)	8.0[a] (1.07)	4.2
	control (C)	0.30[b] (1.07)	
Substrate†	rough (R)	3.40 (0.51)	2.0
	smooth (S)	4.98 (0 51)	
Dispersal × substrate†			2.0
Treatment	T X R	6.54 (0.72)	
	T X S	9.56 (0.72)	
Control	C X R	0.34 (0.72)	
	C X S	0.26 (0.72)	
Age‡	clearcut	5.12 (1.33)	5.0
	young	5.04 (1.38)	
	old growth	2.36 (1.38)	
Age × dispersal‡			4.8
Clearcut	T	1005 (1.82)	
	C	0.19 (1.82)	
Young	T	9 77 (1 88)	
	C	0.30 (1.88)	
Old growth	T	4 34 (1.88)	
	C	0.40 (1.88)	
Age × substrate‡			2.3
Clearcut	R	3.00[ac] (0.86)	
	S	7.24[b] (0.86)	
Young	R	4 56[abc] (0 89)	
	S	5.51[ab] (0.89)	
Old growth	R	2.76[ac] (0.89)	
	S	1.97[c] (0.89)	

Notes Values are least-squares means (with 1 SE in parentheses) of untransformed data (no thalli/dm^2 bark) Means with different superscript letters for a given contrast differed significantly ($P < 0$ 05) The minimum difference (δ) required for a statistical power >80% is shown in rightmost column

† $N = 15$ stands

‡ $N = 5$ stands per age class.

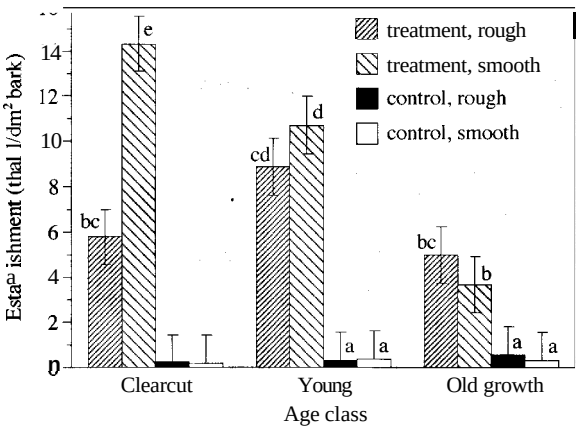

FIG. 1. *Lobaria oregana* establishment after 2 yr by dispersal treatment, substrate type, and stand age class. Data are means ± 1 SE ($n = 5$ stands per age class). Means with different letters differed significantly ($P < 0.05$).

old growth (Fig. 1). Third, stand-to-stand variation in the effect of added propagules was inconsistent across age classes. Specifically, variation among stands was higher in young forests (cv = 88.8%) than in clearcuts (cv = 46.9%) or old growth (cv = 53.7%).

Establishment rates were not uniform within branches. The higher rate of establishment on smooth bark compared to rough bark in clearcuts is attributable to differences in the behavior of propagules on the two substrates. On smooth bark, thalli migrated to the lower surface of the branch where establishment was highest in the dripline. This migration was less evident on rough bark; propagules were trapped in fissures on the upper surface of the branch where they remained fully exposed to direct sunlight and quickly died.

Growth experiment

Lobaria oregana was more sensitive to age class effects than either *L. pulmonaria* or *H. inactiva.* Average annual growth of *L. oregana* was significantly lower in clearcuts than in young forests or old growth (Table 5). Transplanted *L. oregana* thalli lost biomass, on average, in clearcuts, but the biomass of some transplants did increase by >30% (Fig. 2A). Transplanted thalli sustained significantly more injuries in clearcuts than in the other age classes (Table 5). Far fewer thalli remained completely healthy in clearcuts compared to young forests or old growth. Significantly more thalli developed necrosis and bleaching in clearcuts than in young forests or old growth. The area of necrosis and bleaching per injured thallus was significantly higher in clearcuts and old growth than in young forests.

Compared to *L. oregana,* growth of *L. pulmonaria* was relatively unaffected by stand age. Average annual growth rates of *L. pulmonaria* did not differ significantly between age classes (Table 5). Transplanted thalli grew at least as well in clearcuts as in the other age classes. Some *L. pulmonaria* thalli grew very rapidly (>50% annual biomass increase) in all age classes (Fig. 2B). Unlike *L. oregana, L. pulmonaria* transplants sustained significantly more injuries in old growth than in the other age classes (Table 5). Significantly more thalli developed necrosis in old growth than in clearcuts or young forests. The area of bleaching per injured thallus was significantly higher in old growth than in young forests.

