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Distribution of Thalli in a Population of the Epiphytic Lichen *Lobaria oregana* and a Model of Population Dynamics and Production

FREDERICK M. RHOADES

Biology Department, Western Washington University, Bellingham, WA 98225

Abstract. *Data on weight-class distribution, growth rate and asexual propagule (lobule) release are used to analyze populations of the nitrogen-fixing lichen Lobaria oregana in old-growth Douglas fir canopies of western Oregon. A life-table model prepared from observed data is used to produce an estimate of net annual production of biomass, and to analyze the response of a population of this lichen to possible environmental perturbations. The weight-class distribution is similar in each of four trees studied and at different levels within the trees, but differed among the different components of the trees. Survivorship curves (log survivorship versus estimated thallus age) are similar for populations in all trees studied. Estimated net annual production is 31.1% of the standing crop of Lobaria oregana biomass. Mathematical manipulation of matrix formulations of the life-table model indicates that populations would be stable if they recruited 10% of the lobules released each year. In such a configuration, the model population returns to its original size and distribution within 30 years following a simulated storm that removes 90% of the largest thalli and momentarily increases lobule production.*

Study of growth and annual production of lichens has emphasized individual thalli (reviewed by Hale 1973 and Armstrong 1976) or total standing crops of several species in one habitat (reviewed in Pike 1978). There are virtually no studies of the structure of whole lichen populations or the dynamics within them.

Pike (1971) looked at relative numbers and total weight of thalli of *Usnea subfloridana* Stirt. on oak and ash twigs of different ages in Oregon in order to estimate annual production, but did not look at the dynamics of growth of individual thalli. Yarranton (1975) examined the change in distribution of biomass and numbers of podetia of *Cladonia stellaris* (Opiz.) Brodo in successional populations on burnt sites 25 to 55 years of age in Ontario, Canada. Data on the distribution of size classes of podetia were not analyzed because of difficulty in estimating the effect of clonal fragmentation. Armstrong (1978) has examined the pattern of dispersion of *Parmelia glabratula* ssp. *fuliginosa* (Fr. ex Duby) Laund. on slate rock surfaces. He found larger thalli at the top than bottom of the substrate, but identical growth rates among thalli, concluding that colonization had taken place from top to bottom. Further

studies by Armstrong (1981) have shown that substrate topography plays a major role in the entrapment of propagules and their establishment as thalli, and that only a small percentage of propagules become established as thalli.

The dynamics of populations of organisms (growth, mortality, reproduction, potential stability and potential response to environmental perturbations) can be examined by analysis of survivorship curves and life tables (Harper 1977). These types of analyses traditionally have been used to study organisms (insects, birds, seed plants) whose populations show a natural division into ageable groups, and lichens have not been studied in this manner. Lichens are long-lived, reproduce by fragmentation and do not have life histories that fall into specific age classes (Harper & White 1974). Thus, it has been difficult to establish age-specific functions for mortality and reproduction in such populations.

Watson's (1979) study of the variability of populations of mosses is unique, using survivorship curves to analyze the age-class distribution of cryptogams. She was able to show differences among species and among populations of the same species in different environments.

Lefkovich (1965) showed that a modified formulation of life-table analysis developed by Leslie (1945) can be used for a population of organisms grouped in unequal-aged stages. Hartshorn (1975) has used this method in describing the population dynamics of a tropical tree species. Leslie (1945) showed that the dominant root (λ_1) of a matrix of (age-specific) coefficients is equal to e^r , where r is the intrinsic rate of natural increase in the exponential equation of population growth.

$$N_t = N_0 e^{rt}$$

Lefkovich (1965) showed that this was also true no matter how the population was divided up into stages. If $\lambda_1 = e^r = 1$, then $r = 0$ and the population is dynamically stable.

Vandermeer (1975) pointed out the Lefkovich matrix is severely limited, however, because in order to define parameters affecting each stage in the matrix, the population must be assumed to be already stable within each stage. It would be unreasonable to expect a population to be unstable between stages and stable within them, but this possibility is not theoretically prohibited in the Lefkovich model. Ayal and Safriel (1979) stressed the danger of developing circular arguments regarding life table analysis in which some values are derived from others.

Lobaria oregana (Tuck.) Müll. Arg. is an important, nitrogen-fixing, foliose lichen found primarily on conifers in the coastal, Pacific-Northwestern United States and adjacent Canada (Jordan 1973; Pike et al. 1972, 1977; Denison et al. 1972). *Lobaria oregana* may have significant effects on the availability of nitrogen in these forests (Lang et al. 1976; Cooper & Carroll 1978; Caldwell et al. 1979).

Lobaria oregana produces asexual propagules (lobules) on the ridges and margins of older thalli (Jordan 1973), and the mycobiont forms sexual fruiting bodies (apothecia). Samples of thalli from throughout the canopies of Douglas fir record no thalli smaller than the smallest lobules. This supports the view that lobules are responsible for all within-tree and into-neighboring tree propagation and dispersion of this species (Jordan 1973).

Lobaria oregana thalli grow rapidly once they are established, reaching maximum radial rates of almost 10 centimeters per year (Rhoades 1977). Observations of *L. oregana* and many other lichen thalli indicate a maximum thallus size above which thalli are wholly or partly lost to litterfall, or decay of central portions partitions large, old thalli into smaller portions.

The requirement for two mating types for sexual reproduction (heterothallism) has not been demonstrated in lichens (Letrouit-Galinou 1973), but is common in non-lichenized

ascomyetes. If *L. oregana* is heterothallic, ascospores from one mating type would need to germinate in the presence of the necessary algae only rarely to provide a source of genetic recombination for a "clonal" population of another mating type (Bowler & Rundel 1975). There are relatively few lichen species that have both well-developed sexual and asexual reproductive systems. Their mutual presence should give *L. oregana* great ecological versatility in habitats that vary in environmental predictability (Lawrey 1980).

Considering the predominance of asexual reproduction by *L. oregana*, populations of individual thalli are likely to be collections of a few clones rather than of many genetically distinct individuals. Since the amount of genetic exchange is unknown, we chose to regard collections of thalli within one host canopy as functional populations. The distinction made by Harper and White (1974) in separating the effects of genetically different clones from their subunits on population demography and growth could not be resolved here and was disregarded.

We studied the structure of populations of *L. oregana* in order to estimate the annual production of new thallus biomass and the nitrogen supplied as new growth. In addition, an analysis of internal dynamics of a model of the population could be used to test the potential long-term stability of the population and potential reactions of the population to changes in the environment.

In order to assess annual production by populations of *L. oregana*, the following questions were posed. Is the pattern of distribution of thalli of different weights consistent from tree to tree and from branch to branch within a tree? What is the asexual reproductive potential of individual thalli and the population as a whole? Does the pattern of distribution of thallus weights indicate the population has reached a stable structure in the long run? If so, what is the short-term response to major disruptions of the population?

MATERIALS AND METHODS

These studies were made in stands of old-growth conifer forests in the H. J. Andrews Experimental Ecological Preserve, 70 km east of Eugene, Oregon, in the western Cascade mountains. The forests are seral stands typical of moist site *Tsuga heterophylla*/*Rhododendron macrophyllum*/*Berberis nervosa* communities of the *Tsuga heterophylla* zone (Dyrness et al. 1974). Local *Lobaria oregana* populations are dispersed throughout the canopy of these forests.

