

Growth rates of the lichen *Lobaria oregana* as determined from sequential photographs

FREDERICK M. RHOADES

Department of Biology, University of Oregon, Eugene, OR, U.S.A. 97403

Received August 23, 1976

RHOADES, F. M. 1977. Growth rates of the lichen *Lobaria oregana* as determined from sequential photographs. Can. J. Bot. **55**: 2226–2233.

The foliose lichen *Lobaria oregana* (Tuck.) Müll. Arg. is an important nitrogen-fixing component of the canopy epiphyte community in old-growth Douglas fir forests of the Pacific Northwest. This paper presents a non-destructive method for estimating the growth rate (grams per year) for *L. oregana* thalli of different weights.

Photographs were made over a 2-year period of six *in situ* thalli. From a relationship of the photographic thallus area and weight of these and 31 other thalli, the dry weight of each of the six thalli is estimated through time. A growth rate is computed for each thallus and a relationship between growth rate and initial thallus weight is determined. Growth rate (grams per year) = $\exp(-0.8581 + 0.8444 (\log_e \text{initial weight (grams)}))$. The maximum radial growth rate of lobes of *L. oregana* determined from the photographs (9.4 mm/year) is comparable with rates for similar species.

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Le lichen foliacé *Lobaria oregana* (Tuck.) Müll. Arg. est un important fixateur d'azote faisant partie de la communauté des épiphytes de l'étage arboré dans les forêts de sapin de Douglas à maturité, dans le 'Pacific Northwest.' Ce travail décrit une méthode non destructive permettant d'estimer le taux de croissance (grammes par an) des thalles du *L. oregana* de différents poids.

Au cours d'une période de 2 ans l'auteur a photographié six thalles *in situ*. En reliant les surfaces photographées de ces six thalles ainsi que de 31 autres avec leurs poids, un estimé du poids sec de chacun des six thalles, en fonction du temps, a été obtenu. Enfin un taux de croissance est calculé pour chaque thalle et une relation entre le taux de croissance et le poids initial du thalle est établie. Taux de croissance (grammes par an) = $\exp(-0.8581 + 0.8444 (\log_e \text{poids initial (grammes)}))$. Le taux d'accroissement radial maximum des lobes du *L. oregana* déterminé à partir des photographes (9.4 mm/an) est comparable aux taux d'espèces similaires.

[Traduit par le journal]

Introduction

Lobaria oregana (Tuck.) Müll. Arg. is the most abundant lichen in the canopy of many stands of old-growth Douglas fir (*Pseudotsuga menziesii* (Mirbel) Franco) in western Oregon (Pike *et al.* 1972, 1975). Because of its ability to fix atmospheric nitrogen (Marie Roose, unpublished data; Demison *et al.* 1976) and the relatively high proportion (56%) of the total epiphyte nitrogen (Pike *et al.* 1972), we wanted to predict the annual growth of *L. oregana* populations. This paper reports a study designed to estimate growth in dry weight of *Lobaria oregana* thalli. Radial growth rates are also determined since they are commonly discussed in the literature.

Thallus growth has been measured in terms of radial, diametral, or areal dimensions (Hale (1973) and Armstrong (1975) are recent reviews). However, previous studies have neither indicated the relationship of these measures to thallus

weight nor derived estimates of thallus biomass growth from them. Growth rates are best expressed in relative terms, either square centimetres per square centimetre time or grams per gram time (Woolhouse 1968; Farrar 1974).

Recent studies of lichen growth have used photography to record changes in thallus size. This method was first used by Frey (1959) on groups of terrestrial lichens in areas several metres wide and on closeup studies. Hale (1970) has used extreme close-ups to analyze the pattern of growth of lobes of *Pseudoparmelia caperata*. Phillips (1969) examined growth rates of three lichen species (*Lobaria pulmonaria*, *L. quercizans*, and *Menegazzia terebrata*) growing on *Acer rubrum* in Tennessee by photographic methods. Yarranton (1975) has examined clonal growth in populations of *Cladonia stellaris* (Opiz.) Brodo in northern Ontario by tracing clones on a series of photographs over a 6-year period.

