AN ABSTRACT OF THE THESIS OF

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Title: GROWTH IN THE LICHEN LOBARIA OREGANA AS DETERMINED FROM SEQUENTIAL PHOTOGRAPHS

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Abstract approved: William C. Denison

The foliose lichen *Lobaria oregana* (Tuck.) Müll. Arg. is an important component of the upper canopy epiphyte community in old-growth Douglas fir forests of the Pacific Northwest. *L. oregana* contains the secondary phycobiont, *Nostoc* sp., which is capable of fixing nitrogen. This thesis presents a new non-destructive method for estimating the biomass growth rates (g/yr) for *L. oregana* thalli of different dry weights.

Six sequential photographs were made over a two year period of ten *L. oregana* thalli (and thallus lobes considered as thalli) *in situ*. The thallus area (cm^2) of each photograph was measured. From a relationship between "photoarea" and dry weight of these ten thalli and 31 others [Equation (1)], the dry weight of each of the ten thalli was estimated through time. A growth rate was computed and a relationship between growth rate and initial thallus weight was

determined [Equation (2)].

$$\log_{10}(\text{wt.}) = -1.87 + 1.19 \times \log_{10}(\text{photoarea}) \qquad r = 0.98 \qquad (1)$$

$$\log_{10}(\text{growth rate}) = -0.424 + 0.834 \times \log_{10}(\text{initial wt.}) \qquad r = 0.99 \qquad (2)$$

From preliminary data on thalli distribution in the study tree, estimates of productivity of L. oregana and of fixed nitrogen are established. The study tree contained 7.60 kg of L. oregana. These thalli produce 2.56 kg of new thallus biomass per year for a turnover rate of 33.7%. The fixed nitrogen added to the litter from the study tree each year in the form of L. oregana thalli is estimated at 41.8 g.

Growth in the Lichen *Lobaria oregana* as Determined from Sequential Photographs

by

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The OSU Computer Center kindly granted me the funds necessary to carry out the statistical manipulations. Kay Fernald helped in the reproduction of the figures.

This creation is dedicated to Gloria.

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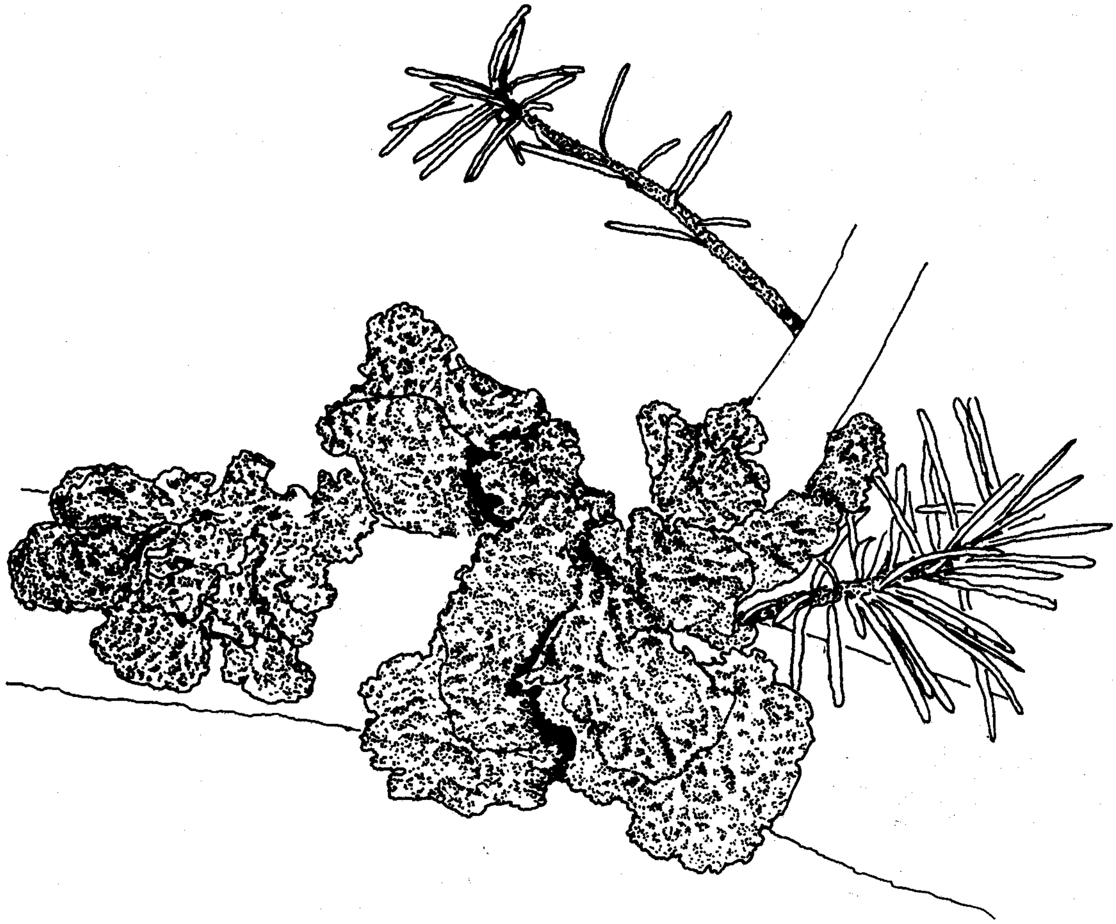


GROWTH IN THE LICHEN *LOBARIA OREGANA* AS DETERMINED FROM SEQUENTIAL PHOTOGRAPHS

I. INTRODUCTION

This thesis presents a new method for the estimation of biomass growth rates and productivity of individual thalli of the lichen *Lobaria oregana* (Tuck.) Mull. Arg. A relationship between the photographic area of a thallus and its dry weight is established. Successive thallus dry weights in photographs of thalli *in situ* can then be estimated and, from a sequential series of such photographs, the biomass growth rates of different thalli can be determined. Studies of linear growth rates were concurrently made for comparison to the traditional literature. Preliminary data on *L. oregana* thallus size distribution is also used to make rough estimates of yearly productivity.

Previous to this study, growth rate determinations have mainly been in terms of linear or areal dimensions (see Hale, 1973, for a review of the literature). A few studies have established biomass productivity for lichens indirectly from destructive sampling of the lichen thalli (Fink, 1917; Scotter, 1963; and Prince, 1974), or from a study of succession of certain species on substrates of known age (Degelius, 1964; and Pike, 1971a and b).

The role played by epiphytes in the Western Coniferous Forest Biome has been under investigation in conjunction with other studies in the U.S. Analysis of Ecosystems -- International Biological Programs. William Denison, Lawrence Pike and students in the Botany and Plant Pathology Department of Oregon State University have undertaken to determine the distribution of species of cryptogamic epiphytes in the crown community of the old-growth Douglas fir habitat type typical of much of the biome. Information has been obtained on biomass and species distribution (Tracy and Nielson, 1971; Pike _et al._, 1972; Denison, 1973; and Pike _et al._, 1974), substrate biomass (Denison _et al._, 1972) and contributions to litterfall and decomposition of the principle lichens and mosses (Rossman, 1972, unpublished data).

Several of the large foliose lichen species of the crown community have been shown to fix atmospheric nitrogen due to the presence of symbiotic blue green algae in their thalli. _L. oregana_, the most abundant species (Pike _et al._, 1974), is the most important nitrogen fixer. Information on the growth rates and size distribution of _L. oregana_ is needed to accurately predict its contribution to epiphytic and fixed nitrogen productivity in this system.

Because of the introduction of a satisfactory technique of access to the crown community (Denison _et al._, 1972) and my own interests in photography, I undertook the following study.

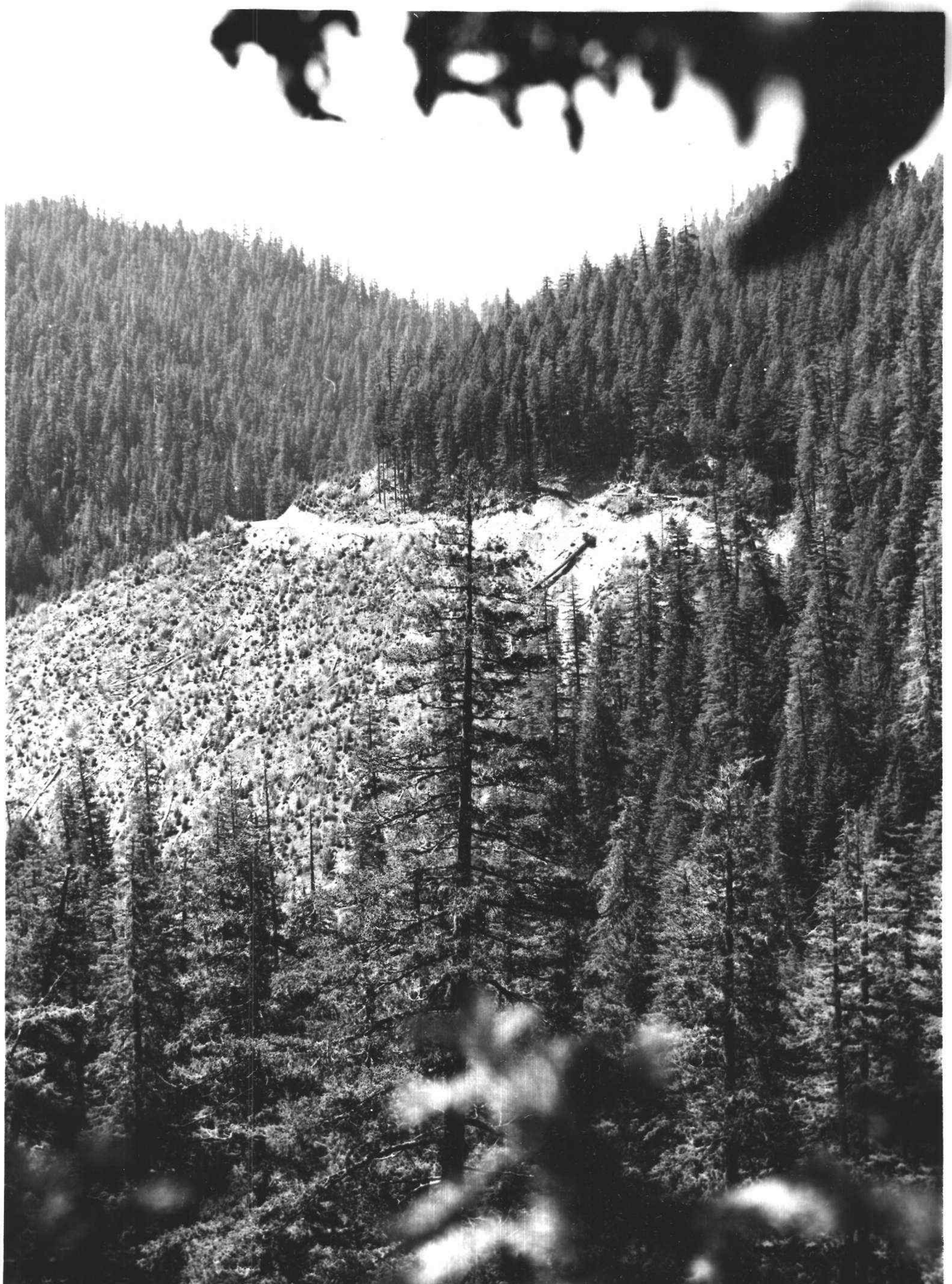
The field work was done between October, 1971 and July, 1973 in a 450-year old Douglas fir located in Watershed 10 of the H. J. Andrews Experimental Forest near Blue River, Oregon.

II. METHODS

A. Study Area

These photographic studies were made on lichens *in situ* in the H. J. Andrews Experimental Forest (44° 10' North Latitude, 122° 20' West Longitude) in the Blue River District of the Willamette National Forest, located in the Western Cascade Mountains approximately 70 km east of Eugene, Oregon. Detailed analyses reported in this thesis were made on the *Lobaria oregana* population in one tree (IBP stem map tree #201, *Pseudotsuga menzesii*: DBH, 130 cm; Ht., 70 m; Age, approximately 450 years), in watershed 10, an approximately ten hectare watershed draining west into Blue River. Tree #201 is located on the southeast bounding ridge of the watershed, approximately 75 m above the mouth of the watershed at an elevation of 500 m above sea level. The tree is growing from a northwest facing slope of about 10° and the surrounding stand of old-growth Douglas fir has an understory which includes western hemlock (*Tsuga heterophylla*) and vine maple (*Acer circinatum*). Figure 1 shows a general view of the area looking southwest out of the top of tree #201. The crown of a tree similar in stature to tree #201 can be seen in the center foreground.

Figure 1. View southwest from the top of tree #201, the study site. The habitat of _Lobaria oregana_ includes most of the crown visible in the tree in the center foreground.



B. Lobaria oregana

L. oregana is a potentially large foliose lichen in the family Stictaceae, commonly found on conifers in moist open woods, and sometimes on mossy rocks or rotting branches in the western portions of northern California, Oregon, Washington and British Columbia. The thallus (Figure 2) is light greenish yellow, loosely attached and has a conspicuously ridged upper surface and a lower surface which is mottled brown and cream and tomentose, particularly around points of contact with the substrate. Neither cyphellae nor pseudocyphellae are present. Apothecia are rare and soredia and isidia are absent (Hale, 1969). The asexual reproductive function of the latter two structures is accomplished by numerous, flat, asexual buds or "lobules" which are produced along the margins and internal reticulation ridges of certain larger thalli (Figure 2). The primary phycobiont is a species of green algae (*Myrmecia*), but a blue green alga (*Nostoc* sp.) is a secondary phycobiont located in internal cephalodia. *L. oregana* is therefore capable of fixing atmospheric nitrogen, and is important in the nitrogen cycle of the type of forest found at the study site (Pike *et al.*, 1972; Pike *et al.*, 1974).

In the study area, *L. oregana* is found as a conspicuous component of the upper trunk (Figure 3), branch system axes (Figures 3 and 4), and branch system branchlet (Figure 4) crown communities

Figure 2. A large Lobaria oregana thallus (#17) in an entire 35 mm frame taken during the study. Note the reticulated upper cortex, the delimitation of several main lobes of active growth and the formation of lobules on the older margins of these lobes. The center point of attachment of this thallus is on the upper right edge of the substrate. This thallus was lost during the winter of 1971-1972.