Thalli in four trees were studied. Three (given the names Neptune—NEPT, El Capitan—CAPT and T201 for convenience) were old-growth *Pseudotsuga menziesii* with diameters of 1.8, 1.8 and 1.1 m at 1 m and heights of 80, 77 and 65 m respectively. One (SLIM) was a younger *P. menziesii* with a diameter of 1.1 m and a height of 55 m. Biomass and structure of these trees and others in the area are discussed by Pike et al. (1977) and Massman (1982). The trees were rigged with climbing ropes and accessed using methods described in Denison et al. (1972). Data were collected during the months between August 1973 and August 1977.

Because we wanted to describe the distribution of individual thalli within the population, and since the sampling was done in conjunction with other studies, a compromise method of sampling weights of thalli was used. This method depended on accurate prediction of the weight of whole thalli from field measurements. Air-dry length (maximum dimension) and width (maximum dimension perpendicular to the length) were recorded for 432 *L. oregana* thalli in situ. These thalli were collected, dried to 85°C overnight, allowed to equilibrate to room temperature for one hour and individually weighed. A computer program was used to produce the following approximately unbiased log-log regression equation (Beauchamp & Olson 1973):

$$\text{weight} = e^{(1.053 \log_e [\text{length} \times \text{width}] - 4.464)} \quad (1)$$

Equation (1) was used to estimate thallus weights from field measurements of air-dry thallus length and width. The variation of actual weights from those estimated by this equation for individual thalli is high (standard error of the $\log_e$ of the estimated weight, $s_{y,x} = 0.482$), but this error cancels out somewhat when making estimates of totals.

The initial sample of thalli showed that numbers of thalli decreased exponentially with increasing

weight. Records of thalli observed in sampling units (as described for various portions of trees below) were grouped into six weight classes (WC 1: 0.0005 g and below; WC 2: 0.0005 + to 0.005 g; WC 3: 0.005 + to 0.05 g; WC 4: 0.05 + to 0.5 g; WC 5: 0.5 + to 5.0 g; and, WC 6: above 5.0 g). In addition, the thalli were scored for the presence of apothecia and lobules.

The weight-class distribution of thalli in the population in each tree was estimated by a modified probability-proportional-to-size sampling method (Pike 1981). Although the mathematical details are not presented here, two stages were involved. First, the tree structure and lichen population were described so that predictions (x_i) of the total weights of *L. oregana* on sampling units in each tree could be made. Second, the predicted total of all sampling units was subdivided into strata, and subsamples were selected with probability proportional to a selection value (v_i) for each sample unit, based on combined predictions of tree structure and lichen biomass. The weight-class distribution of *L. oregana* was determined in each subsample as representative of the stratum from which it was chosen. The information (y_i) from the subsample was then used to modify the original predictions into estimates of the weight-class distribution in the entire tree by equation (2):

$$\hat{Y} = X \frac{\sum_{i=1}^s \frac{y_i}{v_i}}{\sum_{i=1}^s \frac{x_i}{v_i}} \quad (2)$$

where for the i^{th} sampling unit, x_i , y_i and v_i are as defined above, and X is the sum of the x_i 's for the whole tree, $\hat{Y}$ is the tree-total estimate and s is the number of sampling units. Equations used for making predictors and selection values are available from the author. Standard errors for estimates from equation (2) can be approximated by an expression given by Pike (1981).

For convenience of sampling, each of the study trees was divided into three parts: the trunk (the main vertical woody portions), axes (portions of branches greater than four cm in diameter) and branchlets (foliage and the rest of branches less than four cm in diameter). The thalli were sampled separately on each part; the thalli on the trunk and axes were recorded in the field, while a subset of branchlets was returned to the lab for study there. Except where noted below, the details of sampling were as described by Pike et al. (1977).

Lobaria oregana thalli are sparsely dispersed on trunk surfaces of these trees. A record was made of each thallus on trunks of each tree except T201. The height of each thallus was also recorded and the numbers and estimated weights of these few thalli were incorporated into the final tree-totals at the end of calculations for other portions.

On axes, *L. oregana* thalli were recorded on one fifth of the one decimeter-long, belt-shaped sampling units (cylindrats); an initial cylindrical was chosen randomly from the first five adjacent cylindrats, and working sequentially out from the trunk, every fifth cylindrical was sampled. All thalli whose center points of attachment lay inside the cylindrical were recorded.

In the laboratory, portions of the branchlets that were less than four cm in diameter but greater than 15 years of age (by count of terminal bud scars) were sampled by cylindrats in the same manner as the axes were sampled in the field. Portions of the branchlets that were less than 15 years of age were separated from the older wood and the *L. oregana* thalli were recorded on a systematic subsample of these.

The calculations involving estimation of individual thallus weights, keeping accounts of thallus numbers and weights on the various portions of the study trees and the "expansion" of portion-level estimates to tree level estimates by equation (2) were done with computer programs written by R. Rydell and the author. Within each weight class, numbers of thalli and their total weight were tabulated and carried through the sampling and calculations described above. At each level of calculation where fractional numbers of thalli resulted, the values were rounded to the nearest whole number.

In order to examine the dynamics of lobule production and loss on older thalli, 20 *L. oregana* thalli were studied photographically. Thalli with lobules were located throughout the canopies vertically, but were restricted to substrates within two meters of the trunks, including the branch and trunk surfaces. Thalli were photographed in situ periodically for periods up to 1.5 years from October 14, 1975, to July 16, 1977. Photographs were made in situ at one-half life size on 35 mm fine-grain black and white film (H&W Control VTE Pan) using a strobe light source. Prints of previous photos were used to accurately position the view of each thallus in succeeding photographs. To avoid unnatural disturbance of the lobules, the thalli were not sprayed.

At the end of the periods of study, sets of photographs (13×18 cm enlargements) of each thallus were examined. Patches of lobules were delimited on each set of photographs that could be located on each sequential photograph of that thallus (Fig. 1). The locations of patches studied were not chosen

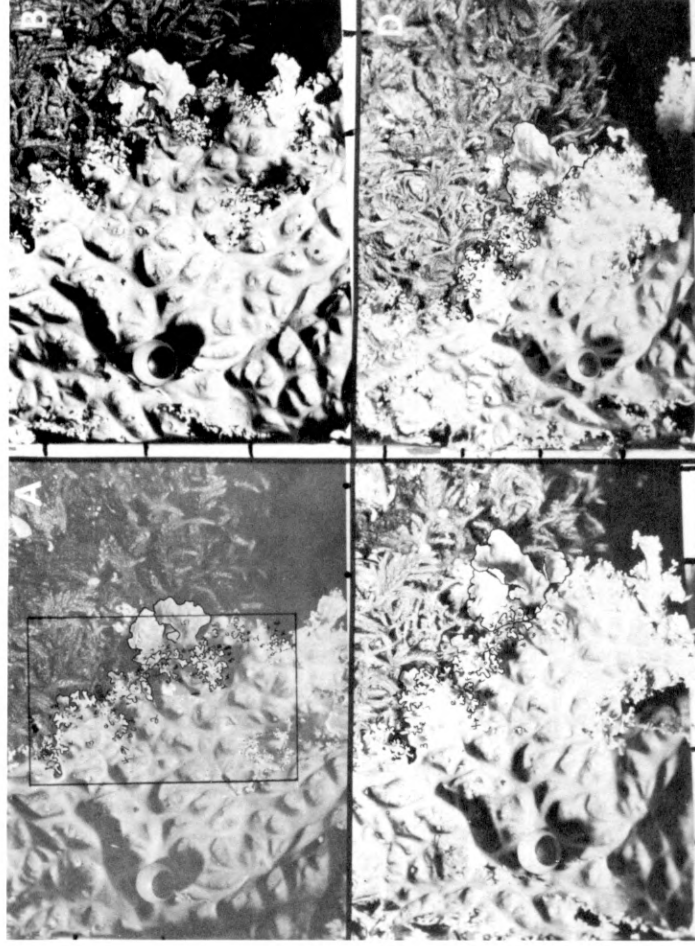


FIGURE 1. Composite photograph showing lobules on surface of the same *Lobaria oregana* thallus and loss of two lobules during a 1.5 year period. Scale markers are 1 cm.