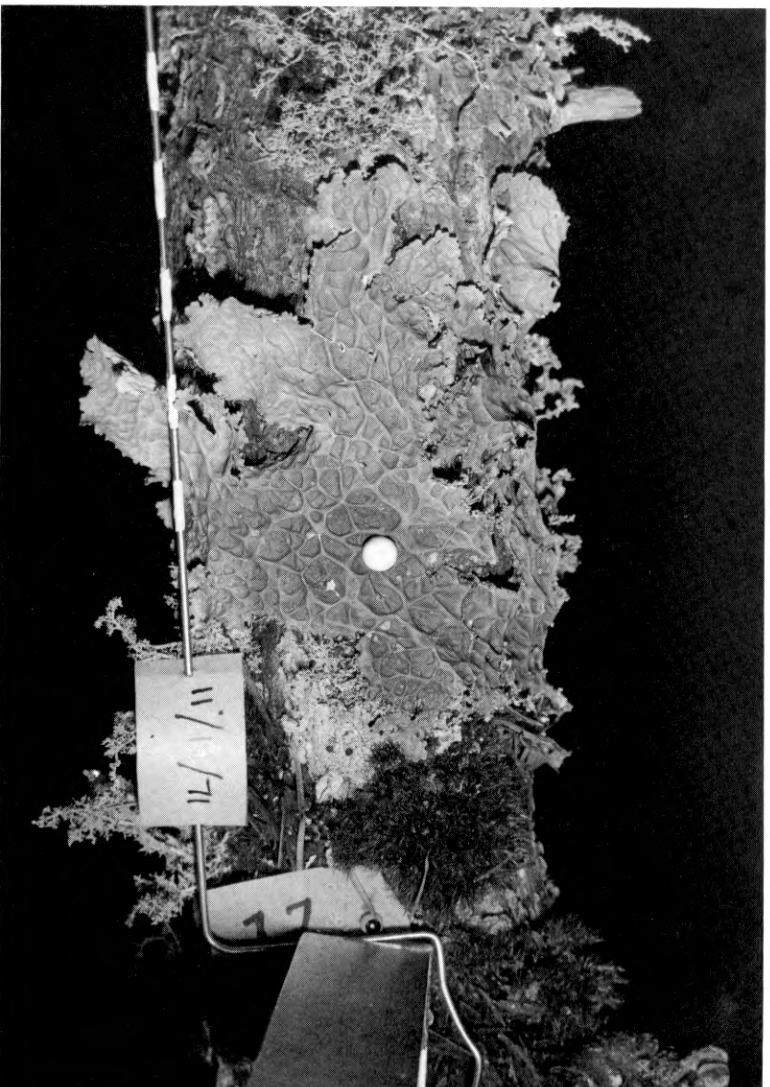


FIG. 1. A large *Lobaria oregana* thallus (No. 17). Note the reticulated thallus, the delimitation of several main lobes of active growth, and the formation of lobules on the older margins of some of these lobes. The center point of attachment is on the upper right edge of the substrate, a Douglas fir branch. Wire scale is in centimetres.

Study Site

The *L. oregana* population of one Douglas fir (International Biological Program (IBP) stem map tree No. 201; diameter at breast height (DBH), 130 cm; height 70 m; age, 473 years) was studied. The study tree was located at an elevation of 500 m in watershed 10 of the H. J. Andrews Experimental Forest in the Blue River District of the Willamette National Forest, located in the western Cascade Mountains about 70 km east of Eugene, Oregon. The surrounding stand of old-growth *Pseudotsuga menziesii*, clear-cut in 1975, had an understory which included *Tsuga heterophylla* (Raf.) Sarg. and *Acer circinatum* Pursh, typical of the *Tsuga heterophylla* zone of the western Cascade mountains (Franklin and Dyrness 1973). Precipitation and temperature data for the period of the study were compared with 20-year (1952–1973) averages for the H. J. Andrews weather station. The precipitation varied from 315 cm during the first

season (August 1971 to July 1972) to 162 cm during the second season (August 1972 to July 1973) compared with the 20-year average of 229 cm for the same period. The monthly averages of daily maximum and minimum temperatures were within 1°C of the 20-year averages for the area.