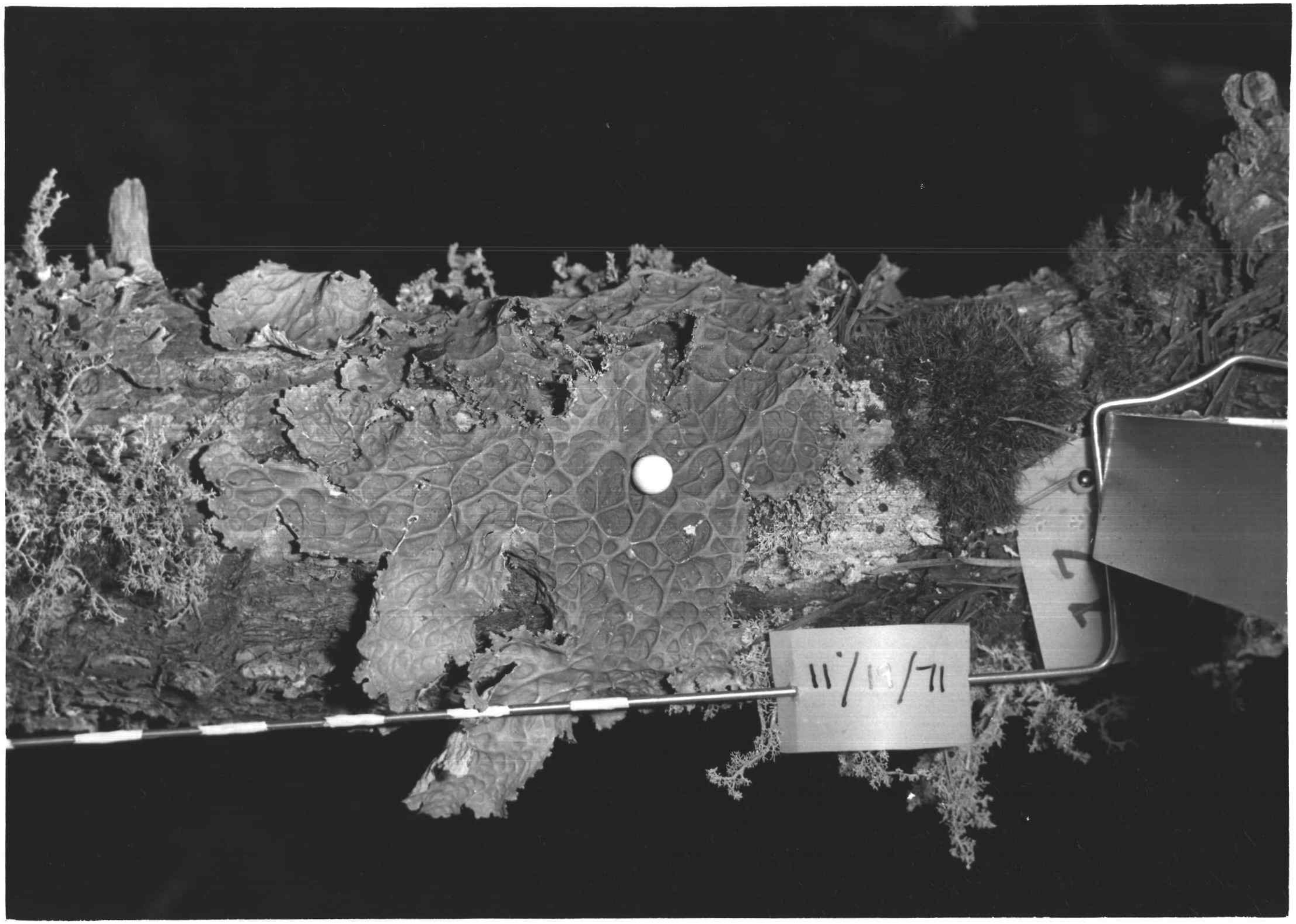

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Figure 3. A view down the trunk of tree #201 from ten meters below the top. Note the large "wads" of *Lobaria oregana* on the upper surfaces of branch system axes, and along the trunk under the climbing rope. The metal ring is a carabiner used in holding the climbing rope to the tree.

Figure 4. A view of a neighboring Douglas fir. Wads of *L. oregana* can be seen on branch system axes and a few thalli can be seen lodged in the outer branchlets and foliage (arrows).

(Pike *et al.*, 1974). The thalli are situated on the upper horizontal or vertical surfaces of the trunk and branch system axes or lodged in the outer branchlet notches. The largest thalli tend to be centered on the upper horizontal surfaces if they occur on branch system axes and drape over either side.

C. Meteorology

Figure 5 presents the precipitation and temperature data for the period of the study, August, 1971 to July, 1973, in comparison to longterm averages (21 year for precipitation; 15 year for temperature) recorded from the main H. J. Andrews weather station located 1 km to the east and at the same elevation as the study area, but in the path of air drainage of the main H. J. Andrews basin. The precipitation was higher than average during the first season and lower than average from August, 1972 to the end of the second season. The monthly averages of daily maximum and minimum temperatures do not show as clear a trend; they are higher than average during late spring and summer, but lower than average during fall and winter of both seasons. Over the entire period, conditions are assumed to be close to normal.

D. Access Technique and Photography

Access to the *L. oregana* population of tree #201 was provided by the use of a modified rock climbing technique described by Denison

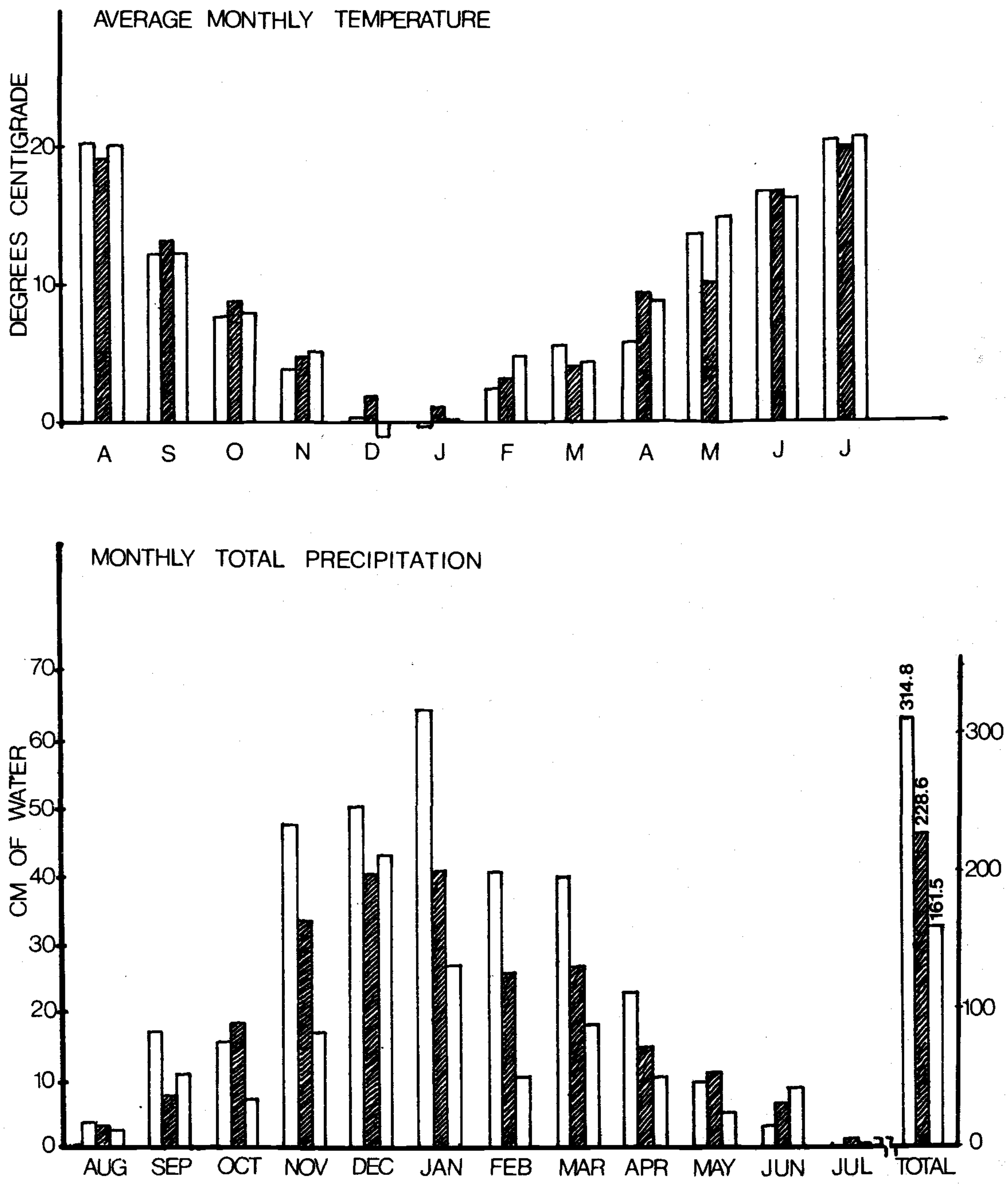


Figure **5**. Meteorological data, one kilometer east of study tree. For each month: shaded bar is the average (1952 – 1973 for precipitation, 1958 – 1973 for temperature); left bar is Aug. 1971 – July 1972; right bar is Aug. 1972 – July 1973. Yearly total (Aug. – July) is graphed lower right.

et al. (1972). The tree was "rigged" with a 75 m length of 11 mm nylon "Goldline" climbing rope along the northeast side of the tree (see Figure 6). This fixed rope remained in place during the course of this study and subsequent climbs were made on it with the aid of "Jumar" ascenders. Following the photographic study reported here, the tree and the *L. oregana* population were analyzed by a modification of the method presented by Denison *et al.* (1972). The diagram in Figure 6 is a simplified presentation of the tree structure at that time. Only the branch system axes (wood greater than 4 cm in diameter) are shown. The angle that the branch systems leave the trunk is an indication of the compass quadrant towards which they face. Secondary leaders are offset to avoid confusion.

On October 22, 1971, 27 stations were established on the trunk and easily accessible branch systems and a first series of photographs were taken. The stations were chosen to include a variety of lichen species, a range of thallus sizes and a range of heights in the tree. Each station consisted of two plastic map tacks and the lichens associated with them. The tacks were positioned on the substrate so that one marked the photographic center of the station and the second, which held an identification label, marked a position such that, when the camera support was adjacent to it and perpendicular to the substrate, the first tack could be centered in the photograph. Figure 7 shows the placement of the tacks and the camera on its support. Figure 2

Figure 6. Tree #201, Watershed 10, H. J. Andrews Experimental Forest, a diagrammatical view from the southeast. Trunk length, diameter and inclination, branch axes (wood to 4 cm in diameter) lengths and compass direction are all drawn to scale. Dashed lines represent dead branches. Secondary leaders are offset to avoid confusion. The upper ten meters of the trunk and branches are not diagrammed because they were not described. Location of the study thalli are represented by the "X's".

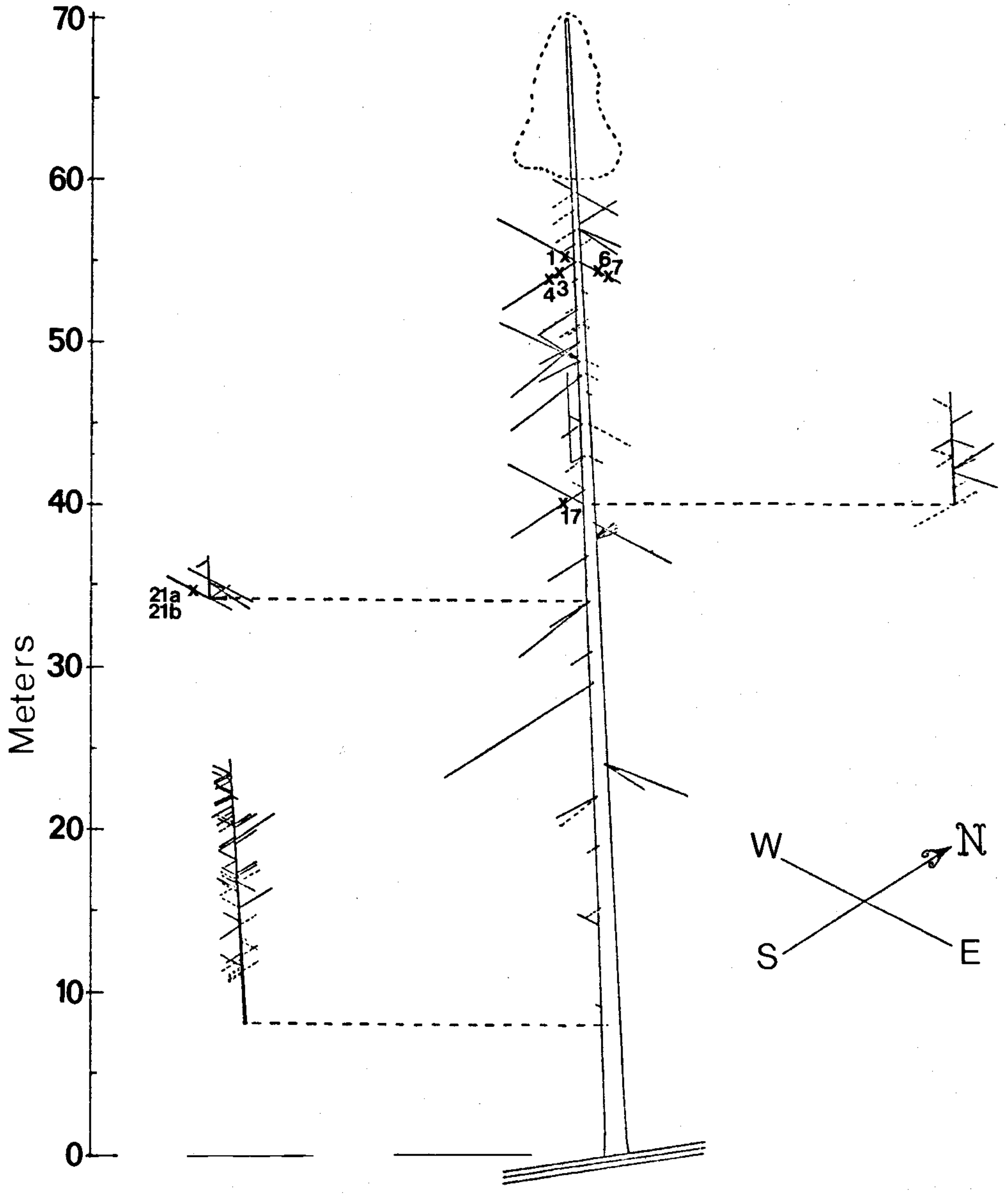
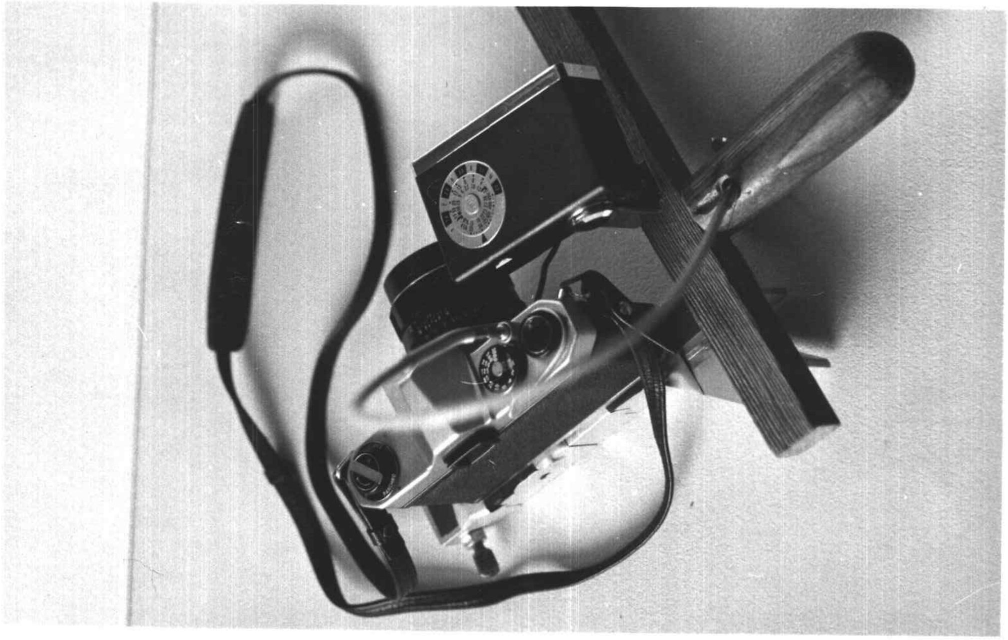
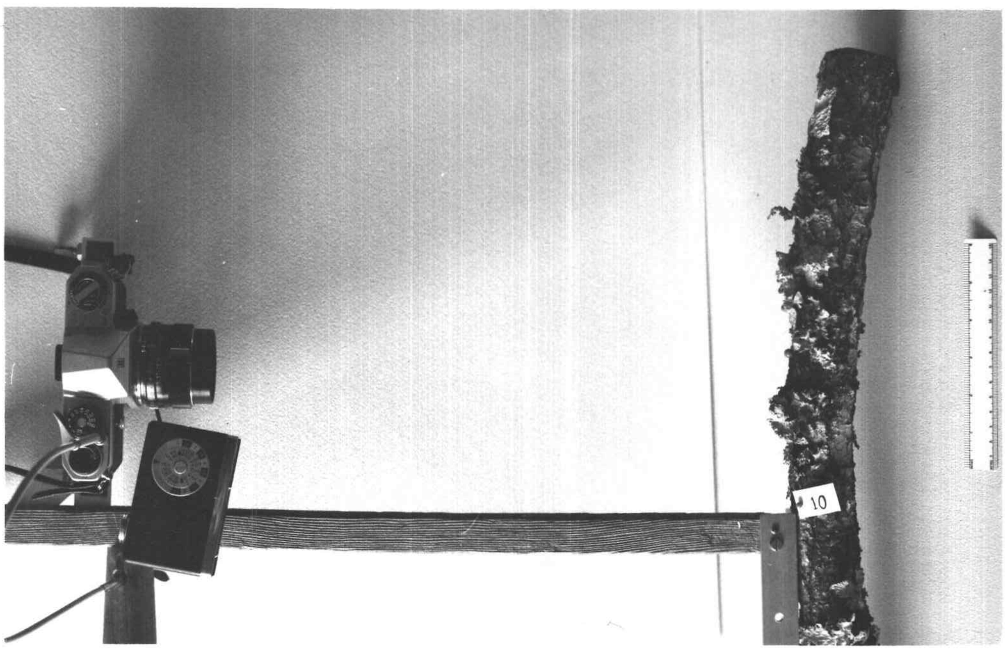