randomly; however, lobules are produced over the entire surface of thalli and a variety of surfaces (both laminal and marginal) were followed. Within the patches, all the lobules less than 4 mm^2 (length $\times$ width) were outlined finely in India ink and lettered. By working with one small area through all the series of photographs, the same lobules could be followed. If a lobule or a part of one was missing, it was scored as lost on the date of that photograph. A rectangular area was drawn on the first photograph of each thallus to enclose all the delimited patches of lobules. Within this area, all lobules were counted, including unmarked lobules. The area of thallus in the rectangle was measured and adjusted to actual cm^2 using the scale included in each photograph. Since there was no attempt to randomize the locations of lobules studied or the rectangular areas in which lobules were counted, estimates of total numbers of lobules may be biased.

RESULTS AND DISCUSSION

Dispersion of thalli in trees. The estimated totals of weights and numbers of *Lobaria oregana* thalli in the four sample trees are presented in Table 1. Because of high standard errors for each weight-class estimate, the distribution patterns are statistically indistinguishable among trees (Kolmogorov-Smirnov Goodness of Fit on relative distribution by weight class). Therefore, the pooled mean-weight-class distribution (separate means of 3 trunks, 4 expanded axes and 4 expanded branchlets, summed at end) is the best estimate for the weight-class distribution for a single tree in the population of Douglas fir from which the sampled trees come (Table 2, Fig. 2). Confidence intervals were calculated for the amounts of the *L. oregana* in each weight class on each tree part as "expanded" to tree totals. The values are not shown in Table 1; they are uniformly as large as the totals themselves.

TABLE 1. Estimated distribution of **total numbers** and total weights (g) of *Lobaria oregana* thalli among weight classes in four sample trees. All values rounded to three significant figures. WC = weight class.

	WC 1	WC 2	WC 3	WC 4	WC 5	WC 6	
Tree	≤0.0005 g	>0.0005 g ≤0.005 g	>0.005 g ≤0.05 g	>0.05 g ≤0.5 g	>0.5 g ≤5.0 g	>5.0 g	Total
SLIM	88,400 5.35	8130 16.7	5790 134.5	3590 406	5420 8970	440 7410	112,000 16,900
T201 ¹	5460 0.88	7960 15.7	5660 88.5	2980 567	1950 3140	107 974	24,100 4790
NEPT	46,000 4.39	11,800 22.3	5200 97.7	3900 674	2500 4450	925 8160	70,400 13,400
CAPT	194,000 17.0	37,100 66.9	20,300 291	10,200 1270	8170 11,500	1210 17,400	271,000 30,550

¹ Trunk was not sampled on T201.

Out of 119,400 thalli weighing a total of 16.4 kg per tree, most thalli (92%) are found in the three smallest weight classes; but these classes account for a negligible portion of the total biomass (1%). The three largest weight classes account for almost all the total biomass, but represent less than a tenth of the total number of thalli in the population.

Separate estimates for total *L. oregana* dry weight were made for three of the sample trees by L. H. Pike (pers. comm.). Although these estimates were obtained using a different sampling procedure, they agree closely with the results presented here. However, several very large thalli were sampled entirely in the largest tree in this study and only partly by Pike (only the portions that fell inside the cylinders were sampled and used to produce estimates for those tree totals). This may have resulted in an overestimation of the number and total weight of thalli in WC 6 in that tree in the present study. Except where indicated below, the mean-weight-class distribution is used in analyzing the structure and dynamics of the *L. oregana* population.

The dispersion of *L. oregana* thalli on the different portions of the tree surface (trunk, axes and branchlets) and the distribution among weight classes on each of these substrates is illustrated in Table 2 and Fig. 3-4. There are very few thalli on trunks of these trees; an average of 13 large thalli (WC 5 and WC 6) accounts for 98% of the biomass found on the trunks, but this biomass is less than 1% of the *L. oregana* biomass on the entire tree. The relatively few thalli on the axes are evenly distributed among weight classes and account for 27% of the total *L. oregana* biomass. Most thalli (97%) are on the branchlets, where small thalli predominate; however, there are enough large thalli to account for 72% of the *L. oregana* biomass estimated for the entire tree. The dispersion of *L. oregana* biomass is similar to that reported by Pike et al. (1977) on a tree not used in this study. The quantities of *L. oregana* on different tree components is a reflection of the relative surface areas of these components (L. H. Pike, pers. comm.), but there is an increase on branchlets over that which would be expected from considering surface area alone. Substrate age on Douglas fir also affects texture, chemistry, light availability, potential for desiccation and potential for damage, fragmentation or loss of thalli by the wind; these are all factors implicated in defining potential habitat for other species in other habitats (Brodo 1973; Armstrong 1981).

Relative distribution of thalli among different weight classes in different levels of the canopy was also examined. Results from sampling units were used to calculate branch-level totals for each of the four sample trees. The numbers and total weights on these

TABLE 2. **Total numbers** and total weight (g) of *Lobaria oregana* thalli in weight classes. Means of four Douglas fir trees (three trunks). Confidence intervals ($\pm 95\%$) for weights were calculated from standard errors associated with the means only. Errors of numbers were of the same relative magnitude for each category. All values rounded to three significant figures. WC = weight class.