Methods

Access to the *Lobaria oregana* population of the study tree was provided by the use of a modified rock-climbing technique described by Denison *et al.* (1972). In October 1971, study thalli were located on the trunk and easily accessible branch systems and the first photographs were taken of each thallus. The thalli were chosen to include a range of sizes and locations in the tree. Tacks were positioned next to the thalli so that the area and orientation of subsequent photographs were identical with the first. Figure 1 is the entire 35-mm frame of thallus No. 17 on November 19, 1971, showing the relationship of the two tacks to the photographic field. The area photographed was saturated with stream water and allowed to rehydrate if necessary. An internal centimetre scale was

TABLE 1. Study thalli, location in tree No. 201, and description. Thalli Nos. 1 and 17 were lost to litter fall during the study. Photoarea and actual and estimated weights as of July 21, 1973

Thallus	Tree height, m	Branch diameter, cm	Photoarea, cm ²	Actual weight, g	Estimated* weight, g
1	55	2	—	—	—
3	55	3	17.18	0.5117	0.495
4	55	2	1.98	0.0639	0.038
6	55	12	73.9	1.7127	2.82
7	55	8	66.3	1.1744	2.48
17	46	7	—	—	—
21a	34	6	0.0528	0.0001	0.000501
21b	34	4	1.62	0.0161	0.0297

*Estimated by equation 1.

TABLE 2. Photoareas, estimated weights (from equation 1), and growth rates of study thalli of *Lobaria oregana*. Growth rate (grams per year) is the slope of the regression line fitted to estimated weight versus time

Thallus	Series	Photoarea, cm ²	Estimated weight, g	Growth rates	
				g/year	g/g·year
3	A	8.31	0.208		
	B	9.69	0.250		
	C	12.66	0.344		
	D	13.19	0.361		
4	E	15.37	0.433		
	F	17.18	0.495	0.160	0.769
6	A	1.00	0.0167		
	B	1.19	0.0205		
	C	1.38	0.0245		
	D	1.47	0.0264		
7	E	1.50	0.0270		
	F	1.98	0.0377	0.00999	0.598
21a	A	48.1	1.69		
	B	53.8	1.93		
	C	57.1	2.07		
	D	64.5	2.39		
21b	E	63.8	2.36		
	F	73.9	2.82	0.578	0.342
21c	A	44.1	1.52		
	B	55.0	1.98		
	C	57.5	2.09		
	D	61.9	2.28		
21d	E	61.7	2.27		
	F	66.3	2.47	0.465	0.306
21e	A	0.0161	0.000122		
	B	0.0216	0.000173		
	C	0.0256	0.000211		
	D	0.0350	0.000307		
21f	E	0.0319	0.000275		
	F	0.0528	0.000501	0.000181	1.49
21g	A	0.624	0.00951		
	B	0.766	0.0121		
	C	1.06	0.0179		
	D	1.22	0.0211		
21h	E	1.33	0.0234		
	F	1.62	0.0296	0.0110	1.15