Figure 6.

Figure 7. Placement of marking tacks on the substrate and camera in position on support over the area to be photographed. The electronic flash unit is purposefully aimed to the side of the area.

Figure 8. Pentax "Spotmatic" 35 mm camera and Vivitar flash unit on the support.

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is the entire 35 mm frame taken of Thallus #17 on November 19, 1971, showing the relationship of the two tacks to the photographic field.

Photographs were made using a Honeywell Pentax "Spotmatic" 35 mm camera with a Super-Takumar f:1.8, 55 mm ("normal") lense and a Vivitar Model 161 electronic flash (except the first series of photographs, which was made in available light). The camera and flash were mounted on a support so that the film plane was 50 cm from the support baseline as shown in Figure 7. This provided a subject to film reproduction ratio of seven to one. When the flash was aimed as in Figure 7, an aperture of f/11 gave the correct exposure with flash duration of 1/1000 second using Kodak Panatomic-X film (ASA 32. Tri-X Pan film, ASA 400, was used for the first series). The exposed film was developed according to Kodak instructions using HC 110 Developer, dilution B and the negatives were enlarged onto 20 cm x 25 cm Polycontrast paper to about life size using a Durst 606 enlarger and an EL-Nikkor f:4 50 mm lense.

During the first season, photographs were made at bimonthly intervals, beginning with Series #1. The area of each station was saturated with stream water using a spray atomizer, except those which were naturally wet. Eleven series were made in all, of which six (numbered 1 to 6 in Table 1), representing about one every three months, were used in the analysis in this thesis. Eight study thalli of _L. oregana_ were selected from the original 27 stations for analysis

(Table 2, Figure 6).

Table 1. Six photographic series analyzed in the study.

Series #	Date	Weeks from start	Precipitation between series
1	10/22/71	0	
			233.3 cm
2	3/08/72	19.7	
			53.3
3	6/26/72	35.4	
			32.8
4	11/15/72	55.7	
			105.0
5	4/15/73	77.3	
			20.9
6	7/21/73	91.1	

An internal centimeter scale was positioned in the plane of focus of the photographs in the first four series as shown in Figure 2. Preliminary analysis of the first series of photographs showed it was difficult to enlarge each photograph to exactly life-size using the internal scale as a guide. For the remaining series (the ones used in this thesis), in each photograph used, two landmarks were chosen on the substrate such that (1) the thalli investigated lay between the two points, and (2) the distance between the points was not likely to change due to substrate growth. The distance between these two points was then used as a standard to transform each linear or areal (using the square of the standard distance) observation made to the scale of the enlargement of the first series' photographs, each of which also included two point landmarks. These computed values are used in the

Table 2. Study thalli: description and location in Tree #201.

Thallus	Refer to figure(s)	Thallus weight at study end	Thallus maximum dimensions at study end	Orientation; vertical (-facing compass) or horizontal	Height in tree	Diameter of substrate
1	--*	--	--	V - S	55 m	2 cm
3	10	2.01 g	10 cm x 12 cm	V - E	55	3
4	11	0.0672	1.6 x 2.1	V - E	55	2
6	12 & 13	8.71	25 x 26	H	55	12
7	14 & 15	16.2	17.5 x 19	H	55	8
17	--*	--	--	V - E	46	7
21a	16	0.0001	0.2 x 0.3	V - N	34	6
21b	16	0.0161	1.4 x 1.5	V - N	34	4

* Thalli 1 and 17 were lost during the course of the study. The implications of this are discussed in the discussion section.

analyses in this thesis and are called "adjusted" values. This method has two advantages: (1) it is unnecessary to enlarge the photographs to exactly natural size and it is also unnecessary to include an internal scale in every photograph, and (2) use of a standard fixed in relationship to the subject compensates for any slight rotation of the camera over the axis of the standard.

E. Linear Measurements

Although linear growth rates have no direct application to a measure of lichen productivity, they are easy to measure, they can be used to analyze the way a lichen grows, and they have been used extensively in the literature. Thus they have a comparative use and were included in this study.

Three types of linear measurements were made on the series of photographs of *L. oregana* thalli: Category A, from the central point of attachment of the thallus (point X in all photographs, Figures 10 to 16) to the tips of actively growing lobes; Category B, from the point of attachment of the thallus to points on the sides of lobes; and Category C, from the point of thallus attachment to various recognizable points within the thallus along the axis of growth. Measurements were made using a pair of compass point calipers and a plastic mm scale. These readings were adjusted to the scale of Series #1 as explained above, by the following equation:

$$\text{Adjusted Value} = \text{Measured Value} \times \frac{\text{Distance between point landmarks, series measured}}{\text{Distance between point landmarks, series \#1}}$$

The adjusted values in Categories A and B are presented in Table 5. Letters refer to points labeled in Series 1 and 6 of each photographed station used. These points are indicated by a dot on each other series (see Figures 10 through 16).

F. Areal Measurements

The outline of each thallus photographed was improved where necessary with a thin black ink line (Figures 10 through 16). Each thallus photoarea was measured by tracing its outline with a Keuffel & Esser Model #620005 Compensating Polar Planimeter. Thalli less than 0.5 cm^2 were circuited 25 times and the result divided by 25 for each measurement. In a similar manner, thalli from 0.5 to 1 cm^2 were circuited ten times, those from 1 to 5 cm^2 were circuited five times, those from 5 to 15 cm^2 were circuited twice and those thalli above 15 cm^2 were circuited once for each measurement. Five separate measurements were made for each thallus and the results averaged. In large thalli, numbers 3, 6 and 7 (Figures 10, and 12 through 15), each thallus was considered an addition of areas of smaller major lobes. If these smaller lobes were not hidden by any other portion of the thallus during the course of the study, they were also considered as separate thalli as explained in the Discussion section. The measurements for each thallus were adjusted to the scale of Series #1 as explained above, by the following equation:

Adjusted Area =

$$\text{Measured Area} \times \frac{(\text{Distance between point landmarks, Series measured})^2}{(\text{Distance between point landmarks, Series \#1})^2}$$

The adjusted areas are presented in Table 4.

In addition to the ten thalli whose growth was followed in these series of photographs ("study" thalli), 31 thalli from a subset of thalli collected from Tree #201 ("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, and the two sets of thalli were oven dried at 40°C overnight, then allowed to equilibrate to room temperature for two hours before recording their dry weight (biomass). The photoareas and dry weights for these 41 thalli are presented in Table 3.

III. LITERATURE REVIEW

In a tree similar to the one studied in this report, Pike *et al.* (1972) estimated the total standing biomass of *L. oregana* to be 6.5 kg or 35.5% of the total epiphyte biomass, and to contain a total of 127 g of nitrogen or about 56.5% of the total epiphyte nitrogen. No other species epiphytic on Douglas fir makes this large a contribution to the total epiphyte nitrogen. Pike was only able to estimate the productivity of *L. oregana* in the Douglas fir system within a range of annual turnover rates for epiphytic lichens from 5 to 25% of the standing crop.

Productivity of a lichen population is a function of the following characteristics of the individual thalli and their arrangement in the population:

a. Increase in biomass of individual thalli is expressed visually as an increase in length of lobes, but also includes an increase in the thickness of older portions of the thalli and often the production of vegetative propagules (Porter, 1927; Hale, 1973).

b. Changes in the rate of growth relative to the size of the thallus (Woolhouse, 1968; Phillips, 1969).

c. Distribution of different sizes (ages) of thalli throughout the population.

d. Differences in growth rate due to different microhabitat locations of thalli (Barkman, 1958; Hale, 1973).

e. Seasonal changes in thallus density and thallus size distribution.

f. Consumption of lichen biomass by herbivores, decomposition *in situ*, and loss of lichen thalli or their lobes to litterfall (Bailey, 1970; Pike, 1972).

These factors are listed in order of increasing difficulty to account for their effects. An extremely accurate analysis might include all of the factors, yet it has only been within the last few years that lichenologists have turned from just concerning themselves with the first factor to a more integrated approach to the problem of productivity. No study has taken all of the factors listed into account.

Three recent estimates of lichen productivity provide a range of values. Pike (1971b), using data from Edwards *et al.* (1960), estimates a value of 33 kg/ha yr for epiphytic lichens (Usneaceae) in the Wells Gray Park, British Columbia, a winter range of caribou. Pike's own estimates for species inhabiting oak and ash twigs in the Willamette Valley, Oregon, are based on a more complete set of data. He (1971b) estimates a value of 480 kg/ha yr. Finally, Prince (1974) calculates a value of 472 kg/ha yr for *Cladonia rangiferina* and *C. arbuscula* in a lichen-rich heath on the Sands of Forvie, Scotland.

Traditionally, radial, diametral or areal dimensions have been used to calculate growth rates. Hale (1973) has contributed an excellent review of this literature and concludes that, "Elongation of thallus part, while not as accurate a measure as mass, does provide a convenient tool for comparative studies and virtually all workers have adopted this method."

Fink (1917) and Linkola (1918) pioneered the study of lichen growth. But Fink hardly studied natural conditions; he cleared an area of *Cladonia* spp. and reseeded the area with their ground up remains, watching how long it took to regenerate the original stand (in Prince, 1974). The slightly more exacting study of lichenometry was begun by Beschel (1950, 1961), who used substrate age to estimate diametral growth rates of closely appressed foliose and crustose rock lichens (particularly *Rhizocarpon geographicum*). These rates are used in turn to estimate ages of other substrates. Lichenometry has come under some attack recently (Jochimsen, 1966 and others); this criticism is discussed along with numerous reports of recent uses of the method in an issue of *Arctic and Alpine Research* (Volume 5, Number 4, 1973) dedicated to Beschel.

By far the majority of recent efforts to establish growth rates for lichens have used photography to record the changes in thallus size. This method was first used by Frey (1959) who made photographs both of areas over several meters wide and close-ups to study growth rates. More recently, Hale (1970) has used extreme close-ups to analyze in elegant detail the pattern of lobe growth in *Parmelia caperata*.

Perhaps the paper of this kind most relevant to the study reported here is Phillips' (1969). He provides data on linear (radial) growth rates of three lichen species (Lobaria pulmonaria, L. quercizans and Menegazzia terebrata) growing on Acer rubrum in Tennessee. Growth was followed photographically on "intermediate sizes" of each species on substrates ranging from 10 to 70 cm in diameter at breast height. Lobes measured were, "(1) those that could be identified and followed during the three year period, (2) those growing directly toward or away from the (aluminum nail) marker, and (3) those perpendicular to the optical axis of small trees." Phillips notes that of lobes originally selected for study, 5 of 20 of M. terebrata and 2 of 7 of L. pulmonaria were lost to excessive decomposition and shedding of bark substrate, respectively. An average linear growth rate for each lichen species was determined by dividing the sum of average annual linear rates for all lobes on all specimens of each by the total number of lobes. The resulting "average growth rates" are 2.54 mm/yr for M. terebrata, 4.82 for L. pulmonaria and 5.62 for L. quercizans. Unfortunately, Phillips provides no information on original lobe length so that the values given have no real meaning and cannot be applied to other collections of the same species; therefore, these rates cannot be used to estimate productivity even if size distribution is known. The procedure used to select lobes for measurement, the loss of some lobes during measurement, and failure to account for these losses in growth rates means that the rates have even less use for predicting productivity.

Traditionally, lichenologists have recognized three arbitrary stages of linear growth in the life cycle of lichens, corresponding to similar stages of the life cycles of many organisms (Hale, 1973). A slow linear growth rate during the establishment and beginning of growth of a reproductive propagule (Juvenile period), a relatively long stage of constant, more rapid growth until the lichen reaches maturity ("Great" period) and a period of growth during which the rate slows down and finally stops (Senescent period). A graph of the increase in linear size of this "average" lichen thus has a sigmoid shape, corresponding to the logarithmic model of growth used to describe the growth of fungi in general and many other organisms (Burnett, 1968).

Lichen growth rates are among the slowest recorded for fungi, but lichen hyphae are also among the longest living fungal organisms. A range in maximum age of 15-20 years for certain foliose lichens to 100-1000 years for rock-inhabiting crustose species is reported by Hale (1973).

Woolhouse (1968) has suggested that the best manner in which to relate growth rates is in relative terms, cm^2/cm^2 x unit time, or even better, g/g x unit time. He concludes, however, that complex mathematical manipulations would be necessary to adjust area calculations on the basis of seasonal differences in thallus density to achieve the latter result. Hale (1973) also dismisses the use of biomass growth rates on the basis of the necessity to destroy the thalli to make the necessary measurements.