Tree component		WC 1		WC 2		WC 3		WC 4		WC 5		WC 6	
Trunk	3	6.37 × 10 ⁻⁴	±1.71 × 10 ⁻³	3	4.74 × 10 ⁻³	±1.71 × 10 ⁻³	8	0.189	1.61	±5.58	8	14.6	73.4
Axes	1020	0.16	±0.17	667	1.46	±2.03	652	74.2	±26.6	435	333	626	294
Branchlets	82,500	6.75	±11.3	15,600	28.9	±40.3	8575	4730	653	4180	374	4690	11,900
Total	83,500	6.91	±11.3	16,300	30.4	±149	9235	5180	729	4520	673	8500	119,000
Ave wt per WC		8.27 × 10 ⁻⁵		1.87 × 10 ⁻³		1.66 × 10 ⁻²		0.141		1.55		12.6	

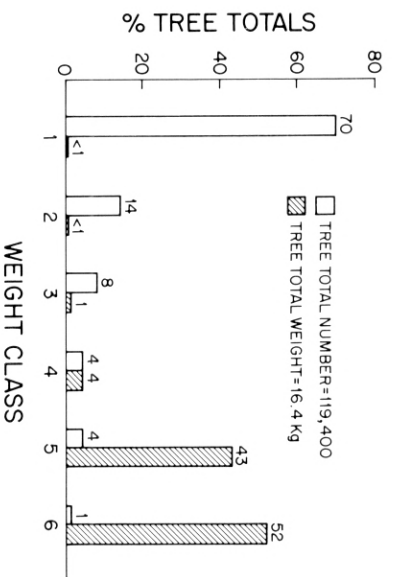


FIGURE 2. Relative distribution of thalli among weight classes in a population of *Lobaria oregana* thalli (mean of four trees). See Tables 1–4 for limits of weight classes.

branches and along the trunk were apportioned among three strata according to their height: upper (above 53 m), middle (40 to 53 m) and lower (below 40 m). Total estimates of numbers of thalli in each weight class on sampling units in each stratum were averaged. Relative distributions of thalli among weight classes within a stratum were calculated from the totals for that stratum (Fig. 5).

The relative distribution in the three different strata is remarkably consistent, even if the lower two weight classes are removed from consideration. Kolmogorov-Smirnov Goodness of Fit tests showed no statistically significant differences between any levels. This is evidence that colonization of the substrate inhabitable by *L. oregana* is height-independent within individual trees and not directed downwards as shown by Armstrong (1978) for *Parmelia glabrata* ssp. *fuliginosa* on slate surfaces in England. It also suggests that there is considerable lateral and vertical movement among different tree canopies. Anyone who has witnessed winter storms in this region would not doubt the potential for even dispersion of lichen propagules by height in these forests.

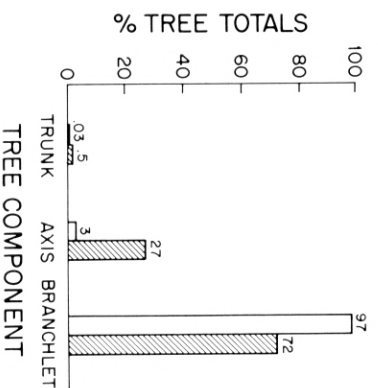


FIGURE 3. Relative dispersion of a population of *Lobaria oregana* thalli on components of the substrate tree. Axes are stems over 4 cm diameter. Branchlets are stems under 4 cm diameter plus foliage. Numbers □ and weights ▨ of thalli in the mean of populations on four observed trees.

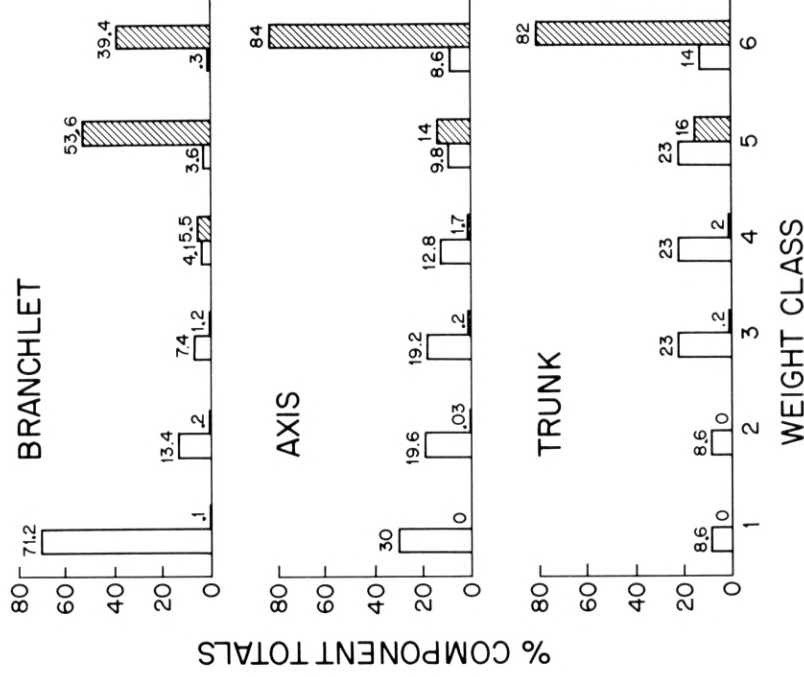


FIGURE 4. Relative distribution of thalli among weight classes on tree components. Axes are stems over 4 cm diameter. Branchlets are stems under 4 cm diameter plus foliage. Numbers □ and ▨ of thalli in the mean of four populations on observed trees for axis and branchlet, and of three observed trunks. See Tables 1-4 for limits of weight classes.

Estimation of thallus age. Analysis of population dynamics by study of survivorship curves requires that the age of individuals be known. Weight-class data recorded here may not be directly related to ages of thalli; however, sequential calculation of the annual growth of a *L. oregana* thallus of age zero (lobule) would produce estimates of the weights of thalli at yearly intervals. Armstrong (1976) used a similar method to estimate ages of thalli of *Parmelia glabratula* subsp. *fuliginosa* from radial growth rates.

The weight of the smallest *L. oregana* thallus recorded during this study is 1×10^{-6} g. Lobules that have been separated from whole thalli and which pass through an 80-mesh screen would have a maximum weight (as calculated by equation (1)) of 2.05×10^{-6} g. 1.5×10^{-6} g is thus a reasonable estimate for the mean weight of the lobules accounting for asexual dispersion of *L. oregana* thalli. Using an equation described previously by Rhoades (1977), annual growth was predicted for this time-zero thallus. This was done sequentially to produce the curve for "average growth" in Fig. 6. Estimates of "minimum-" and "maximum-growth" age-curves were also made by subtracting or adding the 95% confidence intervals to each previous "maximum-" or "minimum-estimate" at each annual iteration. Error bounds associated with ages of larger thalli are considerable when calculated

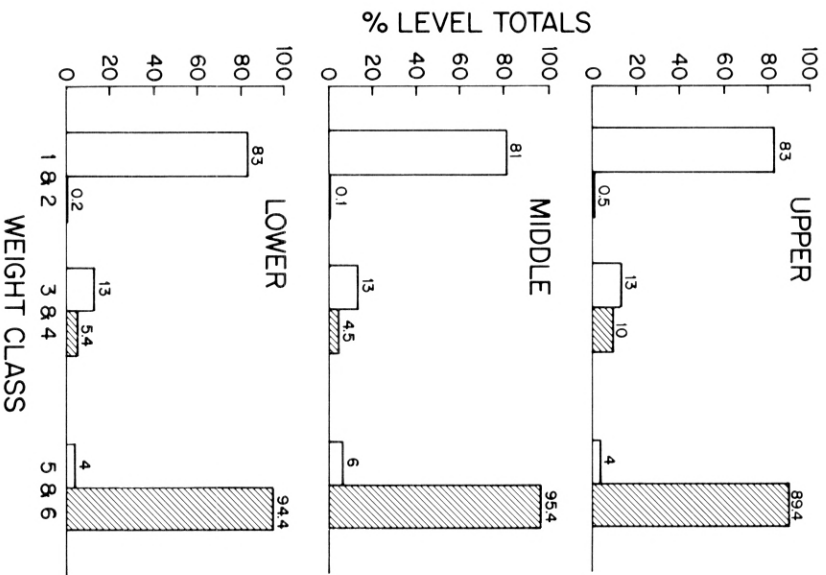


FIGURE 5. Relative weight-class distribution of *Lobaria oregana* thalli from four trees assigned to different strata in the canopy: upper, above 53 m; middle between 40 and 53 m; lower, below 40 m. Percentages of numbers □ and weights ▨ of all thalli observed within each stratum. See Tables 1–4 for limits of weight classes.

in this manner. Since annual growth may vary from year to year around the means predicted, as long as the equation of growth used to make the predictions is unbiased, the actual growth pattern would be closer to the “average” curve than to either error bound.