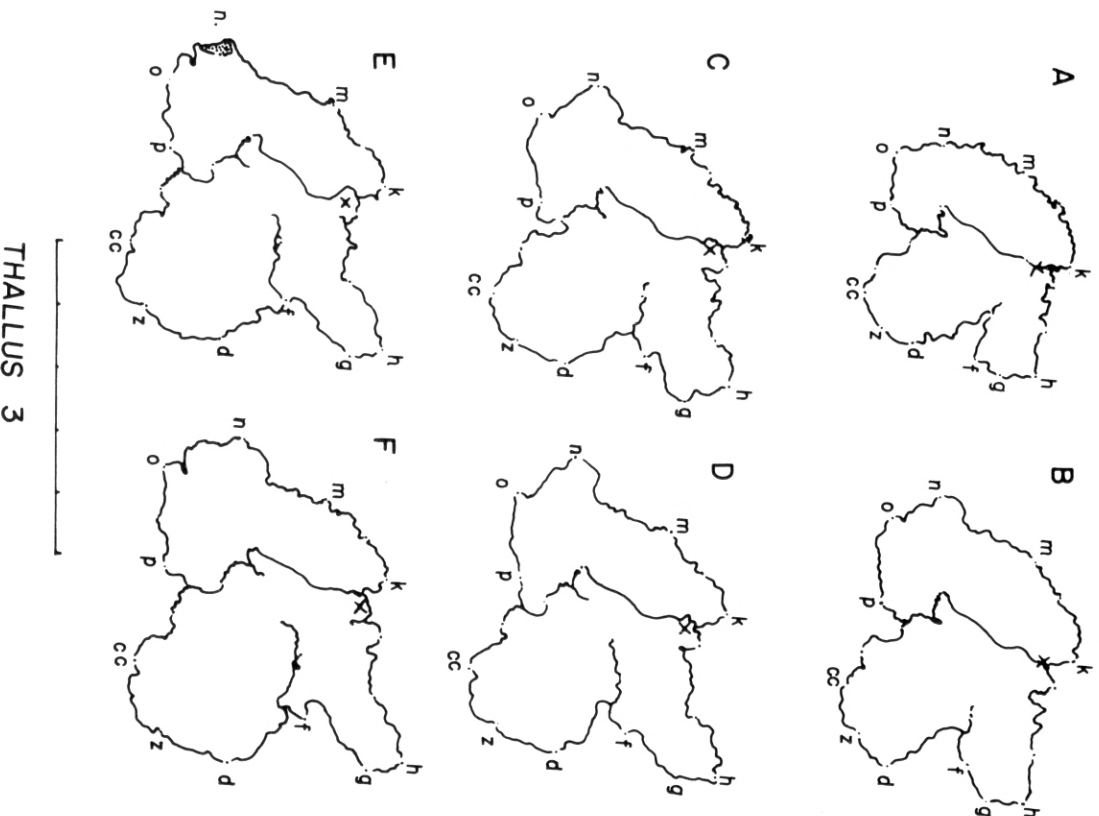


FIG. 2. Tracing of composite photograph used in analysis of growth in thallus 3. Capital letters at upper left refer to series, about 3-month interval between each. Point X was point of attachment. Other letters are points used in radial measurements. Shaded areas are where lobes are folded over in the photographs; those areas are counted twice. Scale is 5 cm.

positioned in the plane of focus in the first photograph and measurements on subsequent photographs were adjusted mathematically to the scale of the first photograph using the distance between landmarks in each photograph. Six series of photographs are analyzed in this study, about one every 3 months (A, 22 October 1971; B, 8 March 1972; C, 26 June 1972; D, 15 November 1972; E, 15 April 1973; F, 21 July 1973). Eight study thalli are analyzed (Table 1).

Figure 2 is a tracing of the photographs used in making the measurements of thallus 3.

Radial measurements from the center point of thallus attachment to various points on lobe tips were made on the photographs and adjusted to constant scale. These

values are grouped into length classes according to the value in series A and averaged.

The photographic area of each thallus was measured by tracing the outer edge of each thallus with a K&E No. 62005 compensating polar planimeter. Thalli less than 0.5 cm² were circled 25 times and the result was divided by 25 for each measurement. In a similar manner, thalli from 0.5 to 1 cm² were circled 10 times, those from 1 to 5 cm² were circled 5 times, those from 5 to 15 cm² were circled twice, and those thalli above 15 cm² were circled once for each measurement. Five separate measurements were made for each thallus and the results were averaged. This method resolves differences in thallus size of 0.005 cm². Error is less than 1% and 10%

TABLE 3. Photoareas and dry weights for 37 *Lobaria oregana* thalli. Study thalli are indicated with an asterisk

Photoarea, cm ²	Dry weight, g	Photoarea, cm ²	Dry weight, g
0.00391	0.00005	2.004	0.0224
0.014	0.00005	1.987	0.0376
0.00706	0.0001	1.9675	0.0430
0.0528*	0.0001	2.8994	0.0484
0.04921	0.0002	3.164	0.0585
0.02578	0.0005	3.8979	0.0591
0.08988	0.0008	1.98*	0.0639
0.2720	0.0008	10.15	0.215
0.210	0.0009	13.911	0.314
0.09068	0.0011	14.23	0.422
0.1331	0.0014	20.593	0.511
0.1411	0.0021	17.18*	0.5117
0.3542	0.0033	40.673	1.11
0.3077	0.0041	66.3*	1.1744
0.4437	0.0049	47.61	1.32
0.7095	0.0085	47.58	1.54
1.62*	0.0161	73.9*	1.7127
0.9352	0.0179	99.82	13.7
1.234	0.0221		

in the measurement of area of 74 cm² (thallus 6) and 0.05 cm² (thallus 21a). Photographic areas for each thallus in each of six series of photographs are given in Table 2.