Nienburg (1919) and Degelius (1964) indirectly measured growth rates of a variety of lichen species on Abies and Fraxinus branches, respectively, by an analysis of the size of lichens growing on different aged twigs between yearly terminal bud scars. This method is similar to the lichenometry developed in 1950 by Beschel for dating rock surfaces. Pike (1971a, b) has extended this indirect method of growth rate determination to arrive at estimates of productivity for the principle components of the epiphytic communities on oak and ash in the Willamette Valley of Oregon. He analyzed biomass of epiphytes on 1 to 20 year-old twigs by determining the average cover of each species on each age class of twig and multiplying by the amount of each age class of twig. This method circumvents the need to describe growth rate and size class distribution for each species, but is only useful where there is a clear trend in succession of epiphyte communities on different age twigs and where the potential substrate for each species is relatively limited (in this case no more than 20 years total of twigs). The sheer size and complexity of the potential habitat for L. oregana in Douglas fir canopies necessitates a different approach to the analysis of its productivity in this community.

IV. RESULTS

A. Relationship of Photoarea to Thallus Dry Weight

Table 3 presents the data and Figure 9 shows the relationship of thallus dry weight (in grams) to thallus photoarea (in square centimeters) for 41 *L. oregana* thalli: 31 "collected" thalli, graphed as "X's" and ten "study" thalli (or lobes considered as thalli), graphed as "O's". The data are graphed as their logarithms. The straight line equation of the regression of the $\log_{10}$ of thallus dry weight on the $\log_{10}$ of thallus photoarea is:

$$\log_{10}(\text{weight}) = -1.87 + 1.19[\log_{10}(\text{photoarea})] \tag{1}$$

The correlation coefficient (r) is 0.98. This relationship is used to estimate dry weights of the study thalli in each of the six series of photographs.

B. The Photographs

The photographs used in making the growth measurements of the ten study thalli are presented in Figures 10 to 16. Each of these composites is reduced by a factor of two, except Figure 11 which is life size. Because of the varied lighting and contrast, the information present in the original prints is not completely recorded in these reproductions. Within the thallus or thalli in each series of

Table 3. Photoarea and dry weight for 41 L. oregana thalli.

"Collected" Thalli			"Collected" Thalli		
	Dry weight	Photoarea		Dry weight	Photoarea
2-32	0.00005g	0.00391 cm^2	2-11	0.0585	3.164
2-14	0.00005	0.014	2-35	0.0591	3.8979
2-10	0.0001	0.00706	2-3	0.215	10.15
2-34	0.0002	0.04921	2-30	0.314	13.911
2-33	0.0005	0.02578	2-20	0.422	14.23
2-37	0.0008	0.08988	2-36	0.511	20.593
2-4	0.0008	0.2720	2-31	1.11	40.673
2-19	0.0009	0.210	2-25	1.32	47.61
2-40	0.0011	0.09068	2-18	1.54	47.58
2-5	0.0014	0.1331	2-1	13.7	99.82
2-24	0.0021	0.1411	"Study" Thalli		
2-7	0.0033	0.3542	21a	0.0001	0.0710
2-39	0.0041	0.3077	21b	0.0161	2.179
2-22	0.0049	0.4437	3a	0.2074	8.25
2-23	0.0085	0.7095	3b	0.3043	14.57
2-38	0.0179	0.9352	7b	0.3083	11.70
2-16	0.0221	1.234	3	0.5117	22.82
2-26	0.0224	2.004	6a	0.5343	24.90
2-2	0.0376	1.987	7a	0.6457	29.86
2-42	0.0430	1.9675	7	1.1744	46.76
2-21	0.0484	2.8994	6	1.7127	78.09

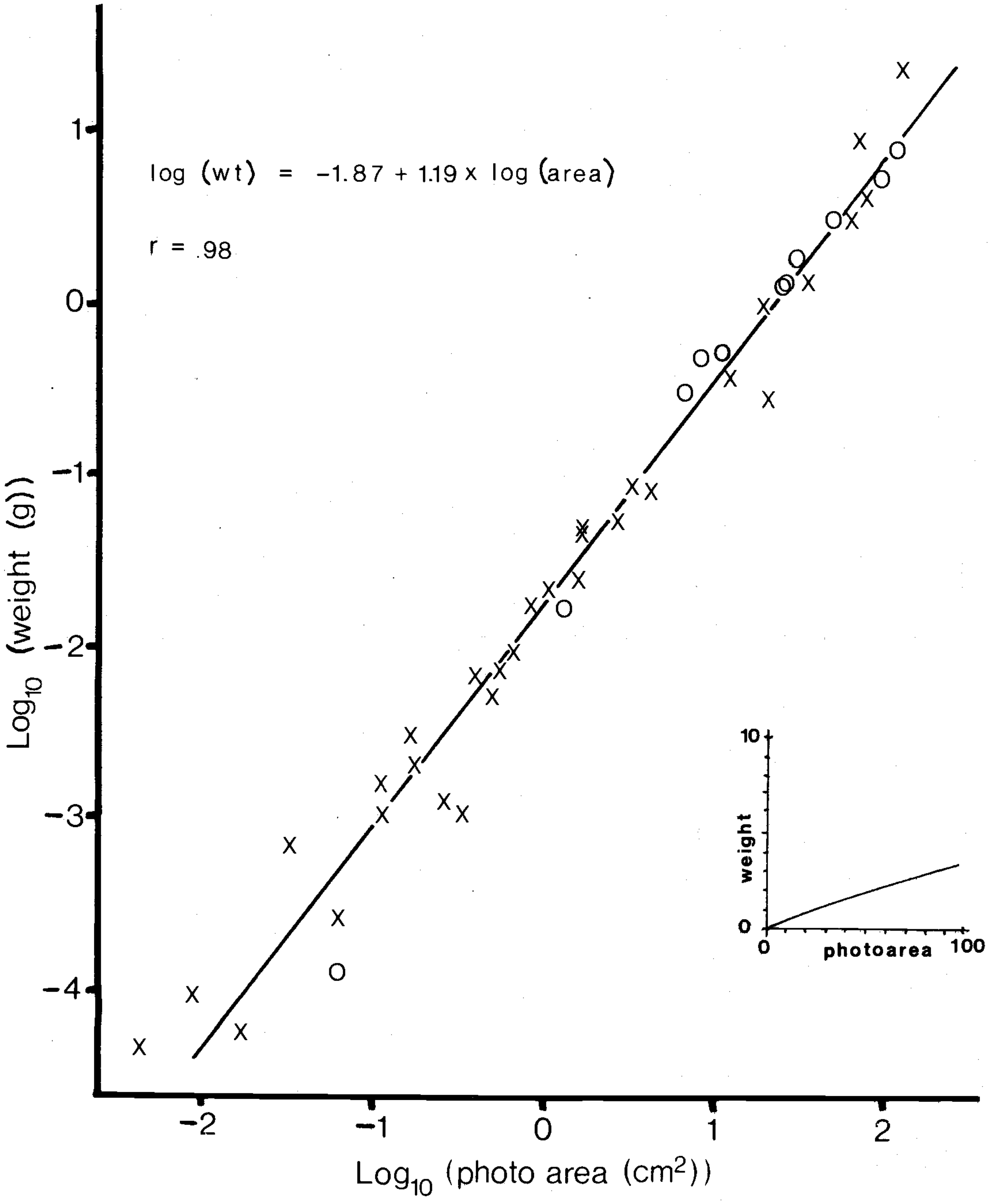


Figure **9**. Regression of log (dry weight) on log (photo area) for 41 <u>Lobaria</u> thalli. x = collected thalli. o = study thalli.

Figures 10 through 16.

Composites of the photographs originally used to obtain measurements for analysis of growth in the study thalli. All but Figure 11 are reduced one-half life size. Numbers in the upper left corner of each section refer to the series. Points used in analysis of linear growth are identified in Series 1 and 6.

Figure 10. Thallus 3. Lobes 3a and 3b are identified in Series 2.

Figure 11. Thallus 4.

Figures 12 and 13. Thallus 6. Lobe 6a is identified in Series 2.

Figures 14 and 15. Thallus 7. Lobes 7a and 7b are identified in Series 2.

Figure 16. Thalli 21a and 21b. These are identified in Series 2.

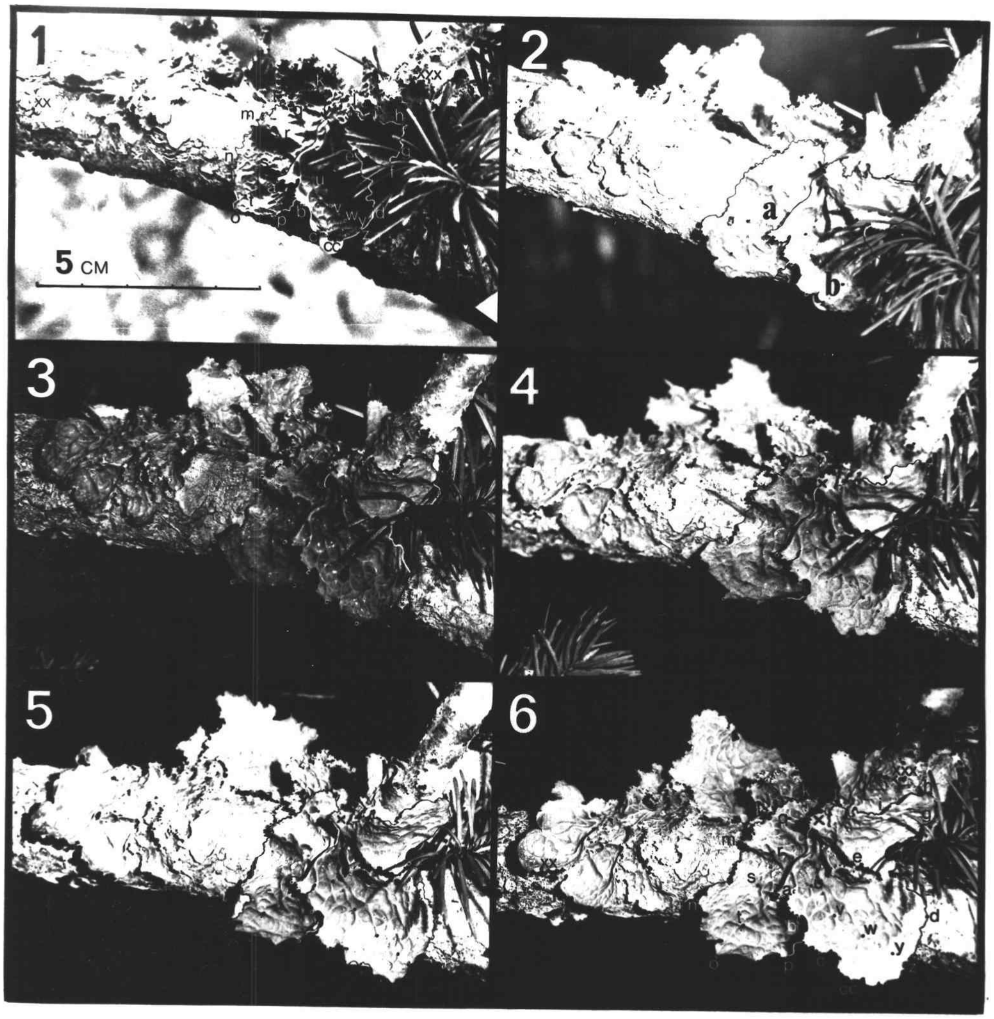


Figure 10. Thallus 3

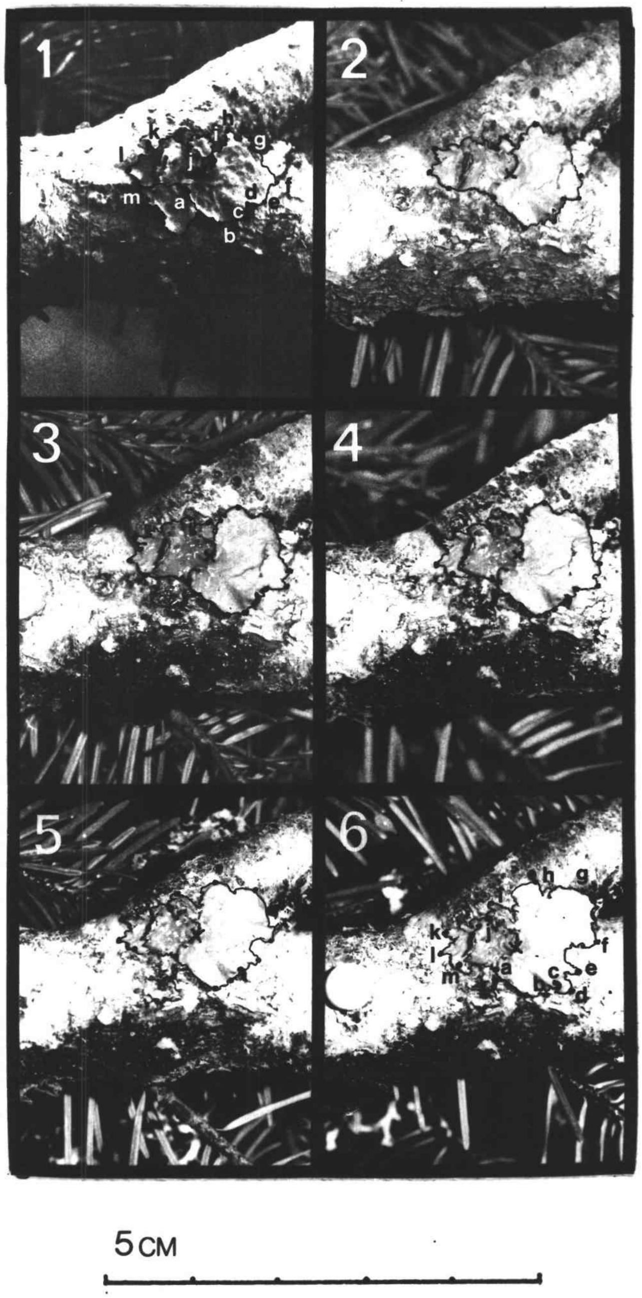
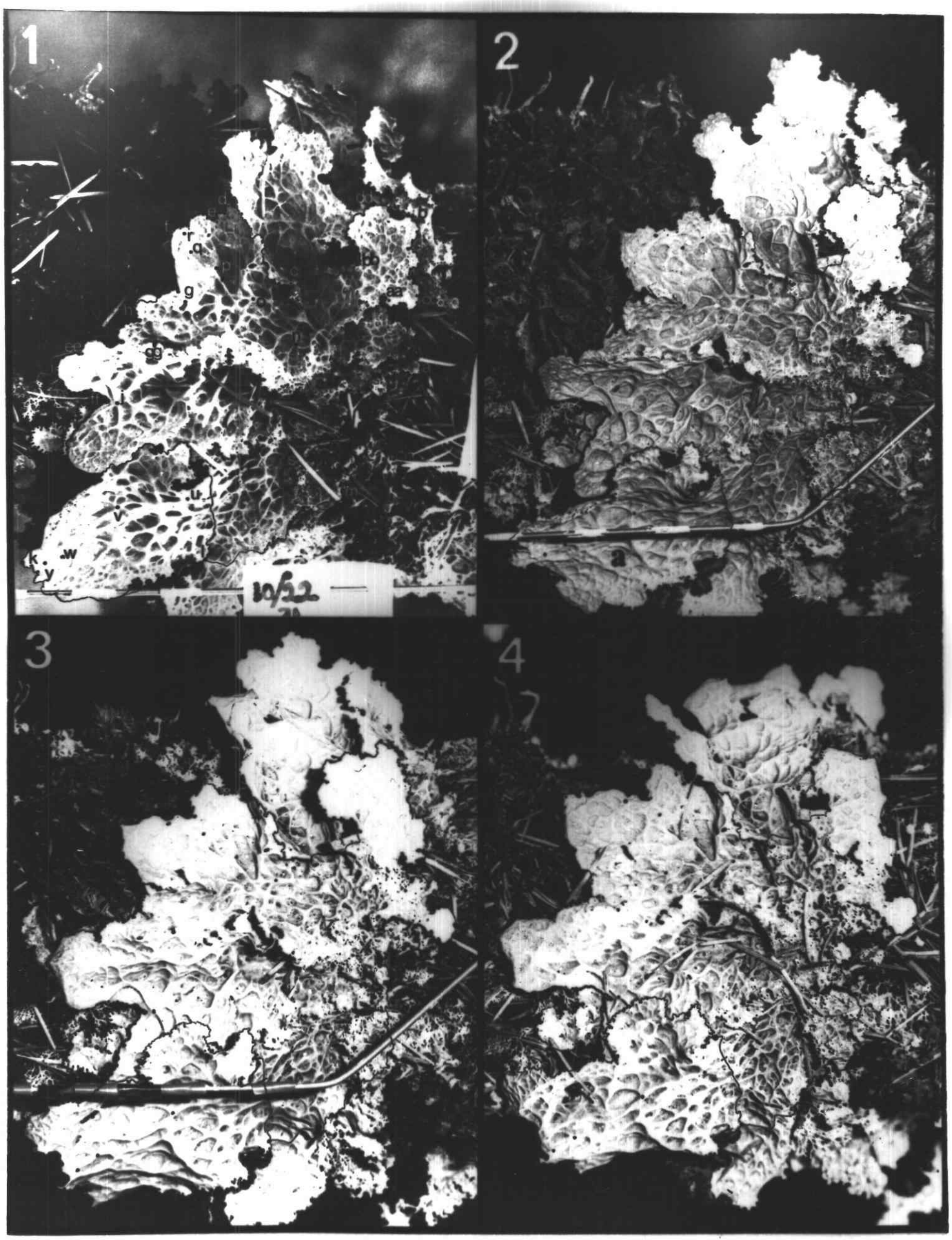