A model of survivorship. Ages were estimated from data used to make Fig. 6 for thalli at each weight-class lower limit in the estimated populations from each of the four trees and for those thalli in the mean *L. oregana* population. Assuming that the population is stable over time, the distribution of thalli among weight classes is a reflection of the survival of thalli as they increase in age. Survivorship data can then be determined for these populations (Table 3). Survivorship curves (log survivorship versus estimated age) for the four individual populations and the mean population are shown in Fig. 7–8, respectively. Survivorship curves for the individual populations are remarkably similar, being nearly linear over the intervals up to WC 5. This indicates mortality is a fixed fraction of the thalli whose weights fall into those intervals. Further analysis of survivorship was done on the data for the mean population (Fig. 8, Table 3).

Somewhere above the lower limit of WC 5, the slope of the curve changes because

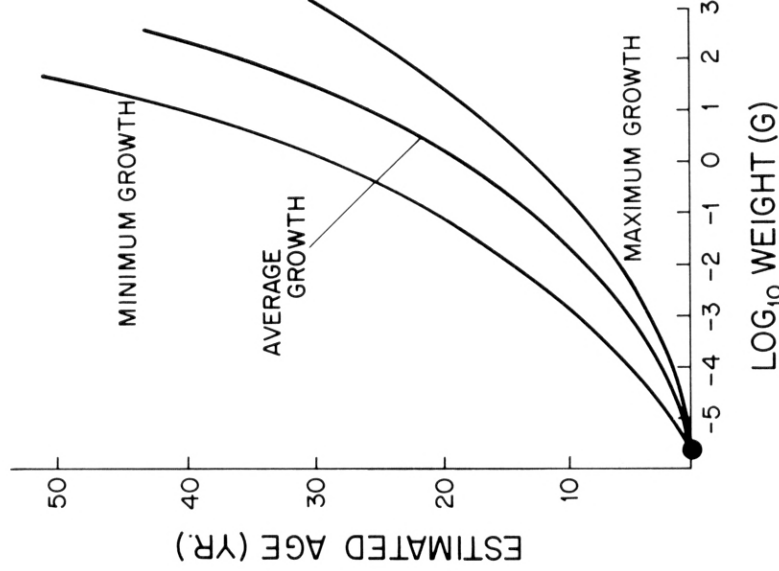


FIGURE 6. Age estimation for *Lobaria oregana* thalli. Average growth from iteration of growth equation in Rhoades (1977) over successive years starting with a thallus weighing 1.5×10^{-6} g. 95% confidence interval estimates of growth at each iteration were added and subtracted for maximum and minimum estimates respectively.

survivorship at the lower limit of WC 6 is consistently lower than would be expected if the linear trend continued within WC 5. Survivorship cannot be calculated directly from the numbers of thalli within WC 6, since it is an open-ended class. The exact nature of the distribution of thallus weights within the three largest weight classes must be known to estimate production. Since thalli in those classes account for 99% of the total biomass, it was expected they would account for most of the production. Thus, further analysis of the survivorship structure in WC 5 and WC 6 was needed. Following is a discussion of how this internal distribution was estimated for the mean population.

The average thallus weight within each class reflects the distribution of weights within that class: the smaller the mantissa of the observed weight, the more skewed towards the lower end of the interval is the distribution. For WC 6, the survivorship at the lower limit age, the total weight of thalli, and the average thallus weight are known. The survivorship of the upper limit of the class (and the entire population) was made arbitrarily small ($\frac{1}{N}$ where N is the number of thalli in the population).

The model of survivorship for *L. oregana* populations was completed by making the following assumptions of the behavior of the survivorship curve in weight classes 5 and

TABLE 3. Estimated age and survivorship values for a population of *Lobaria oregana*, based on mean estimated values for numbers of thalli in four trees. WC = weight class.

	WC 1	WC 2	WC 3	WC 4	WC 5	WC 6
	≤0.0005 g	>0.0005 g & ≤0.005 g	>0.005 g & ≤0.05 g	>0.05 g & ≤0.5 g	>0.5 g & ≤5.0 g	>5.0 g
Age (yr) estimate of lower WC limit	0	4.78	7.66	11.4	16.5	23.3
Number in all classes above lower WC limit	119,393	35,856	19,605	10,370	5194	673
Proportional survivorship at lower limit	1.00	0.300	0.164	0.0869	0.0435	0.00564

6. The weight (age) of the largest thallus in the model population was assumed to be the mean of estimates for the largest thallus produced by two model distributions of thalli in WC 6: one where there was a linear decrease within the weight class of log survivorship against *weight*, such that the mean weight of all the thalli in this distribution was equal to the observed mean weight; the other where there was a linear decrease within the weight class of log survivorship against *estimated age*, such that a thallus of mean age of all the thalli in the distribution would have the weight equal to the observed mean weight. Since survivorship changes curvilinearly within WC 5 rather than abruptly at either limit of the weight class, a transition point within WC 5 was calculated at the intersection of lines extrapolated from WC 4 and WC 6. The actual change in survivorship would lie within the triangle formed by this point and the limits of WC 5. Figure 8 incorporates these assumptions. Of several models that were examined, that used here yields values for total population weight, weight-class-total weights and weight-class-average weights closest to those observed in the mean population (Table 4). Further calculations are based on this model distribution.

Estimate of annual production by growth. The similar age distribution of *L. oregana* from trees of vastly different ages suggests the age structure of *L. oregana* populations is stable with respect to age of host within a broad range of host ages. Since sampling was done at one time and climatic influences supposedly operate on all trees simultaneously, these data cannot shed light on whether age distribution is similar from year to year. If catastrophic environmental perturbations have affected mortality of thalli at different times in the recent past, the survivorship curves do not show it. The old-growth Douglas fir forests of the age studied here produce a slight, annual increase in total biomass (Franklin & Waring 1980), but probably offer little or no change in the total size of habitats available to *L. oregana*. It seems reasonable to think that the population of thalli of *L. oregana* in these old trees has reached a stage of dynamic equilibrium. Thus, in the long run, annual growth of the population is balanced by mortality (litterfall, consumption and decomposition). If the population is assumed to be stable from one year to the next, then the decrease in survivorship with age is an indication of the amount of mortality occurring within each year.