At the end of the study, the six 'study' thalli were removed from their substrates. In addition, 31 thalli ('collected' thalli) were harvested at the end of the photographic study. The photographic area of the 31 'collected' thalli was determined using a planimeter as above. The two sets of thalli were oven-dried at 40°C overnight and allowed to equilibrate to room temperature for 2 h before recording their weight (Table 3).

Results

The relationship of thallus dry weight to thallus 'photoarea' for 37 'study' and 'collected' thalli is shown in Fig. 3. The data are graphed as their natural logarithms to reduce the variance of the weights of larger thalli for regression purposes. The straight-line equation of the regression of the log_e thallus dry weight (grams) on the log_e thallus photoarea (square centimetres) is as follows:

log_e (weight) = -4.256 + 1.191 log_e (area).

To correct for bias in estimates based on log-log regressions (Finney 1941; Beauchamp and Olson 1973), an equation which gives approximations of the unbiased estimates (fit to terms 1/n of Beauchamp and Olson (1973) is used:

[1] weight = exp (-4.093 + 1.192 log_e (area)).

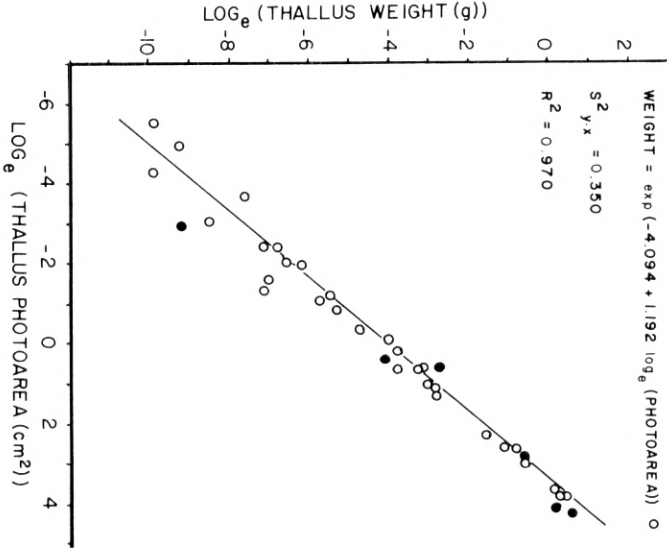


FIG. 3. Regression of log_e (thallus dry weight) on log_e (photoarea) for 37 *Lobaria oregana* thalli. ○, collected thalli; ●, study thalli.

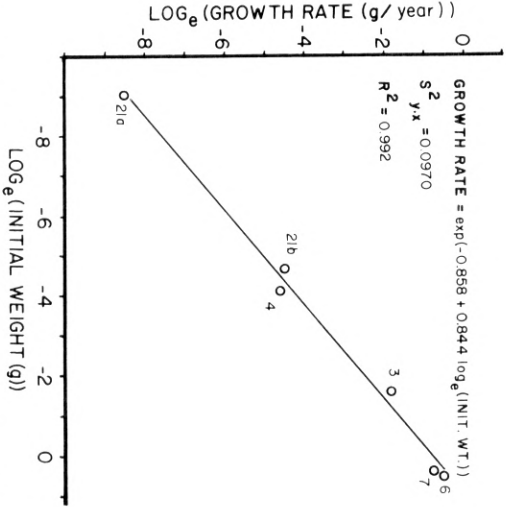


FIG. 4. Regression of log_e (growth rate) on log_e (initial thallus weight) for study thalli of *Lobaria oregana*. INIT. WT. = initial weight.