Figure **11**. Thallus 4



5 CM

Figure 12. Thallus 6

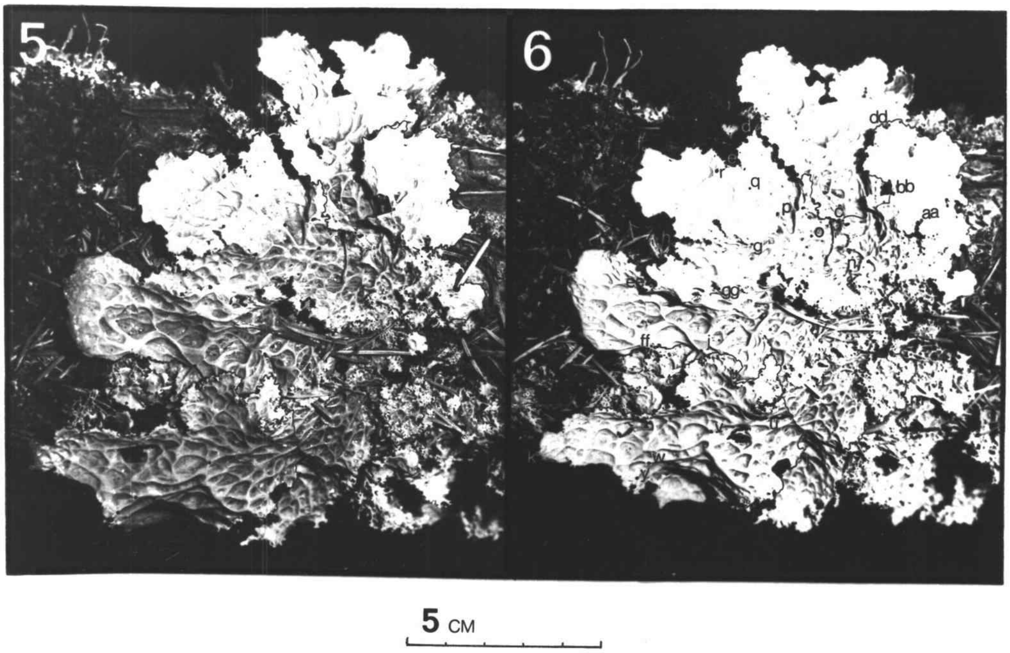


Figure 13.

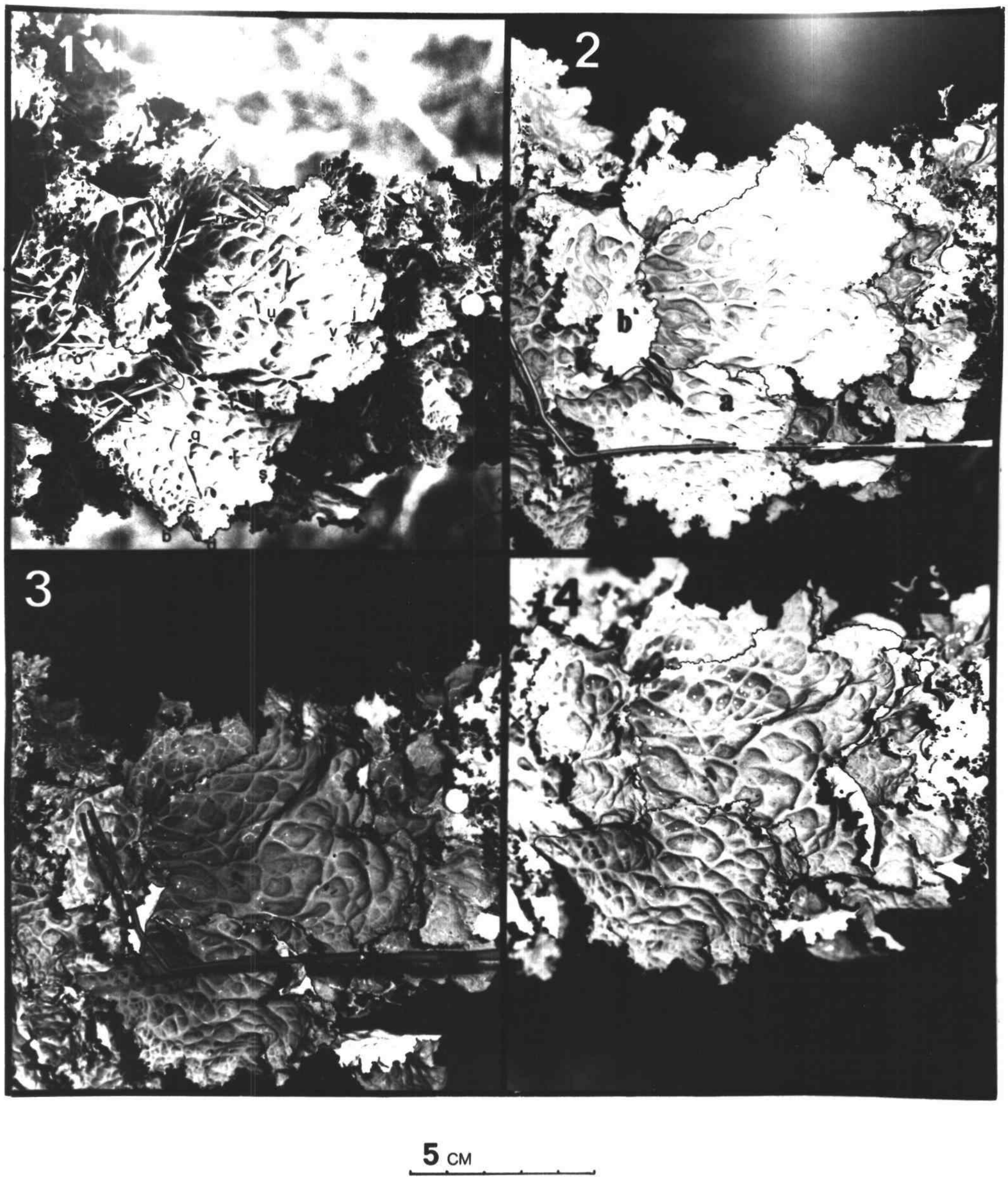


Figure 14. Thallus 7

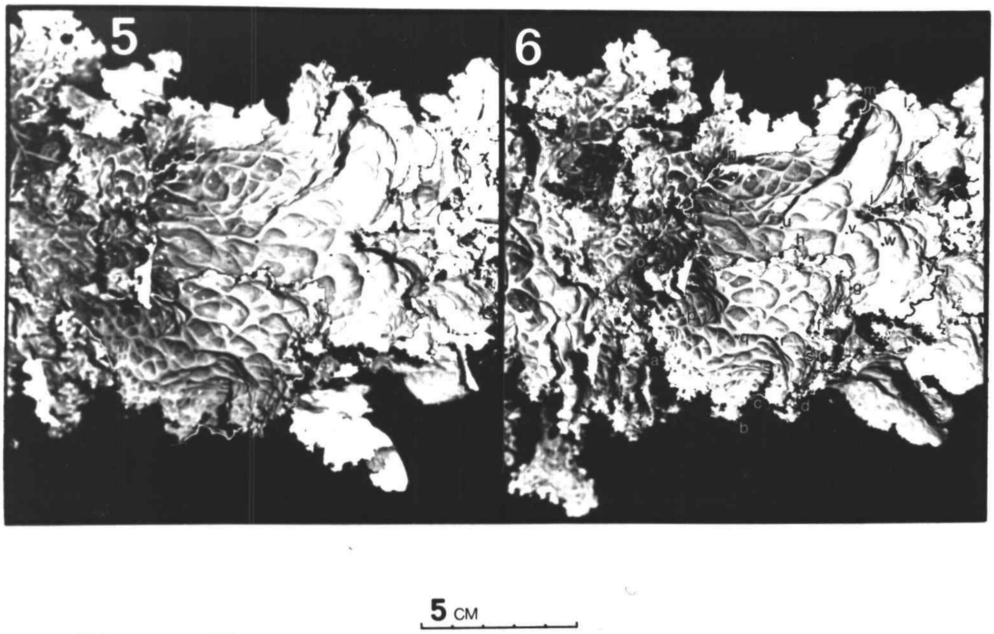


Figure 15.

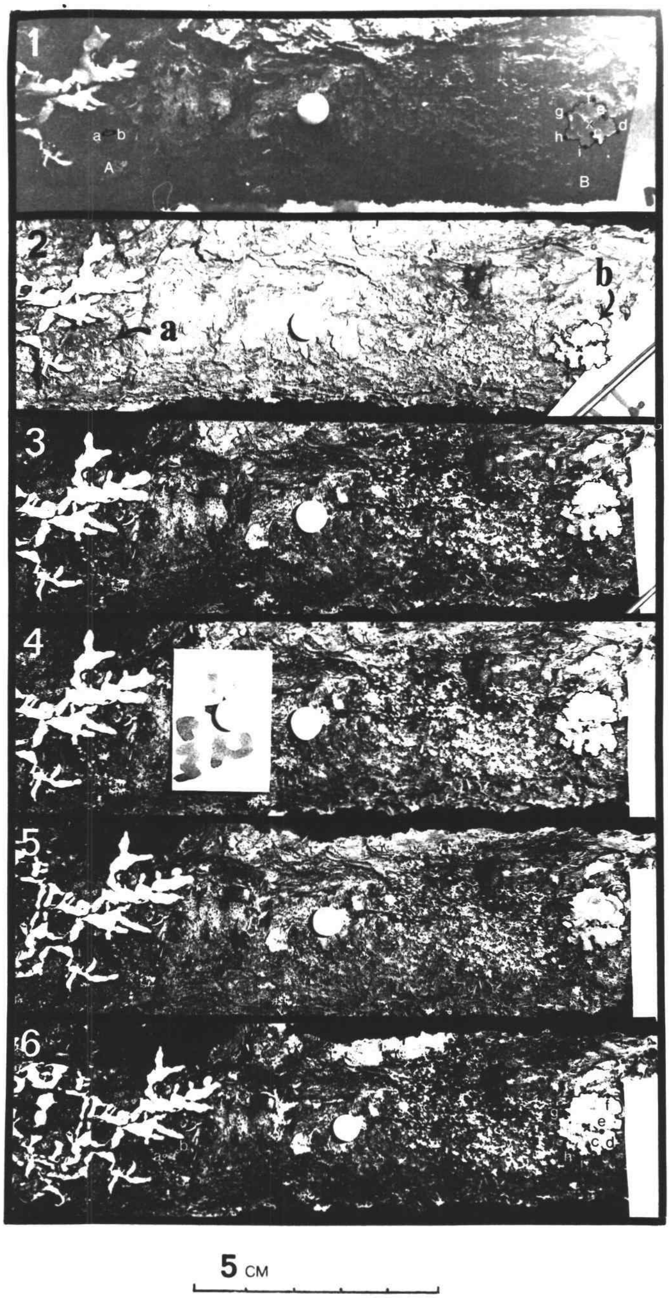


Figure 16. Thalli 21a&b

photographs, selected recognizable points are identified through the time sequence by black dots, which are lettered in Series 1 and 6. Distances between some of these points are used in the analysis of linear growth rates. On every thallus, point "X" is the central point of attachment to the substrate. The edge of each thallus photograph is outlined where necessary with white or black ink for facilitating areal measurements; these measurements are used in the analysis of areal growth. Tables 1 and 2 list the pertinent information concerning each series of photographs and each thallus used in the following analyses.

C. Areal and Biomass Growth

The adjusted photoareas of each study thallus in each of the six series of photographs (Figures 10 to 16) are presented in Table 4, followed by an estimated dry weight, using Equation (1) above. The last two columns of Table 4 show the absolute growth rate (g/yr) and the relative growth rate (percent of initial weight (in g)/yr) for each thallus or thallus-lobe, determined from the slope of the linear regression line equation of each relationship of estimated thallus dry weight to time.

The absolute growth rate can be related to the initial estimated thallus dry weight. Figure 17 shows the regression of the logarithm of yearly growth rate (g/yr) on the logarithm of the initial estimated weight (g). The straight line equation of the relationship is:

Table 4. Adjusted photoareas of study thalli. Estimates of thallus dry weights and growth rates.