Hypogymnia inactiva performed poorly in this experiment. Transplanted thalli lost biomass, on average, in all age classes (Table 5) even though — 30% of thalli gained biomass in clearcuts (Fig. 2C). Unlike either

TABLE 5. Summary of stand age effects on growth and injury of lichen transplants.

Deoendent variable	Age class			*P*	δ
	Clearcut	Young	Old growth		
Lobaria oregana					
Percentage average annual growth	– 10.4[a] (3.2)	4.4[b] (3.4)	9.0[b] (3.4)	0.002	10.1
Percentage transplants healthy	24.2[a] (9.7)	62.8[b] (10.8)	62.0[b] (9.7)	0.028	20.7
Percentage transplants necrotic	65.1[a] (5.8)	3.2[b] (6.4)	14.0[b] (5.8)	<0.0001	12.4
Percentage necrosis/thallus	70.1[a] (7.6)	7.5[b] (8.5)	54.5[a] (7.6)	<0.001	16.3
Percentage transplants bleached	46.4[a] (6.5)	4.7[b] (7.3)	21.3[b] (6.5)	0.004	14.0
Percentage bleaching/thallus	65.6[a] (6.7)	20.0[b] (7.5)	45.9[a] (6.7)	0.003	14.5
Lobaria pulmonaria					
Percentage average annual growth	14.8 (3.6)	10.3 (4.0)	15.2 (3.7)	0.639	11.6
Percentage transplants healthy	69.9 (7.5)	68.2 (8.4)	55.0 (7.5)	0.351	16.1
Percentage transplants necrotic	9.1[a] (4.4)	7.8[a] (4.9)	24.8b (4.4)	0.039	9.5
Percentage necrosis/thallus	40.3 (11.6)	31.0 (13.0)	46.9 (11.6)	0.671	24.9
Percentage transplants bleached	10.6 (4.0)	2.2 (4.5)	18.6 (4.0)	0.059	8.7
Percentage bleaching/thallus	46.3[ab] (7.4)	21.2[a] (8.2)	64.4[b] (7.4)	0.008	15.8
Hypogymnia inactiva					
Percentage average annual growth	– 14.9 (3.8)	–21.5 (4.2)	–18.5 (3.9)	0.508	12.2
Percentage transplants healthy	79.9 (4.3)	84.9 (4.8)	85.7 (4.3)	0.609	9.3

Notes: Values are least-squares means (with 1 SE in parentheses) of untransformed data; $N = 5$ stands per age class. Means with different superscript letters for a given dependent variable differed significantly ($P < 0.05$). The minimum difference between means (δ) required for a statistical power >80% is shown in rightmost column.