This relationship is used to estimate dry weights of the study thalli in each of the six series of photographs. The area of a thallus in each photograph is adjusted to the scale of the first

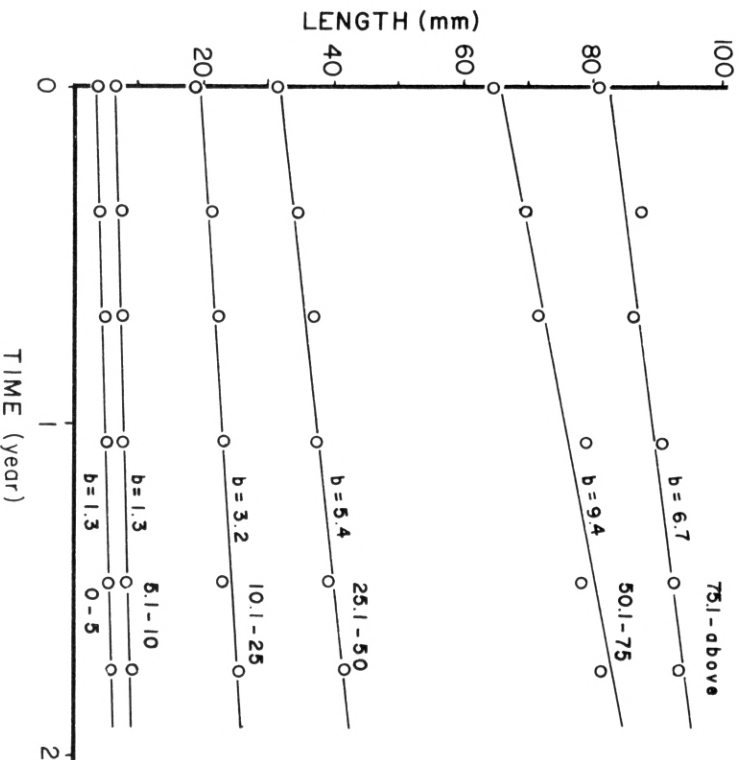


FIG. 5. Increases in radial measurements on photographs of *Lobaria oreghana*. Each point is an average of the lengths in its class (labelled to the right) at each time. Regression lines are fitted through the data for each class; b , slope of the regression equation (millimetres per year).

photograph and the weight is estimated using [1]. A growth rate for each thallus is computed as the slope of the straight-line regression equation

$$\text{weight} = a + b (\text{time})$$

for its sequence of weights over time from October 1971 to July 1973 (Table 3).

The absolute growth rate of a thallus is related to its initial size (Fig. 4). The straight-line equation of the regression of the $\log_e$ yearly growth rate (grams per year) on the $\log_e$ initial estimated weight (grams), adjusted for bias in log-log regressions, is as follows:

$$\begin{aligned} [2] \quad & \text{growth rate} + \exp (-0.8581 \\ & + 0.8444 \log_e (\text{initial weight})). \end{aligned}$$

Alternatively, the following relationship between relative growth rate (grams per gram year) and initial weight can be determined by linear regression of $\log_e$ -transformed data (corrected for bias):

$$[3] \quad \text{relative growth rate} =$$

$$\exp (-0.860 - 0.156 \log_e (\text{initial weight})),$$

$$r^2 = 0.811, \quad s^2_{y.x} = 0.0958.$$

Equations 2 and 3 can be used to predict the rates of dry weight increase for any *L. oreghana* thallus if its initial weight or (with [1]) photoarea are known.

Figure 5 compares the changes in average lobe length of six length classes based on the length in series A: 0-5.0 mm, 5.1-10.0 mm, 19.1-25.0 mm, 25.1-50.0 mm, 50.1-75.0 mm, and 75.1 mm and above. The average radial growth rate (millimetres per year) for each length class is the slope of the linear regression line fitted to the data average length versus time. Growth in the top two length classes is indistinguishable by the t -test but there is a suggestion that growth reaches a peak in the 50.1- to 75-mm class of 9.4 mm per year and decreases with increasing size.