Thallus or lobe of thallus	Photo series (weeks from start)	Averaged adjusted photoarea	Estimated dry weight	Linear regression growth rate	Relative growth rate
3a	1 (0)	3.64 cm^2	0.0697 g		
	2 (19.7)	4.31	0.0853		
	3 (35.4)	4.87	0.0986		
	4 (55.7)	4.91	0.0996		
	5 (77.3)	5.42	0.112		
	6 (91.1)	6.21	0.132	0.0313 g/yr	44.9 % initial wt./yr.
3b	1	4.67	0.0938		
	2	5.38	0.111		
	3	7.79	0.172		
	4	8.28	0.185		
	5	9.95	0.230		
	6	10.97	0.258	0.0956	101.9
3	1	8.31	0.186		
	2	9.69	0.223		
	3	12.66	0.306		
	4	13.19	0.322		
	5	15.37	0.386		
	6	17.18	0.440	0.142	76.3
4	1	1.00	0.0151		
	2	1.19	0.0185		
	3	1.38	0.0221		
	4	1.47	0.0238		
	5	1.50	0.0244		
	6	1.98	0.0339	0.00900	59.6
6a	1	10.4	0.243		
	2	12.3	0.297		
	3	14.4	0.357		
	4	15.0	0.375		
	5	15.1	0.378		
	6	17.9	0.462	0.108	44.4

Table 4. (Continued)

Thallus or lobe of thallus	Photo series (weeks from start)	Averaged adjusted photoarea	Estimated dry weight	Linear regression growth rate	Relative growth rate
6	1(0)	48.1 cm^2	1.49 g		
	2 (19.7)	53.8	1.71		
	3 (35.4)	57.1	1.83		
	4 (55.7)	64.5	2.11		
	5 (77.3)	63.8	2.09		
	6 (91.1)	73.9	2.49	0.512 g/yr	34.4 % initial wt/yr.
7a	1	13.9	0.342		
	2	17.0	0.435		
	3	18.3	0.474		
	4	20.1	0.530		
	5	19.8	0.521		
	6	22.4	0.603	0.129	37.7
7b	1	7.76	0.171		
	2	9.08	0.207		
	3	9.55	0.219		
	4	10.4	0.243	0.0652	38.1
	5	7.71	0.170	lobe broken	
	6	8.77	0.198		
7	1	44.1	1.35		
	2	55.0	1.75		
	3	57.5	1.85		
	4	61.9	2.01		
	5	61.7	2.01		
	6	66.3	2.19	0.412	30.5
21a	1	0.0161	0.000112		
	2	0.0216	0.000159		
	3	0.0256	0.000195		
	4	0.0350	0.000282		
	5	0.0319	0.000253		
	6	0.0528	0.000460	0.000167	149.1
21b	1	0.624	0.00861		
	2	0.766	0.0110		
	3	1.06	0.0161		
	4	1.22	0.0191		
	5	1.33	0.0211		
	6	1.62	0.0267	0.00991	115.1

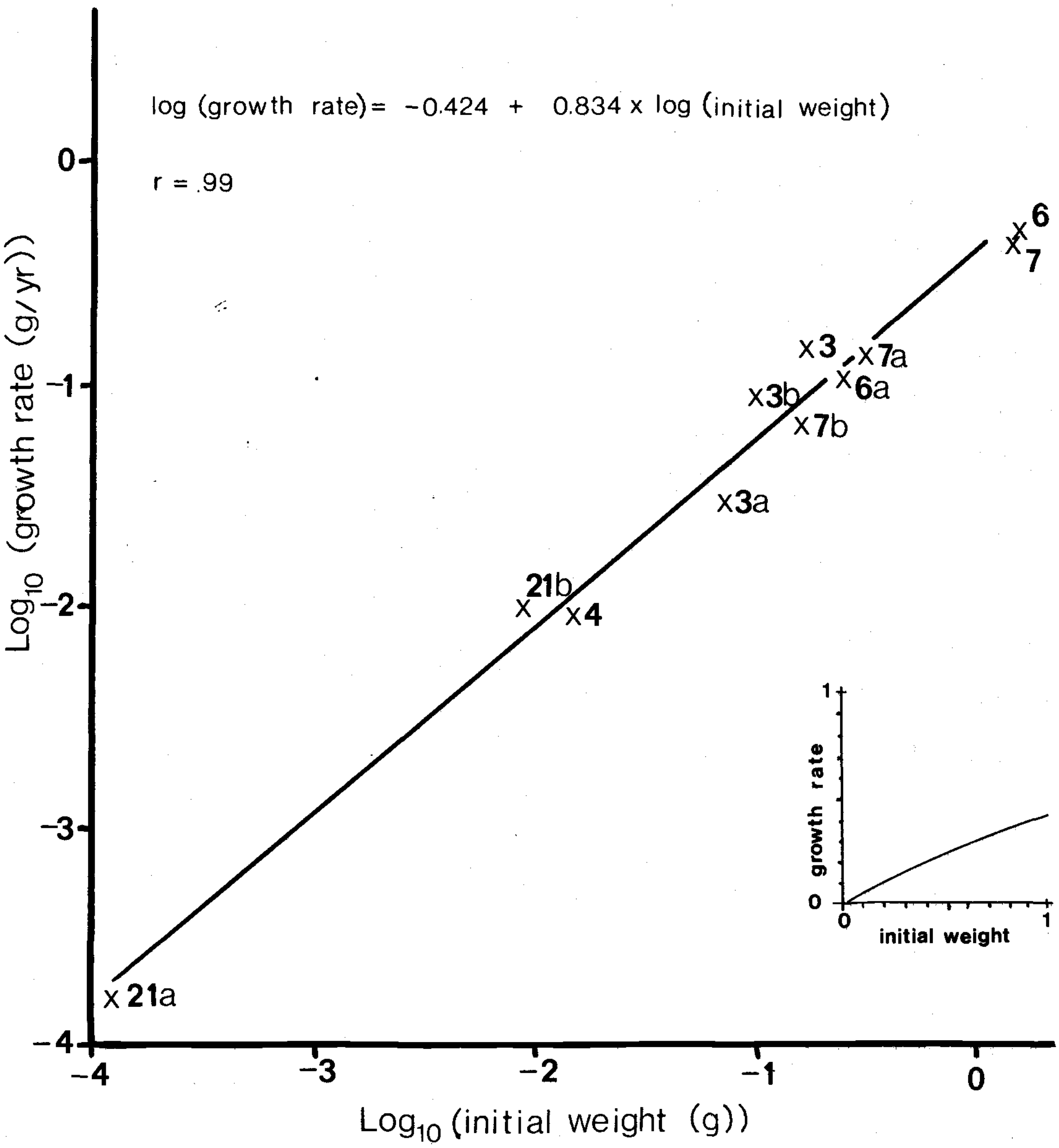


Figure **17**. Regression of log (growth rate) on log (initial weight) for thalli and lobes of Lobaria oregana. **3**a, **3**b, **6**a, **7**a & **7**b are lobes.

$$\log_{10}(\text{growth rate}) = -0.424 + 0.834[\log_{10}(\text{initial weight})] \quad (2)$$

The correlation coefficient (r) for this relationship is 0.99. This equation can be used to produce estimates of the absolute rate of biomass growth for any L. oregana thallus if its initial weight (or by combining equations (1) and (2), if its photoarea) is known.

The graph of the relationship between relative growth rate and initial thallus weight is presented in Figure 18.

D. Thallus Age

Besides estimating growth rates, Equation (2) can be used to estimate ages of thalli. If we assume that a thallus begins its life as a lobule of dry weight of 0.0002 g, the weight of this thallus at the end of each year's growth [rate for each year determined from Equation (2)] describes the curve presented in Figure 19. A thallus of ten grams is therefore approximately 22 years old.

E. Linear Growth Rates

Table 5 lists the various adjusted linear dimensions followed through the photographic series shown in Figures 10 to 16. For further analysis, these dimensions were grouped into three categories as explained above. Only Categories A and B are presented in Table 5. The averages for each of six size classes (beginning dimension: size

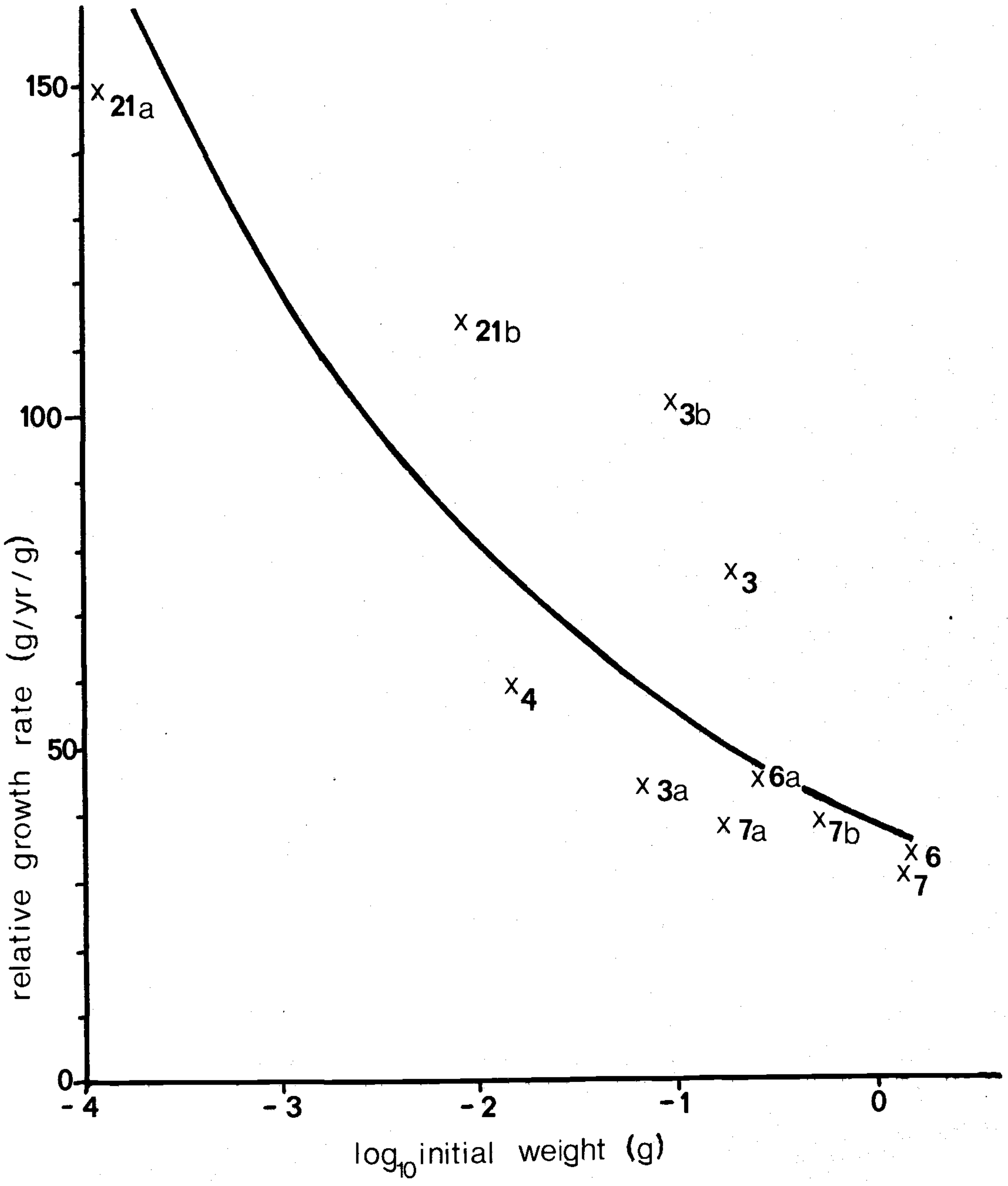


Figure **18**. Relative growth rate (% initial weight per year) as a function of initial thallus weight for L. oregana. Curve predicted from equation (**2**).

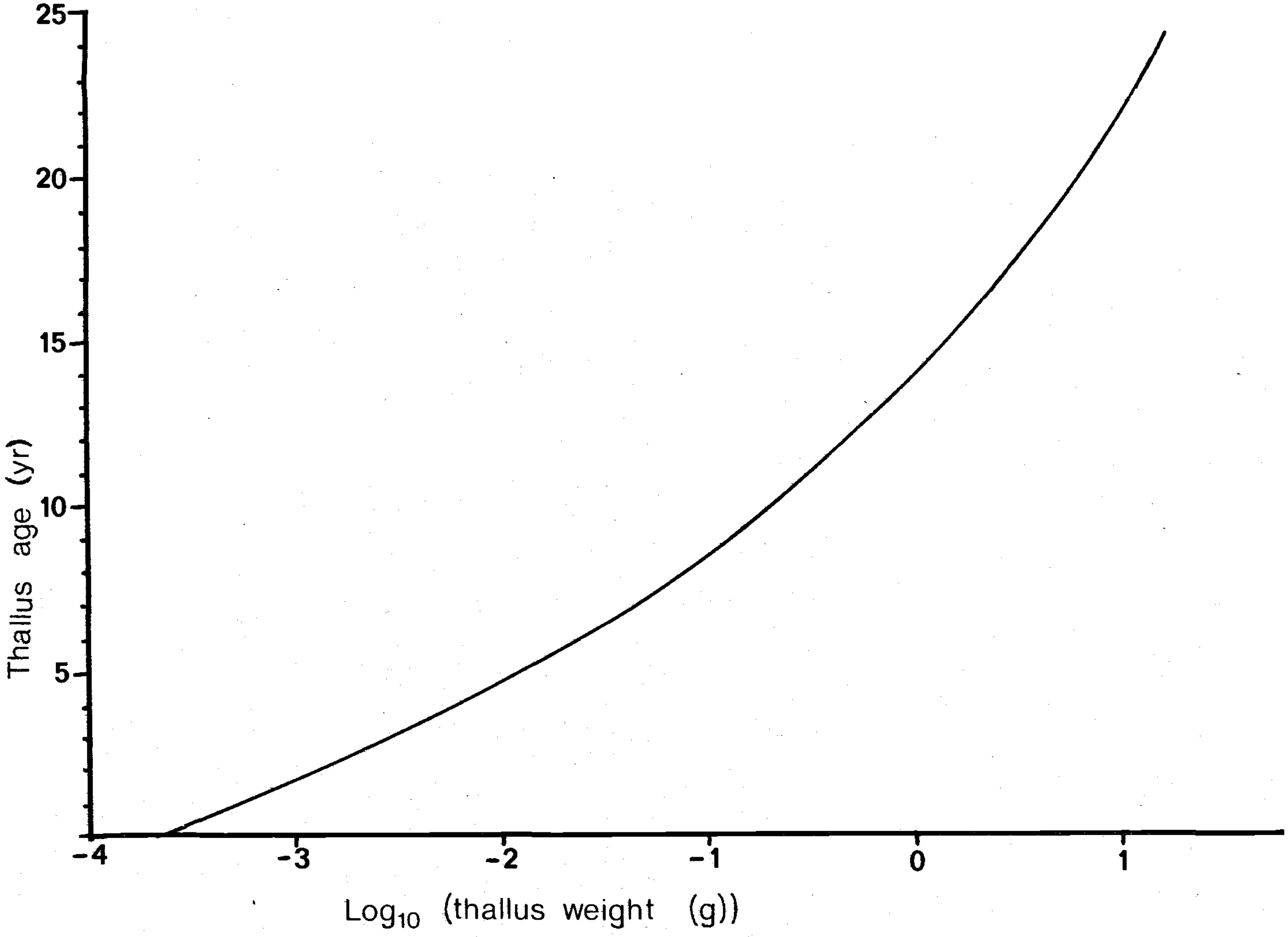


Figure **19**. Estimation of thallus age from logarithm of thallus dry weight.