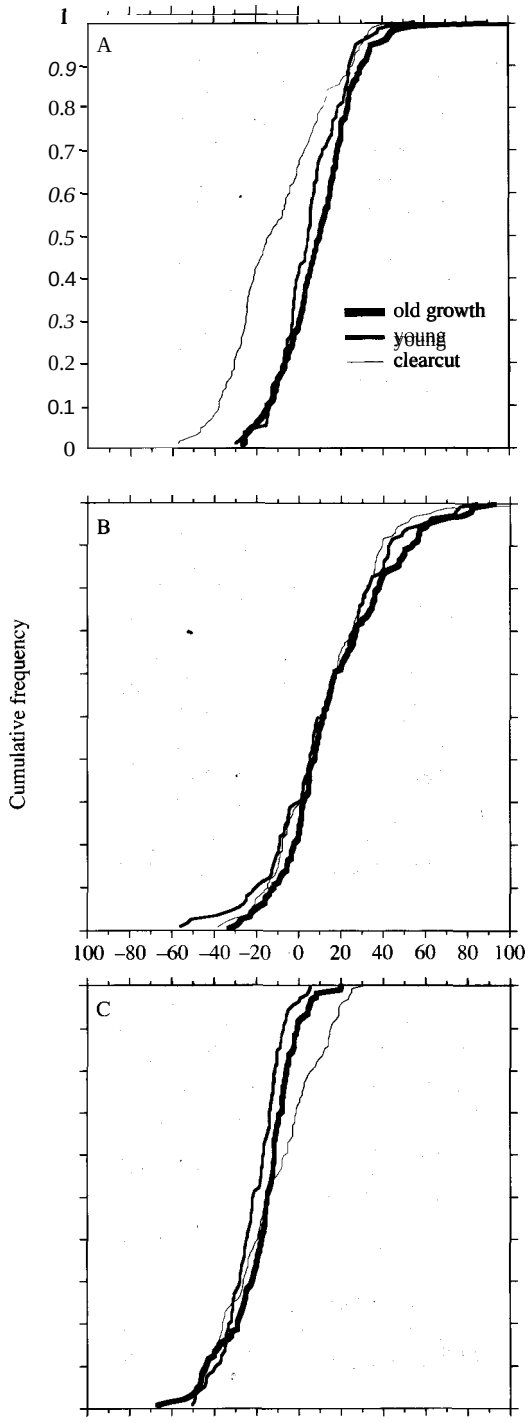

FIG. *2.* Cumulative frequency distribution of transplant biomass changes by stand age class for three lichen species: (A) *Lobaria oregana* (n = 130 transplanted thalli for old growth. n = 116 for young, and n = 137 for clearcut), (B) *Lobaria pulmonaria* (n = 147 transplanted thalli for old growth, n = 116 for young, and n = 152 for clearcut), and (C) *Hypogymnia inactiva* (n = 128 transplanted thalli for old growth, n = 112 for young, and n = 126 for clearcut).

Lobaria species, there were no significant differences in injuries between age classes for *H. inactiva* (Table 5). This may be partly attributable to a difficulty detecting injuries on its finely dissected thalli; too few injuries were recorded to permit statistical analyses of all but one injury variable for this species.

DISCUSSION

The cause of failure of any species to flourish in a habitat can be identified by dividing its life cycle into phases and then examining which of those phases limit population development. We conceptualized the life cycle of an epiphytic lichen as occurring in three distinct phases: dispersal of propagules, establishment of thalli, and growth of established thalli. Our experiments test-

accumulate humus, and form a spongy surface that could either promote or inhibit lichens, Some old-growth associated lichens are strongly associated with moss mats (e.g., *Pseudocyphellaria rainierensis* and *Peltigera britannica*), but *L. oregana* avoids thick moss mats (Sillett 1995) and grows just as well on bare bark as it does on moss (Sillett and McCune 1998). Based on field observations, we rejected the hypothesis that

previous colonization by mosses is required for establishment of *L. oregana* and many other old-growth associated lichcns. We have frequently observed small thalli establishing on moss-free bark, and we have often found vigorous thalli of old-growth associated species on smooth-barked twigs and branches.

Dispersal limitations

The literature on dispersal of lichens is very sparse and speculative. Previous studies (e.g., Bailey 1976, Tapper 1976, Armstrong 1990, 1991, 1992) shed little light on the effectiveness of lichen dispersal at the landscape level. However, poor dispersal has been frequently postulated as limiting the development of populations of old-growth associated lichens (e.g., FEMAT 1993, Sillett and Neitlich 1996, Dettki and Esseen 1998, Sillett and McCune 1998). Our experiment confirms this hypothesis for *L. oregana* by demonstrating establishment of sown propagules in clearcuts, young forests, and old growth.

Observational studies also support this hypothesis. Lichen populations show markedly better development in young forests regenerating from clearcuts near the edges of old-growth forests than in central areas of the clearcuts (Neitlich 1993). Lichen litterfall drops off exponentially as one moves away from cut edges toward the interior of clearcuts (Dettki 1998; B. McCune, *unpublished d ata)*. Large, isolated remnant trees appear to inoculate surrounding younger trees in multi-aged stands such that populations of some old-growth associated species are highest near remnant trees (Peck and McCune 1997, Sillett and Goslin 1999).

Many old-growth associated lichens reproduce primarily by thallus fragmentation or the production of lobules that readily detach. In the case of *L. oregana,* these fragments are hundreds of times larger and presumably less easily dispersed than typical fungal spores (1–3 mm long vs. 10–20 μm long). Other old-growth associated species in the Cascade Range have similarly large propagules (e.g., *Alectoria sarmentosa, Pseudocyphellaria rainierensis, Sticta weigelii, Usnea longissima)* or have sparse, coarse soredia (e.g., *Nephroma occultum).* We also expect these species to be dispersal limited.

In contrast, some old-growth associated lichens appear to be relatively mobile but have specific substrate requirements, such as old bark surfaces or standing coarse woody debris (snags). Many of the Caliciales, lichens well known as old-growth associates (Tibell 1992, FEMAT 1993), invest heavily in thc production of small spores that are probably dispersed by arthropods and birds (Tibell 1994). Thus, our results should not be extended to all old-growth associated lichen species.