Discussion

The method described here can probably be used for estimation of growth characteristics of other *in situ* foliose lichen thalli. The data provided in Table 3 (estimated weight versus time for each thallus) can be used in several ways to produce estimates of growth rates. Since there appears to be some imprecision in any one series in the values of photoarea (because of changes in thallus orientation and thallus hydration), I felt that the best estimation of growth rate is a straight-line regression which uses all the data. Since the study spans slightly less than 2 years and ends in the middle of the dry summer period when growth is expected to be slower, the growth rates predicted by linear-regression equations may be lower than if there were a final point of data in November 1973 after growth had sped up with the beginning of the rainy weather. Another method of data analysis could take this into account: growth rates are estimated as the average of the difference in estimated weight between series D and A and the differences between series F and C, each spanning a time of 1.067 years. The values obtained from this analysis are comparable with those presented above, but only four of the six series are used in making the estimation.

Another method of analysis involves the calculation of the mean relative growth rate (MRGR) for each thallus (Woolhouse 1968; Farrar 1974; Armstrong 1974):

$$\text{MRGR} = \int_{t_1}^{t_2} \frac{1}{W} \frac{dW}{dt} = \frac{\log_e W_2 - \log_e W_1}{t_2 - t_1},$$

where W = thallus weight and t = time.

MRGRs can be calculated from the data in Table 3 and are comparable with the results shown by Armstrong (1973, 1974) and Farrar (1974); that is, there is a decrease in MRGR with an increase in thallus weight. However, MRGR is a less intuitive measure of relative growth than that shown in Table 2 and predicted by [3] since it compresses the magnitude of changes in larger thalli.

Analysis of covariance and the Newman-Keuls multiple-range test (Zar 1974) show that there is a significant difference between the absolute growth rates of the thalli in Table 2. Those thalli underlined together, below, do not

differ significantly (at 95% confidence level) in their growth rates: 6 7 3 21b 4 21a ← increasing growth rate.

In the thalli used to derive equations 2 and 3, there was no visible indication of consumption, decomposition, or loss to litter fall. Thalli Nos. 1 and 17 were large thalli among the original sample which were lost to litter fall during the course of this study and not used in the analysis. It is expected that the probability of thallus loss increases with size (preliminary analysis of thallus distribution in the study tree confirms but does not quantify this). Decomposition of central portions of very old thalli is often seen, but none of the thalli used in this study showed loss of thallus to decomposition. A portion of the growth effort of older thalli results in lobe production, but this productivity is below the limit of resolution of this photographic method, although the weight of lobules present is included in the original dry weights. Lobules may represent a significant portion of the litter fall and may be an important food source for canopy mammals and invertebrates. All these factors suggest that thallus productivity might be somewhat higher than the value provided by these equations.

If it is assumed that the old-growth Douglas fir *L. oregana* populations are in a state of dynamic equilibrium, losing whole thalli and fragments to decomposition, consumption, and litter fall and gaining an equal amount of dry weight by thallus growth (which is assumed to be uncomplicated by seasonal density changes or production of lobules), these estimates can be used with population thallus weight distribution to predict productivity of this species for entire trees.

The rates of radial growth for lobes of *L. oregana* are comparable with those for other species presented in Hale (1973) and support the general concept of the sigmoid growth curve for lichen growth. Growth rates increase with thallus size. Phillips' (1969) data are comparable: radial growth of *L. pulmonaria* varies from 1.86 to 8.60 mm/year and for *L. quercizans*, from 3.7 to 8.5 mm/year over a 3-year period for different lobes of six different thalli for each species. Although Phillips does not compare the growth rates with the lobes' initial lengths, the ranges are comparable with those presented here and it may be assumed that the pattern of radial growth and probably areal and dry weight

growth for *L. pulmonaria* and *L. quercizans* is similar to that shown here for *Lobaria oregana*.

Acknowledgments

This work was done under support from the Coniferous Forest Biome, U.S. Analysis of Ecosystems, International Biological Program. This is contribution No. 248 to the Coniferous Forest Biome. The author acknowledges the assistance of Dr. L. Pike, Dr. W. Denison, Dr. J. Farrar, and Dr. G. Carroll, who reviewed copies of the manuscript and made helpful suggestions. The work has been in part published as the author's thesis, partial requirement for the degree of Master of Science at Oregon State University.

The following climbers also supported me in this work: Tom Denison, Kathy Lee, Tom Verhoeven, Bruce Caldwell, and Larry Bartell.