The best estimate of production by the *L. oregana* population is made by summing the annual growth of each individual in the population, then removing from the total that production by thalli not living to grow the entire year. In order to make this estimate the following assumptions are implicit:

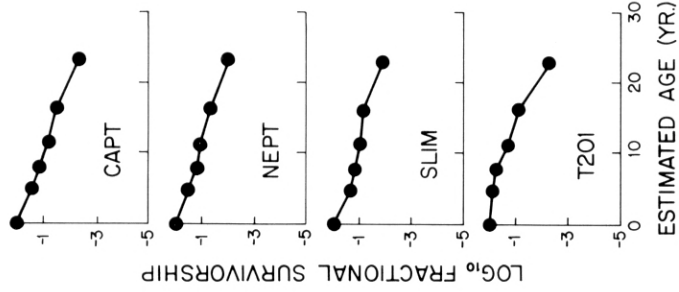


FIGURE 7. Survivorship curves for *Lobaria oregana* populations of each of four trees. ● = Observed values.

- 1) An age-class distribution is defined by the survivorship curve model for the mean population in Fig. 8 and Table 4. Between points where survivorship is calculated directly from the data, or indirectly by other assumptions (within weight classes 5 and 6), log survivorship is inferred to decrease linearly with increasing age.
- 2) The population is in steady state and the difference in survivorship from one age class (thalli grouped into estimated yearly intervals) to the next equals the annual mortality for the younger class.
- 3) Growth, as estimated for individual thalli from the equation given by Rhoades (1977), shows no year-to-year variability and is expressed as annual increases in biomass from August to August.
- 4) Growth is applied to a thallus of average weight within each age class, where the average weight is equal to the mean of the lowest weight and the highest weight found in the class.
- 5) Since growth and mortality are both correlated with moisture (pers. observation of data used by Rhoades 1977 and from litterfall; Rhoades 1978), when some growth occurs, some mortality also occurs. Each can thus be assumed to occur linearly within the year, since production is being estimated from year to year, despite the fact that their individual effects actually may be concentrated during the winter. For purposes of calculation, half the mortality is assumed to occur at the beginning of the year and the other half at the end of the year after growth of all remaining thalli.

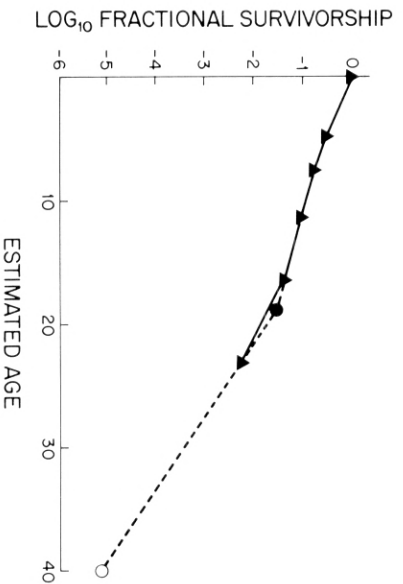


FIGURE 8. Model survivorship curve for mean population of *Lobaria oregana* thalli in four trees. ▲ = observed values, ○ = assumed survivorship and age for last thallus in the population, ● = estimated transition point in WC 5. See discussion.

These assumptions were incorporated into the following equations:

$$N_i = N(S_{i+1} - S_i)$$

$$A_i = \frac{W_i + W_{i+1}}{2}$$

$$W = \sum_{i=1}^n N_i A_i$$

$$P = \sum_{i=1}^n f(A_i) \frac{(N_i + N_{i+1})}{2}$$

$$M_i = N_i - N_{i+1}$$

where N_i is the total number of thalli in age class, S_i is the survivorship at the beginning of the age class, N is the number of thalli in the entire model population, A_i is the average weight of a thallus in age class, W_i is the weight of a thallus at the beginning of age class, W is the weight of the entire model population, P is the total annual production by the population, $f(A_i)$ is the equation of thallus growth from Rhoades (1977) applied to the average thallus weight in age class, M_i is the mortality that occurs within age class, and n is the age of the oldest thallus calculated for the model population.

Estimates of annual production by the studied *L. oregana* populations were calculated from these equations using a computer program. Sample computer output for the various model populations is available from the author. A comparison of the relative rate of production by models of populations in each sample tree is presented in Table 5. Despite the differences in absolute size of these populations, the relative production values are similar. Overall production estimated for the model mean population is 31.1% of the standing crop of *L. oregana*. Estimates of total weight of *L. oregana* in a number of trees show no significant correlation with basal diameter of the trees (Pike 1981). Using his value for the total standing crop of *L. oregana* of 508 kg ha⁻¹ and the relative production value of 31.1% produces an estimate of annual production of 158 kg ha⁻¹ yr⁻¹ for entire watersheds

TABLE 4. Observed and model¹ weight-class distributions of thalli in a population of *Lobaria oregana*. WC = weight class.

WC 1		WC 2		WC 3		WC 4		WC 5		WC 6	
		>0.0005 g		>0.0005 g		>0.005 g		>0.5 g		>5.0 g	
Total wt (g)	Observed	6.9	30.4	153	729	7020	8500	16,450	17,260	119,393	119,392
per class	Model	6.0	30.3	169	973	7808	8273				
Number	Observed	83,537	16,251	9235	5176	4521	673				
per class	Model	83,141	16,393	9377	5321	4509	651				
Ave thallus	Observed	8.27 × 10 ⁻⁵	1.87 × 10 ⁻³	1.66 × 10 ⁻²	1.41 × 10 ⁻¹	1.55	12.6				
wt (g)	Model	7.34 × 10 ⁻⁵	1.85 × 10 ⁻³	1.80 × 10 ⁻²	1.83 × 10 ⁻¹	1.73	12.7				

¹ Survivorship within WC 5 and WC 6 as described by model distribution with the maximum age of a thallus of 40 years (see Fig. 8).

TABLE 5. Annual production by models of *Lobaria oregana* populations in four Douglas fir trees and the four-tree mean.

	CAPT	NEPT	SLIM	T201	Four-tree mean
Model total weight (kg tree ⁻¹)	31.6	13.6	15.3	4.675	17.3
Model production (kg tree ⁻¹ yr ⁻¹)	9.44	4.12	4.55	1.61	5.37
Relative production (% total wt yr ⁻¹)	29.9	30.2	29.8	34.3	31.1

(assuming 40 trees of the size sampled here per hectare old-growth forest: Grier & Logan 1977).

Because the growth-rate equation from Rhoades (1977) is based on thalli that were healthy at the time of measurement, growth for larger thalli may be overestimated since decomposition occurs in particularly large thalli while they are still in place, lowering their effective growth rates. The increase in mortality in WC 6 also suggests this. Although the proportion of *L. oregana* thalli that were beginning to decompose was not measured during the census of the population, climbers estimated that from 5 to 10% of the surface area of larger thalli were necrotic (G. Carroll, pers. comm.). If 10% of the thalli in weight classes 4, 5 and 6 were not growing at the time of the determination of the weight-class distribution, the estimated annual production drops to 28.0% of the standing crop.

Several different models were used initially to test the sensitivity of annual production of a population to changes in several of the parameters which describe the population. Annual production was insensitive to the way survivorship was made to change within a weight class in order to determine survivorship at age-class boundaries (particularly in WC 5 and WC 6. Annual production was estimated for populations assumed to be growing at maximum and minimum limits of growth (as shown by the error bounds in Fig. 6). In formulating these models, not only were the maximum or minimum growth rates estimated for each age class, but the age-class distributions themselves were based on these rates. Annual production is quite sensitive to these changes, even though total population weight is not: annual relative production varied from 18.9% by a population growing at the minimum rate to 52% by a population growing at the maximum rate. Since there are no better estimates of error in the growth-rate equation, these should be regarded as the absolute error bounds for production by *L. oregana* populations. However, since growth is being estimated for a population rather than individual thalli, these bounds are over-liberal.