Table 5. Linear dimensions analyzed on study thalli. Refer to letters on Figures 10 to 16.

Thallus	Dimension	Category-size class	Adjusted length (mm) Series 1	2	3	4	5	6
3	x-a	B-3	18.5	18.9	20.5	19.8	19.6	20.5
Fig. 10	-b	B-3	20.8	22.1	24.5	23.7	24.0	24.3
	-c	B-4	26.1	27.7	30.9	30.1	31.8	32.4
	-cc	A-4	28.3	30.1	36.3	36.0	37.6	40.0
	-z	A-4	27.0	30.2	34.6	34.5	38.6	40.2
	-d	A-4	23.3	28.7	30.1	29.7	32.1	35.1
	-e	B-3	10.4	13.7	13.3	13.3	13.0	12.9
	-f	A-3	17.9	19.6	20.4	19.8	19.6	21.4
	-g	A-3	18.3	23.0	24.8	24.6	26.4	27.9
	-h	A-3	17.7	22.1	22.8	24.7	26.3	28.0
	-i	B-3	10.7	14.5	14.8	14.9	13.8	15.7
	-j	B-1	4.3	4.5	3.8	3.9	3.7	6.3
	-k	B-2	5.5	4.6	6.5	7.0	7.7	6.8
	-l	B-3	11.2	10.0	12.3	9.7	10.2	16.6
	-m	B-3	15.5	15.4	16.7	16.0	16.6	19.5
	-n	A-4	25.7	29.8	32.3	33.1	34.6	35.0
	-o	A-4	29.3	31.9	35.1	35.1	37.0	41.5
	-p	A-4	25.7	26.1	28.6	28.3	31.3	34.3
4	X-a	B-1	2.6	3.4	3.7	4.1	3.8	4.0
Fig. 11	-b	B-2	6.3	6.5	7.0	7.4	8.1	7.3
	-c	B-2	7.3	7.4	7.8	7.5	8.1	7.1
	-d	A-2	6.4	6.7	7.4	7.8	8.0	9.4
	-e	B-2	7.8	8.2	9.5	9.9	8.5	9.1
	-f	B-2	8.6	8.1	9.4	9.6	9.5	10.9
	-g	A-2	6.7	8.0	8.2	8.8	9.4	11.8
	-h	A-2	5.6	6.4	6.6	7.0	8.0	9.4
	-i	A-1	4.2	4.4	4.1	4.7	5.6	6.9
	-j	B-1	3.1	3.5	3.5	4.4	4.7	5.3
	-k	A-2	7.0	9.3	9.1	9.2	9.6	10.0
	-l	A-2	8.7	9.5	9.5	9.6	9.7	10.2
	-m	B-2	7.5	7.4	7.9	7.8	8.0	8.3

Table 5 (Continued)

Thallus	Dimension	Category-size class	Adjusted length (mm) Series 1	2	3	4	5	6
6	x-a	A-3	20.4	20.3	21.0	23.0	19.6	24.8
Figs. 12	-b	A-4	42.3	44.6	47.4	43.5	46.7	48.3
and 13	-c	B-3	24.4	24.5	23.4	25.0	23.3	24.5
	-d	B-4	46.7	50.6	52.5	57.5	56.4	58.5
	-e	B-4	45.0	50.2	49.3	53.0	53.0	53.9
	-f	A-5	50.1	60.9	62.6	70.7	69.7	77.6
	-g	B-4	38.4	38.9	36.6	40.7	38.4	39.4
	-h	A-4	48.5	52.0	52.0	57.7	56.5	59.6
	-i	A-5	63.6	70.2	72.1	79.5	81.6	86.9
	-j	B-5	50.0	51.9	50.4	53.0	51.4	52.3
	-k	A-6	83.1	88.7	87.7	87.7	96.7	104.2
	-l	B-5	51.2	49.7	49.4	52.4	46.2	48.3
	-m	B-4	27.4	28.6	27.9	31.3	27.4	29.5
7	x-a	B-4	47.7	47.3	43.8	49.3	45.0	47.3
Figs. 14	-b	B-5	70.6	72.9	66.5	71.6	70.2	74.3
and 15	-c	B-5	68.7	70.8	69.4	73.7	69.6	71.0
	-d	A-6	77.2	80.0	79.8	85.8	81.3	81.5
	-e	A-6	78.9	83.2	81.8	87.8	82.0	80.9
	-f	B-5	71.0	73.9	74.9	77.3	73.2	72.6
	-g	A-5	72.5	72.8	76.3	82.4	79.6	76.5
	-h	B-5	59.1	60.7	58.3	61.6	58.9	57.4
	-i	A-6	86.1	94.4	95.7	97.7	103.5	103.3
	-j	B-6	75.8	79.7	78.3	80.4	82.8	78.6
	-k	A-6	83.5	90.3	87.8	91.2	97.0	93.6
	-l	A-6	76.9	87.4	84.5	93.9	95.6	96.0
	-m	A-5	72.2	74.9	75.1	83.5	82.6	83.8
	-n	B-4	42.4	42.9	41.4	41.0	37.8	37.8

class (1) = 0 - 5 mm; (2) = 5 - 10; (3) = 10 - 25; (4) = 25 - 50; (5) = 50 - 75; and (6) = greater than 75 mm) is given in Table 6.

Figure 20 shows a comparison of the changes in length of the average dimensions in these six size classes. Categories A and B are computed separately. The average linear growth rate (mm/yr) for each size class is computed from the linear regression of linear dimension on time and is presented in the last column in Table 6.

Figures 21 and 22 compare the growth of dimensions in Category C: point of thallus attachment to various points along lines parallel to the axis of growth within each of the four lobe tips, two lobes of Thallus 6 (Figures 12 and 13) and two lobes of Thallus 7 (Figures 14 and 15). The data have been manipulated some to take into account some changes in perspective which occurred due to lobe movement. Nevertheless, some generalizations about the nature of the growth of L. oregana can be made on the basis of these graphs (see below).

F. Relationship of Growth Rates to Meteorological Pattern

It was hoped that growth data would be sufficiently accurate to resolve effects due to changes in weather from the first season to the second. This does not seem to be possible.

Table 6. Averages of linear dimensions in six size classes and two categories in Table 5. Linear growth rates.

Category-size class	Average adjusted length (mm)						Number of dimensions averaged	Linear growth rate (mm/yr)
	Series							
	1	2	3	4	5	6		
A-1	3.6	3.9	4.8	4.9	5.1	6.1	4	1.28
A-2	6.4	7.4	7.7	8.0	8.3	9.4	7	1.44
A-3	18.6	21.3	22.3	23.0	23.0	25.5	4	3.21
A-4	31.3	34.2	37.1	37.2	39.3	41.8	8	5.42
A-5	64.6	69.7	71.5	79.0	78.4	81.2	4	9.40
A-6	81.0	87.3	86.2	90.7	92.7	93.3	6	6.68
B-1	3.0	3.3	3.4	4.3	3.6	4.6	5	0.77
B-2	6.9	6.8	7.7	7.8	8.0	7.9	7	0.70
B-3	15.9	17.0	17.9	17.5	17.2	19.1	7	1.26
B-4	39.1	40.9	40.3	43.3	41.4	42.7	7	1.81
B-5	61.8	63.3	61.5	64.9	61.6	62.7	6	2.17
B-6	75.8	79.7	78.3	80.4	82.8	78.6	1	---

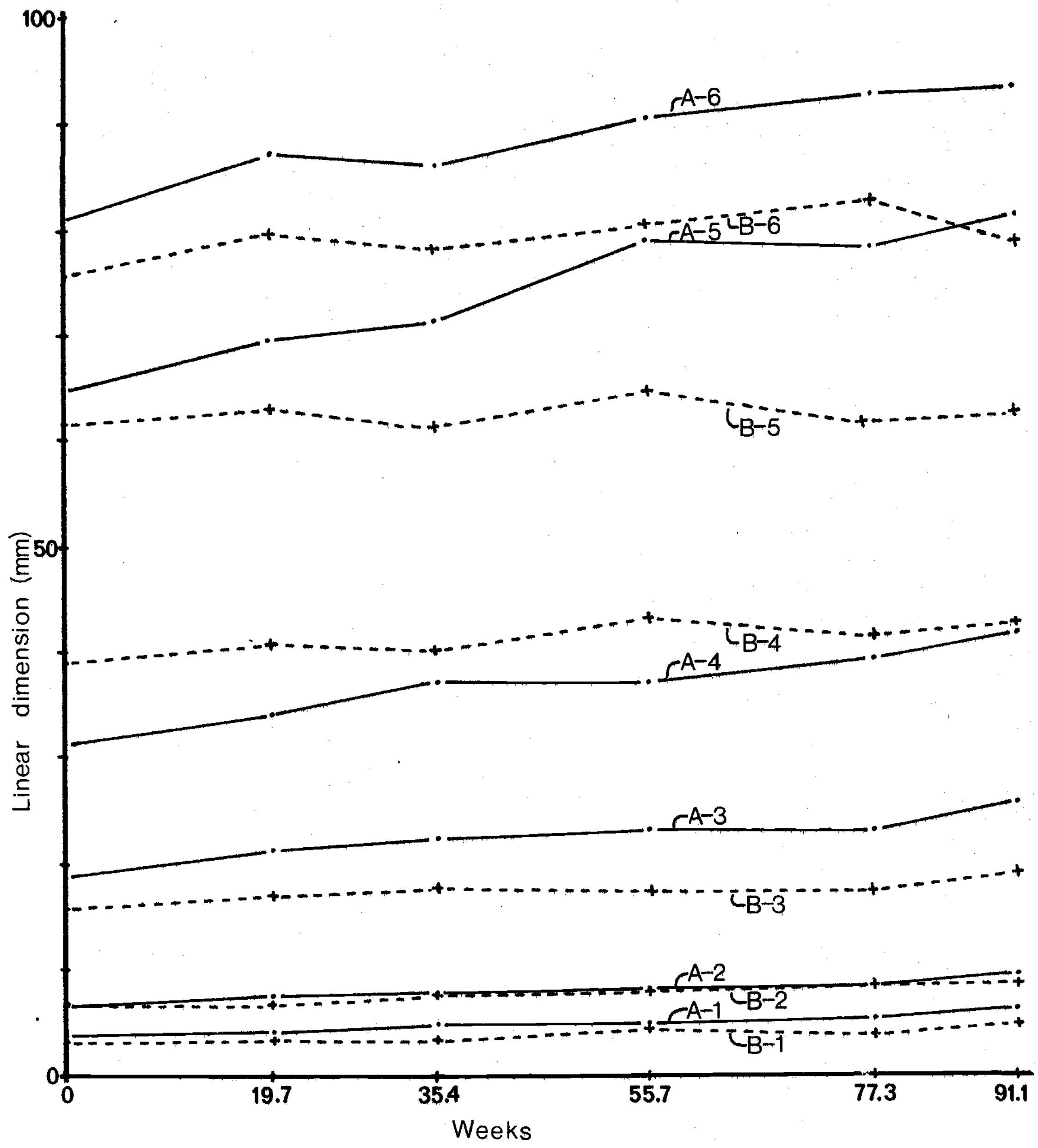


Figure **20**. Increase in distance from point of substrate attachment to points on edges of lobes. Category A: actively growing lobe tips. Category B: sides of growing lobes. Lines connect series averages for each of six starting size classes. Refer to Tables **5** & **6**.

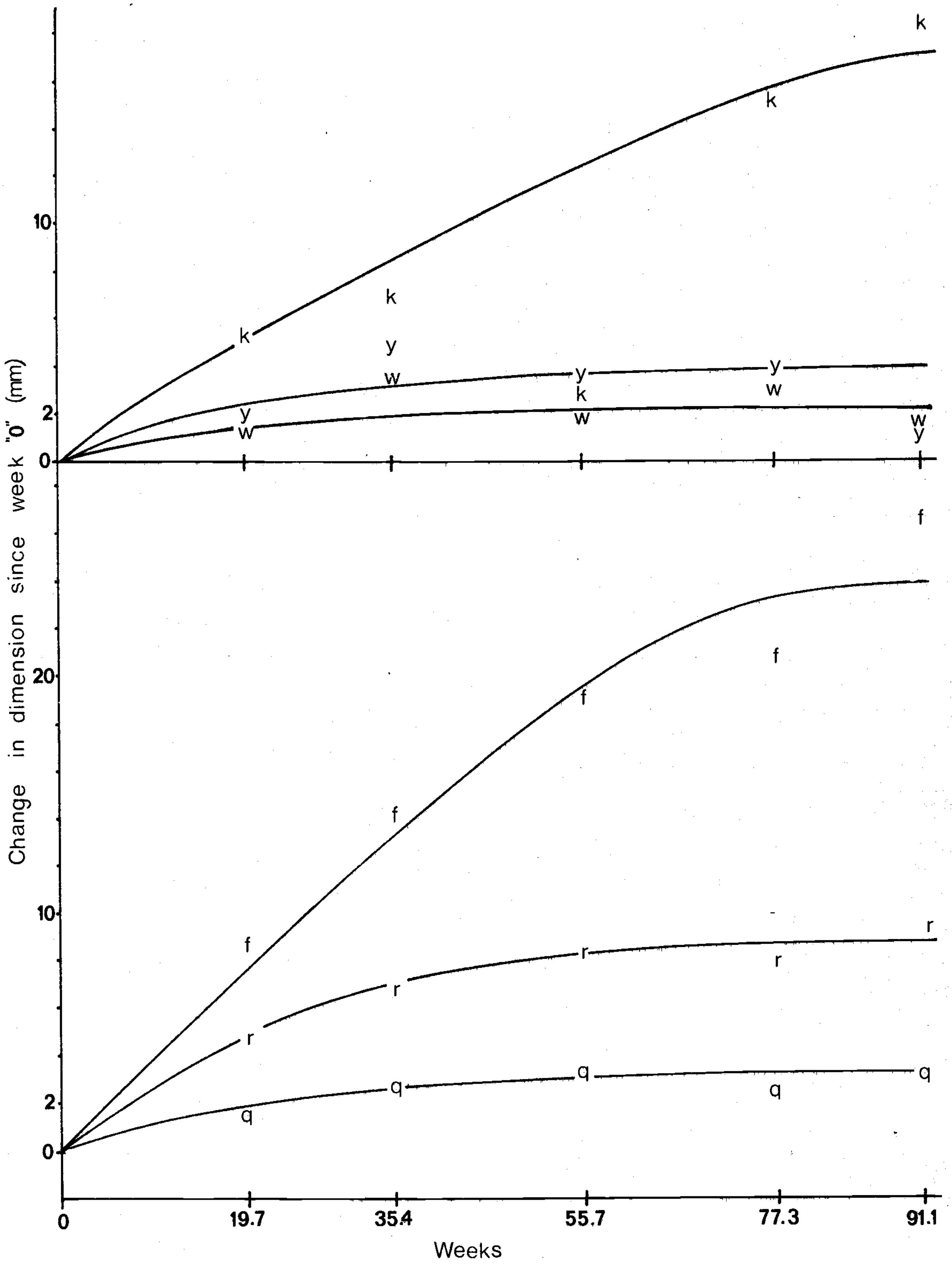


Figure **21**. Lobe growth in Thallus 6. Changes in adjusted linear dimensions with time. Letters refer to points labeled on Figures **12** & **13**. Curves fitted by eye.