Unsuitable microenvironments

Conventional wisdom says that there are important microenvironmental differences between young forests and old growth. These differences presumably arise from structural attributes such as the frequency and size of canopy gaps, abundance of coarse woody debris, and complexity of canopy architecture. These characteristics develop slowly from young, even-aged forests (Kuiper 1988, Spies and Franklin 1991, Van Pelt and North 1996). Humid old-growth Douglas-fir forests also support a large biomass of epiphytic mosses (Sillett 1995), which stores water and ameliorates humidity fluctuations in the canopy (Veneklaas et al. 1990). The important proximal environmental factors operating on epiphytic lichens are moisture regime (i.e., average humidity, frequency of wetting and drying) and availability of diffuse but fairly bright light (Barkman 1958, Stone 1989, Rose 1992, Renhorn et al. 1997). Nutrient availability may also be important (Sillett and Goward 1998, Goward and Arsenault 1999).

Despite all the imaginable distinguishing microenvironmental characteristics of old-growth forests affecting epiphytic lichens, we found that *L. oregana* grew as rapidly in young forests as it did in old growth, confirming the results of Sillett and McCune (1998), who measured average annual growth rates of 16% and 15% for *L. oregana* in young forests and old growth, respectively. Transplants of *L. oregana* survived in clearcuts, but they decreased in biomass and suffered more injuries than in forests. *Lobaria pulmonaria* also performed at least as well in young forests as it did in old growth. Unlike *L. oregana,* however, transplants of *L. pulmonaria* grew rapidly and remained healthy in clearcuts. We conclude that *L. oregana* is less tolerant of wide-open habitats than *L. pulmonaria,* but both species can survive and grow in the full range of habitats included in this study. The poor performance of *H. inactiva* transplants in this study has no clear explanation and needs further study.

Other field observations support our finding that old-growth associated lichens can tolerate young forests and open habitats (see Sillett 1994, Neitlich and McCune 1997, Renhorn et al. 1997). These species frequently flourish in relatively open, stable habitats such as the edges of large gaps, openings along streams, oak savannas, and old shrubs in rocky areas. We occasionally find vigorous thalli of normally old-growth restricted species in young forests. Populations of some old-growth associatcd lichens (e.g., *Alectoria sarmentosa),* however, decline when they are suddenly exposed along the edges of clearcuts (Esseen and Renhorn 1998).

Implications for forest management

Since remnant trees must now be left after many logging operations on Federal lands in the Pacific Northwest (R.O.D. 1994), specific recommendations on the spatial pattern and density of remnant trees are urgently needed in order to take full advantage of their potential as a source of lichen propagules. The problem can be represented by a simple decision matrix (Table

TABLE 6. Decision matrix for maintenance of old-growth-associated epiphytes in managed forests, depending on the factors limiting rates of population development. Our conclusion for *Lobaria oregana* is indicated in boldface type.

Dispersal strongly limiting?	Microenvironments strongly limiting?	
	Yes	No
Yes	Maximize number of retained trees using closely spaced clumps of retention.	Maximize number of retained trees using dispersed pattern.
No	Retain trees as aggregates to conserve as much of the intact habitat as possible.	Green tree retention would not affect epiphyte recovery.

6). For example, if the microenvironments provided by an intact, old-growth forest were necessary to maintain old-growth associated lichens, then leaving trees in aggregates rather than as isolated, dispersed remnants would be important. We found dispersal rate to be the primary factor limiting development of *L. oregana* populations in Douglas-fir forests. Particular substrates and microenvironments found only in old growth do not appear to be essential for establishment and growth of this species in the forest canopy. Therefore, we conclude that maximizing the number and dispersion of remnant trees will maximize the rate of accumulation of *L. oregana* biomass in regenerating forests. If dispersal strongly limits population development of old-growth associated epiphytes, then maintaining an adequate local source of propagules is crucial to the resilience of these species in a managed forest landscape.

Our success at establishing propagules of *L. oregana* begs the question of whether this and other old-growth associated species can be restored in young forests by artificially sowing propagules. It may indeed be possible on a small scale (Scheidegger et al. 1995). Consider, however, the vast area of young forests and the large number of epiphyte species. We can never hope to restore all of them to the landscape by such single-species interventions. Instead, we advocate forest management that recognizes the likelihood of dispersal limitations in epiphytic lichens. The single most important action promoting the propagation of old-growth associated lichens in managed forests will be the retention of propagule sources in and near all cutting units. Maintaining a full complement of epiphytic lichens in managed forests will not only increase biodiversity, but it will also greatly benefit a wide variety of other organisms utilizing lichens.

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