Reproductive potential. The presence of reproductive structures on thalli from trees distributed among different weight classes shows that the incidence of reproductive thalli was low in weight classes 1, 2 and 3 (0, 0.6 and 1.2% respectively). Larger thalli are proportionately more active reproductively, with some form of reproduction occurring in 29% of thalli in WC 4, 77% of thalli in WC 5 and 88% of thalli in WC 6. Lobulate thalli accounted for 20.8%, 56.6% and 70.6% of the thalli recorded in each of weight classes 4, 5 and 6 respectively.

The results of a contingency table χ^2 analysis of the occurrence of apothecia and lobules on thalli shows that for all thalli recorded, there is a significant interrelationship because of the interrelationship of the occurrence of each form of reproduction and weight class. Analysis of thalli within weight classes shows, in general, that apothecia and lobules are not significantly interrelated.

Contingency table analyses were made between presence of reproductive structures and

TABLE 6. Lobule density and loss from *Lobaria oregana* thalli in two Douglas fir trees (SLIM & CAPT).

Thallus identification	Weight class	Density (lobules cm ⁻²)	Lobules lost (lobule ⁻¹ yr ⁻¹)	Lobules lost (cm ⁻² yr ⁻¹)
SL5	6	15.62	0.137	2.14
SL6	5	22.78	0	0
SL11	6	13.20	0.127	1.68
SL12	5	24.75	0.090	2.23
SL13	6	22.27	0.042	0.935
SL14	5	28.71	0	0
SL15	6	12.32	0.114	1.40
SL20	6	29.71	0	0
SLIM mean		21.17	0.0638	1.05
±95%		±5.5	±0.049	±0.80
CP1	6	24.44	0.488	11.9
CP2	6	25.06	0.135	3.38
CP3	5	28.69	0	0
CP4	6	24.97	0.218	5.44
CP5	6	8.95	0.099	0.866
CP6	6	30.48	0	0
CP7	6	35.27	0.110	3.88
CP10	6	18.88	0.128	2.42
CP11	5	19.85	0.158	3.14
CP12	6	15.20	0.368	5.59
CP15	6	21.93	0	0
CP17	6	16.82	0.202	3.40
CAPT mean		22.54	0.159	3.34
±95%		±4.53	±0.093	±2.13

characteristics of the location of thalli within the canopy (height, aspect and substrate diameter). There is no statistically significant interrelationship shown for the presence of any reproductive structures and the characteristics of locations in trees.

Lobule creation and growth were not noticeable on the thalli studied. Once lobules are initiated, they must grow very quickly, comparable to rates as high as 200% annually for very small thalli (Rhoades 1977) and then stop when they reach a certain size. Thus, all thalli examined in this study had already produced their crop of lobules. Most lobules followed did not increase in size during the period of the study.

The density of lobules varied from 9 to 35 per cm² with a mean number of 22 per cm² on 20 thalli in both CAPT and SLIM (Table 6). The relative number of lobules lost in CAPT (0.159 lobule per lobule per year) was three times the value for SLIM (0.0638 lobule per lobule per year). This may have been due to the higher stature of the former tree (thus exposing thalli to a greater amount of weather), but more likely it was due to inadvertent disturbance of thalli by other climbers in CAPT. For this reason, the mean value for lobules lost from thalli in SLIM was used for further calculations. Estimates of lobule loss by thalli in each of the three larger weight classes of the mean population of *L. oregana* were made using the following equation:

$$\frac{\text{lobules lost}}{\text{thallus}_{\text{wci}} \text{ year}} = \frac{\text{lobules lost}}{\text{cm}^2} \times \frac{\text{estimated cm}^2}{\text{thallus}_{\text{wci}}} \times \frac{\text{proportion of}}{\text{thalli with lobules}}$$

where equation (1) of Rhoades (1977) is used to estimate the photographic area of the average thallus in each weight class. The results of these calculations are shown in Table 7.

TABLE 7. Annual lobule production by *Lobaria oregana* thalli in different weight classes in the model population, using the value of lobule loss in tree, SLIM.

Weight class ¹	Average weight	Estimated area	Lobules lost per year		
			Proportion of lobulate thalli	per thallus	per total population
1-3	0.00175 g	0.155 cm ²	0.012	0.0017	181
4	0.141	5.99	0.208	1.23	6370
5	1.55	44.8	0.567	61.5	113,000
6	12.6	260.0	0.706	444	109,000

¹ See Tables 1-4 for limits of weight classes.

Loss of lobules was low relative to the numbers of lobules followed. There was no significant correlation of loss of lobules to either precipitation or estimated number of storms preceding the date of loss. This suggests that asexual reproduction in *L. oregana* is a random event. However, it undoubtedly is influenced by climatic factors to some degree as has been reported previously for other species (Jahns 1973; Pyatt 1973; Bowler & Rundel 1975).

A crude calculation of the annual dry matter production by the mean population in the form of lobule loss, assuming a lobule weight of 1.5×10^{-6} g and using the rate of loss for thalli in SLIM, is 0.34 g yr⁻¹, clearly an insignificant amount. The values for rates of loss calculated here are obviously imprecise and may be in error on the low side due to the location of thalli studied (close to the trunk and away from the effects of high wind). They suggest a relative order of magnitude for this type of event.

Lefkovich projection matrix model of population dynamics. The Lefkovich projection matrix is a formulation, in vector form, of the population at time *t*:

$$N_t = \begin{bmatrix} n_1 \\ n_2 \\ n_3 \\ \vdots \\ n_s \end{bmatrix}_t$$

where *n*₁, *n*₂, . . . , *n*_s are the number of units in the population in each of *s* stages in the population at time *t*. The numbers at time *t* + 1 are predicted by multiplying *N*_{*t*} by a matrix *M*:

$$N_{t+1} = M_t \cdot N_t$$

where *M* includes as coefficients, fractional probabilities of the effects of each stage on all other stages:

$$M_t = \begin{bmatrix} m_{11}, & m_{12}, & \dots, & m_{1s} \\ m_{21}, & m_{22}, & \dots, & m_{2s} \\ \vdots & \vdots & \ddots & \vdots \\ m_{s1}, & m_{s2}, & \dots, & m_{ss} \end{bmatrix}_t$$

where, the coefficients in row 1 (*m*₁₁, *m*₁₂, . . . , *m*_{1s}) represent the influences of stages 1, 2,

TABLE 8. Life table for the model population of *Lobaria oregana* thalli. WC = weight class.

Number of released lobules										
	WC 1 ¹	WC 2	WC 3	WC 4	WC 5	WC 6	Total number	Fractional mortality ²	Fractional survival ("S")	Weight above which thallus graduates (g)
	unknown	83,537	16,251	9235	5176	4521	673	0	0.234	0.765
								0	0.766	0.805
								1	0.878	0.876
								—	0.333	3.72
								1	0.0515	0
								0	0.874	0.948
								0	0.800	1
								0	1.23	25.0
								0	0	162

¹ See Tables 1-4 for limits of weight classes.