- ARMSTRONG, R. A. 1973. Seasonal growth and growth rate-colony size relationships in six species of saxicolous lichens. *New Phytol.* **72**: 1023–1030.
- . 1974. Growth phases in the life of a lichen thallus. *New Phytol.* **73**: 913–918.
- . 1975. Studies on the growth rates of lichens. *In* Lichenology: progress and problems. *Edited by* D. H. Brown, D. L. Hawksworth, and R. H. Bailey. Academic Press, New York. pp. 309–322.
- BEAUCHAMP, J. J., and J. S. OLSON. 1973. Corrections for bias in regression estimates after logarithmic transformation. *Ecology*, **54**: 1403–1407.
- DENISON, R. F., B. CALDWELL, B. BORMAN, L. ELDRED, C. SWANBERG, and S. ANDERSON. 1976. Effects of acid rain on nitrogen-fixation in Washington coniferous forests. *In* Proceedings of the First International Symposium on Acid Precipitation and the Forest Ecosystem. *Edited by* L. S. Dochinger and T. A. Seliga. U.S. Dep. Agric. Gen. Tech. Rep. NE-23, pp. 933–949.
- DENISON, W. C., D. M. TRACY, F. M. RHOADES, and M. SHERWOOD. 1972. Direct nondestructive measurement of biomass and structure in living old-growth Douglas fir.

- In* Proceedings—research on coniferous forest ecosystems—a symposium. *Edited by* J. F. Franklin, L. J. Dempster, and R. H. Waring. U.S. For. Serv. Pac. Northwest For. Range Exp. Stn., Portland, OR. pp. 147–158.
- FARRAR, J. F. 1974. A method for investigating lichen growth rates and succession. *Lichenologist*, **6**: 151–155.
- FINNEY, D. J. 1941. On the distribution of a variate whose logarithm is normally distributed. *J. R. Stat. Soc. Ser. B*, **7**: 155–161.
- FRANKLIN, J. F., and C. T. DYRNES. 1973. Natural vegetation of Oregon and Washington. U.S. Dep. Agric. For. Serv. Gen. Tech. Rep. PNW-8. Pac. Northwest For. Range Exp. Stn., Portland, OR.
- FREY, E. 1959. Die Flechtenflora und -vegetation des Nationalparks im Untergarin. II. Teil: Die Entwicklung der Flechtenvegetation auf photogrammetrisch kontrollierten Dauerflächen. *Ergebn. Wiss. Untersuch. Schweiz. Nationalparks*, **6**: 241–320.
- HALE, M. E., Jr. 1970. Single lobe growth-rate patterns in the lichen *Parmelia cupressata*. *Bryologist*, **73**: 72–81.
- . 1973. Growth. *In* The lichens. *Edited by* V. Ahmadjian and M. E. Hale. Academic Press, New York. pp. 473–492.
- PHILLIPS, H. C. 1969. Annual growth rate of three species of foliose lichens determined photographically. *Bull. Torr. Bot. Club*, **96**: 202–206.
- PIKE, L. H., W. C. DENISON, D. M. TRACY, M. A. SHERWOOD, and F. M. RHOADES. 1975. Floristic survey of epiphytic lichens and bryophytes growing on old-growth conifers in western Oregon. *Bryologist*, **78**: 389–402.
- PIKE, L. H., D. M. TRACY, M. A. SHERWOOD, and D. NIELSON. 1972. Estimates of biomass and fixed nitrogen of epiphytes from old-growth Douglas fir. *In* Proceedings—research on coniferous forest ecosystems—a symposium. *Edited by* J. F. Franklin, L. J. Dempster, and R. H. Waring. U.S. For. Serv. Pac. Northwest For. Range Exp. Stn., Portland, OR. pp. 177–187.
- WOOLHOUSE, H. W. 1968. The measurement of growth rates in lichens. *Lichenologist*, **4**: 32–33.
- YARRANTON, G. A. 1975. Population growth in *Cladonia stellaris* (Opiz.) Pouz. & Vezda. *New Phytol.* **75**: 99–110.
- ZAR, J. H. 1974. Biostatistical analysis. Prentice-Hall, Englewood Cliffs, NJ.