² Mortality as a fraction of the total number of thalli in a weight class. See Table 5.

TABLE 9. Lefkovich matrix for the model population of *Lobaria oregana* thalli.

	0 ¹	1 ^{2,4}	0	0	0	1.23	25.0	162 ³
0 ¹	0	0.679	0	0	0	0	0	0
1 ^{2,4}	0	0.0873	0.540	0	0	0	0	0
0	0	0	0.225	0	0.644	0	0	0
0	0	0	0	0.161	0.767	0	0	0
0	0	0	0	0	0.111	0.830	0	0
0	0	0	0	0	0	0.0451	0.679	0

¹ First diagonal = Annual survival ("S" × "R" in Table 8).
² Second diagonal = Annual graduation ("S" × "G" in Table 8).
³ First row = Annual fecundity ("F" in Table 8).
⁴ Coefficient m₂₁ = Annual fractional recruitment (see text).

... , s on stage 1 at time t + 1, etc. If stage 1 represents offspring, the coefficients in row 1 represent the number of offspring (fecundity) of each member of each stage. Each diagonal coefficient (m₁₁, m₂₂, etc.) is the proportion of the individuals remaining in each stage multiplied by the survival rate of the stage (survival). Each subdiagonal coefficient (m₂₁, m₃₂, etc.) is the proportion of individuals that move up to the next stage multiplied by the survival rate of the lower stage (graduation). For most organisms, all other coefficients are zero, because individuals do not regress into previous stages (upper right triangle of zeros), nor do they pass through two stages in one time interval (lower left triangle of zeros). The former situation is possible for a lichen such as *L. oregana*, where older, larger thalli fragment or decompose to give rise to slightly smaller thalli which continue to grow in place. The population of *L. oregana* studied here has been divided into different classes based on weight. In order to use life-table analysis to examine this population the following parameters need to be determined:

- 1) The number of individuals in each weight class at time zero.
- 2) The fraction of each weight class that survives each year whether or not the individuals grow enough to move into the next weight class.
- 3) The fraction of those surviving in each weight class that graduate to the next class each year.
- 4) The fraction of the survivors in each weight class that remain in the class each year.
- 5) The fecundity of each weight class.

The first four of these parameters have been determined by field measurements and assumptions based on thallus growth and have been incorporated into the model of the population presented above. In *L. oregana*, parameter 5 (fecundity) includes both reproduction by lobule dispersion and by fragmentation of larger thalli to give slightly smaller thalli. Field data did not distinguish between small thalli that had grown up from lobules and those that were fragments of larger thalli. Survivorship between classes was derived from the weight-class distribution assuming that the overall population was stable. Thus the fragmentation of larger thalli to give smaller thalli (which would appear as actual values in the upper right corner of zeros in the Lefkovich matrix M) is incorporated into graduation values (diagonal parameters of matrix M) which are probably slightly higher than they really would be for the smaller classes. A test of the final matrix showed that its performance as a model of population dynamics did not change if values for survival and graduation were adjusted to account for hypothetical fragmentation.

In the *L. oregana* populations studied, growth and reproduction were measured at least

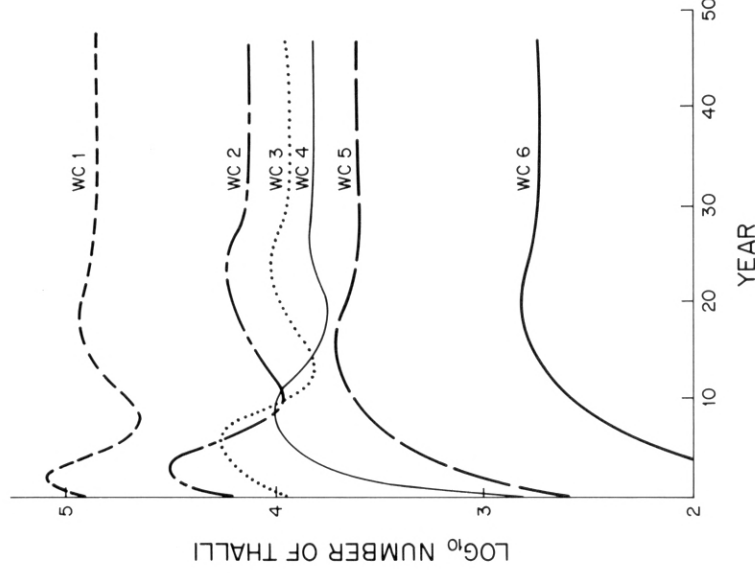


FIGURE 9. Reestablishment of model *Lobaria oregana* population-weight-class distribution following loss of 90% of thalli in WC 4–WC 6 and increase in released lobules (10 times normal – not diagrammed). Data were obtained by successive multiplication of population vector by projection matrix. See discussion. See Tables 1–4 for limits of weight classes.

partly independently of the weight-class distribution. Annual mortality was calculated for each weight class assuming stable age-class distributions from model survivorship curves in conjunction with the estimation of annual production. Unlike Hartshorn (1975) and others who have used independent sets of data in setting up life tables, it has been necessary here to assume overall stability of the population to derive some values for parameters of the life table. The Lefkovich matrix can not be used to prove stability, but it can be used to compare the form of stable models of different populations, to help define other parameters that have not been measured or derived and to test the response of these models to perturbations of the populations.

Table 8 is the life table, and Table 9 the Lefkovich matrix formulation of it, for the model mean population of *L. oregana* with seven stages. Stage “number of released lobules” is an extra stage included to assess the “recruitment” of dispersed lobules. Other stages are weight classes as previously defined. The matrix includes the undefined parameter m_{21} , annual fractional recruitment of lobules. Initial solution of the matrix for λ_1 (the dominant root, equivalent to e^r of the equation of exponential population growth) with m_{21} set at 1 (all lobules are recruited into the population), gave a value of 1.13, indicating the population would not be stable in this configuration. Stability is achieved if m_{21} is set at 0.12. This

indicates that approximately 10% of the dispersed lobules would need to be trapped to cause stability in the population. Armstrong (1981) found that less than 5% of artificially disseminated isidia actually grew into *Parmelia* thalli on slate surfaces.

Similar matrix models were constructed for each of the individual model population distributions from the four sample trees. Values for m_{21} were 0.13, 0.09 and 0.18 for three of the trees studied. These values are close enough to suggest that the populations were behaving similarly. In the model of the population in the fourth tree, no value gave a stable configuration. This is due to a negative mortality in WC 1 for that tree, since there were more thalli in WC 2 than WC 1.

These mathematical formulations of the *L. oregana* population can be used to test the response of the population to environmental perturbations. The results of an unusually violent storm might change the weight class distribution as follows (a somewhat arbitrary set of changes in the model distribution for the sake of illustration):

Dispersed lobule pool increased to ten times the normal (2.5 million):

- WC 1 remains the same
- WC 2 remains the same
- WC 3 remains the same
- WC 4 drops 90% to 518
- WC 5 drops 90% to 452
- WC 6 drops 90% to 67.

Successive annual changes in the population vector by multiplying by the projection matrix M (with $m_{21} = 0.12$) showed that the model population would stabilize within 30 years to its original size and distribution (Fig. 9). Similar results occur with more rapid stabilization if the model is perturbed less violently.

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