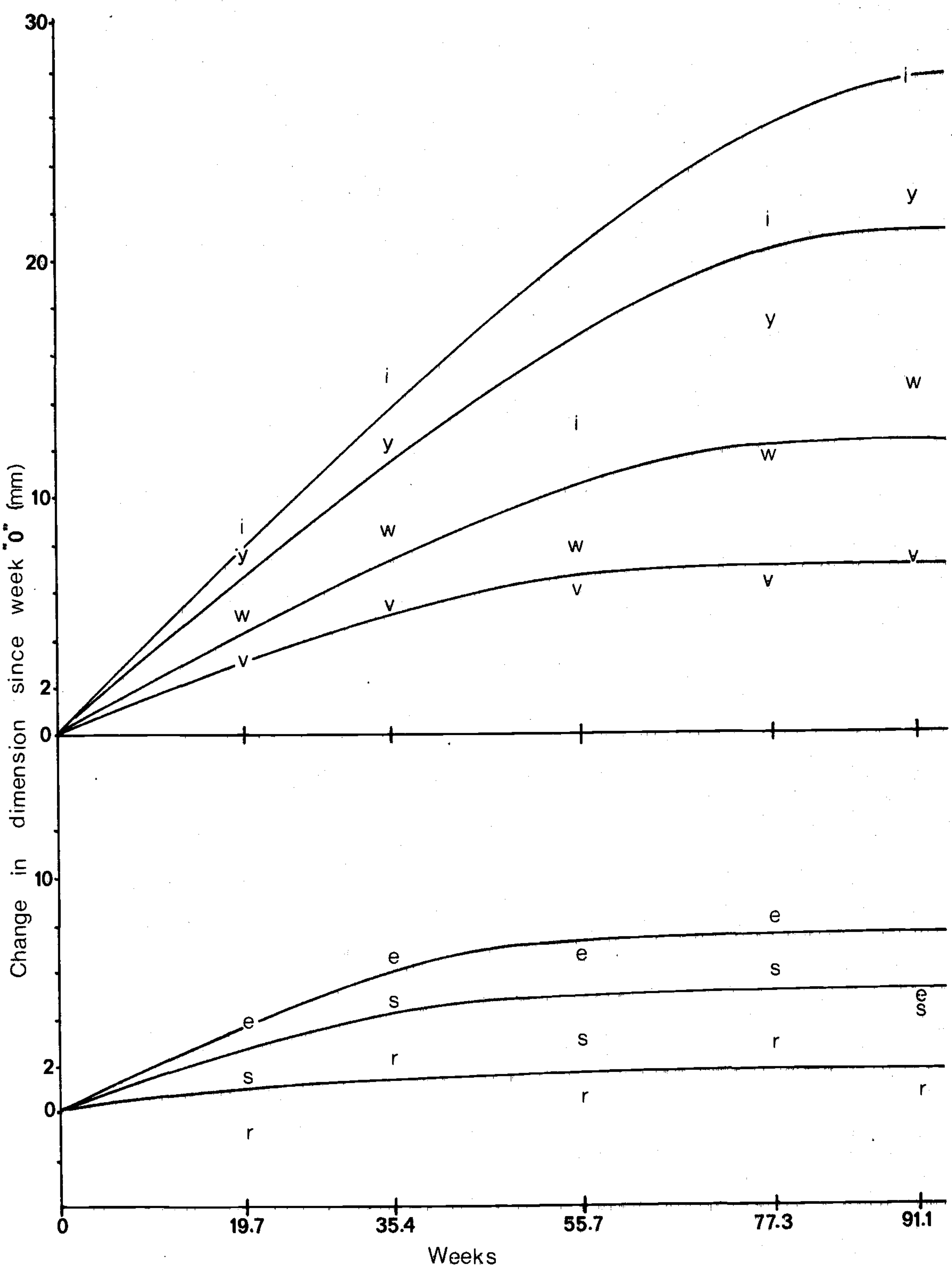


Figure **22**. Lobe growth in Thallus 7. Changes in adjusted linear dimensions with time. Letters refer to points labeled on Figures **14 & 15**. Curves fitted by eye.

V. DISCUSSION

A. Assessment of Errors in the Method and Their Implications

As Woolhouse (1968) says, the best comparative measure of lichen growth would be the increase in biomass per unit thallus (area or weight) in a given time interval. Although Woolhouse thought it necessary to destroy the thallus to get these measurements, it has been shown here that an accurate measure of biomass increase can be made without destroying the thalli measured. The results shown in Figure 17 provide, for the first time, a direct method for the estimation of the growth of individual foliose lichen thalli. Before discussing potential uses of these estimates, I will examine some of the sources of error of the method, and some of their consequences.

As shown in Table 2, eight thalli were originally chosen for this study. Thallus #17 was a large thallus that was no longer in position on its substrate after the winter of 1971-1972. It has not been used in the calculation of growth rates above. In addition, Thallus #1, another large thallus, was sequentially in several different orientations and could provide no consistent data for growth rate calculations. These two cases are similar to what Phillips (1969) found for *Lobaria pulmonaria* and support the view that the *L. oregana* population is in constant movement. There is no way to include this information within the present calculation, since the set of thalli observed for growth rates is so small in number and no data have been collected on thallus movement. The omission of cases such as Thallus #17 implies that the growth rates estimated from Figure 17 and equation (2) are for potential growth for those thalli which remain in position. Natural loss of thalli to litterfall, consumption and decomposition tend to increase with increasing thallus size, due to the increases in weight, exposed surface area, lobule production, and thallus weakening due to decomposition of the central portions. There appears to be a natural limit to the size to which L. oregana thalli can grow. The decrease in relative growth rate, apparent in Figure 18, should be accentuated by these natural forces, so that one would expect an upper limit of between 10 and 100 g thallus dry weight.

The accuracy of the Polar Planimeter was tested by measuring graph paper squares of known size. The accuracy and reproducibility are very good (Table 7), better for larger than for smaller areas. The method appears capable of resolving differences in thallus size of the order of 0.005 cm^2.

Table 7. Accuracy test of the K & E polar planimeter.

Area of square	Circuits per measurement	Measurement 1	2	3	4	5	Average
0.06 cm^2	25	0.06	0.064	0.064	0.06	0.064	0.0624 cm^2
1.0	5	1.00	0.98	1.00	1.00	1.00	0.996
16.0	2	16.0	16.0	16.0	16.0	16.0	16.0
100.0	1	99.9	100.2	100.0	99.9	100.0	100.0

Error due to mismeasurement tends to average out. In Figure 9 the distribution of measured thalli appears to be well scattered about the regression line at the small area values (less than 0.1 cm^2).

In the analyses that led to the graph in Figure 9, two sets of thalli were used: 31 "collected" thalli, dry at the time of the photograph, and ten "study" thalli or lobes, wet at the time of the last series of photographs. In the relationship of these two sets of thalli to their dry weights, it might be expected that the regression line for the ten study thalli would have a smaller slope than the regression line for the 31 collected thalli, since a thallus of given area when dry should be larger when wet. A separate regression line for the ten study thalli was slightly below a separate line computed for the 31 collected thalli. However, there was no statistically significant difference (at the 95% confidence interval) between the slopes of the two lines as indicated by the "t" test of Steel and Torrie (1960). The data were pooled and the resulting regression line (Equation (1), Figure 9) was used for further computations. The expected difference in the groups of data may not be great enough to show if, as a thallus wets up, its photoarea remains approximately the same because of buckling of the expanding thallus along existing lines of the thallus ridges.

After the analysis of the data presented here was largely completed, the paper by Beauchamp and Olson (1973) came to my attention. Their correction factor for the bias inherent in using regressions involving logarithms has not been included in this analysis. Use of their method of correction for this bias would tend to increase the slopes of the regression equations (1) and (2). So the estimates for growth rates presented here are underestimates because of this error.

When analysis of the original stations in tree #201 began it became apparent that the sample size of L. oregana thalli was extremely small (six thalli). Partly to increase the sample size, but also to make measuring more convenient on the larger thalli (3, 6 and 7), it was decided to divide these thalli into a combination of smaller parts. This seemed reasonable since it appeared that larger thalli grow as a result of the individual growth of smaller lobes. This was apparent from preliminary analysis of the photographs and also of the manner of growth of lobes (see below, under linear growth). The scatter of points representing both thalli and lobes along the regression line in Figure 17 appears to support the assumption that there is no difference between the growth of small thalli and that of smaller lobes of larger thalli.

B. Estimation of Productivity

The relationship in Figure 17 of biomass growth to initial thallus weight (or photoarea) can be used to estimate yearly productivity of L. oregana populations. This can be done if the distribution (by weight or photoarea) of the L. oregana thalli in a given population is known. It is assumed, that the old-growth Douglas fir substrate which was studied is sufficiently old, that the Lobaria populations are in a state of dynamic equilibrium, losing biomass to decomposition, consumption and litterfall that is equalled by biomass produced by thallus growth. At least some of thallus growth may be predicted by the relationship developed here. However, a good deal of the growth of older thalli may go into lobule formation, which has not been measured by this method: it is not sensitive enough to resolve changes in the numbers or existence of lobules. Lobules represent a large portion of the litterfall and may be an important food source of insects and other animals during certain periods of the year (Bailey, 1970). Carroll (1973) reports that under some circumstances over 90% of insect frass collected in throughfall precipitation under Douglas fir canopies is fungal in nature. The possibility of L. oregana productivity entering the system in this manner should be examined further.

Nevertheless, using the relationship in Figure 17 and applying it to some preliminary data on L. oregana weight class distribution in tree #201 (Table 8), some interesting approximate values of productivity for this species can be obtained. Since these growth rate estimates do not include values for lobule production, they are probably underestimates.

Table 8. Approximate distribution of Lobaria oregana thalli in six weight classes and L. oregana productivity in Tree #201.

Dry weight class	Average* weight/ class	Average age (from Figure 19)	Thalli+ Number/ class	Thalli+ Percent total/ class	Standing biomass weight/ class	Standing biomass Percent total/ class	Productivity ǂ weight/ class	Productivity ǂ Percent total/ class
0-0.0005g	0.000212g	0.2 yr	6551	26.7%	1.39g	0.0183%	2.13g	0.083%
0.0005-0.005	0.00232	2.5	6579	26.8	15.3	0.201	15.7	0.613
0.005-0.05	0.0178	5.5	5205	21.2	92.6	1.21	68.2	2.66
0.05-0.5	0.204	10	3480	14.2	709.9	9.34	348.0	13.6
0.5-5.0	1.81	15	2517	10.3	4556	60.0	1556	60.7
5.0 & above	10.11	22	220	0.9	2224	29.3	569.8	22.3
Totals			24552		7599g		2559g	

+ The numbers of thalli in each weight class were obtained by a method of branch system subsampling similar to that used by Pike et al. (1972). They are "ball park" estimates.

* Because of the distribution of thalli within weight classes, the average weight in each class is different than the mean of the end values.

ǂ Productivity is computed by obtaining the growth rate (g/yr) from equation (2) for each "average" thallus in a weight class and multiplying by the number of thalli in that weight class.

The estimates presented in Table 8 are approximate but are accurate enough to illustrate two points:

1. Proportionally larger numbers of smaller thalli.
2. Because of the interaction between numbers of thalli per weight class and the growth rates of the different average weights, the 0.5 - 5.0 g weight class (average weight, 1.81 g) is responsible for the most productivity. From Figure 19, this average weight class represents thalli from 12 to 18 years old (average is 15 yr).

A further extension of the productivity estimate can be made using the figures presented by Pike *et al.* (1972) concerning the "standing crop" of nitrogen in *L. oregana* thalli on a per tree and a per hectare (assuming 60 old-growth trees per hectare) basis. These estimates are presented in Table 9.

Table 9. Productivity of *L. oregana* dry weight and standing crop nitrogen on per tree and per hectare bases.

	Thallus dry weight		Kjeldahl nitrogen	
	per tree	per hectare	per tree	per hectare
Standing population	7.6 kg	456 kg	0.124 kg	7.5 kg
Yearly productivity	2.56	154	0.0418	2.51

Two additional assumptions are made here: (1) *L. oregana* adds nitrogen to the system only through its yearly contribution to the litterfall, and (2) the percent of nitrogen remains constant in the thalli during the year and is equal to a level measured in August. Both these assumptions tend to lower the estimate since thallus leaching by throughfall may take place and the percent nitrogen is undoubtedly higher during the times of the year when the nitrogen fixing phycobionts in L. oregana are more metabolically active, that is during the winter months.

C. Linear Growth Rates

Two trends are apparent from Table 6 and Figure 20. One is that linear growth away from the center of thallus attachment of the tips of actively growing lobes is faster than that of points along the sides of these lobes. This supports the picture in Figures 21 and 22, where most of the growth in length of lobes is shown to take place at the lobe tips. The second trend seen in Table 6 and Figure 20 is that the rate of linear growth of the lobe tips away from the point of thallus attachment changes with the distance from the point of attachment. Lobe tips in category A-5 (average distance at the start is between 50 and 75 mm) grow at the fastest rate (9.4 mm/yr), shorter lobes grow at slower rates, and longer lobes (Category A-6) also grow slower. This supports the generalized concept of the sigmoidal nature of the lichen growth curve (Hale, 1973). The implications of this are interesting: is there lateral transport of nutrition and water from the center of an established lobe to its growing margin, or is this difference in growth rates due to physical changes in the structure of the thallus?

These data point out the drawback of measuring linear growth rates, as pointed out by Woolhouse (1968): it is a meaningless measure unless one knows the size of the lobe that is growing. The fastest rate of lobe tip growth away from the point of attachment (about 9.4 mm/yr) appears to be comparable to the rates presented by Phillips (1969). Linear growth of L. pulmonaria varies from 1.86 to 8.60 mm/yr and for L. quercizans, from 3.7 to 8.5 mm/yr over a three year period for different lobes of six different thalli for each species. Unfortunately, no information is given on initial lobe lengths. Since these ranges are comparable to that given in this study, it may be assumed that linear growth rates in all three Lobaria species are comparable, and that areal and dry weight growth rates of L. pulmonaria and L. quercizans probably follow the pattern shown for L. oregana.

The graphs in Figures 21 and 22, showing growth within lobe tips along axes of growth in thalli 6 and 7, have been estimated since there were problems with lobe reorientation in some cases (particularly s-w, s-y and s-k in Thallus #6 and x-v, x-w, x-y and x-i in Thallus #7). Only an approximation of the pattern of linear growth can be seen. It appears, however, that lobe growth is maximal at the lobe tip and rapidly reaches zero growth about 15 to 20 mm behind the tip. The relative changes in the dimensions x-q, x-r and x-t in Thallus 6 (Figure 21) show this particularly well. Furthermore, it appears, although it is impossible to measure this from the photographs, that "linear" growth continues for a time behind this zone, but is taken up by increases in depth and complexity of the reticulations, which effectively increases the mass per unit area (photoarea) of the thallus.

There is no information in the literature concerning the detailed analysis of growth of lichen thalli. Hale (1970) analyzed in minute detail the growth of a single lobe of _Parmelia caperata._ Although he did not make the measurements made in this study, it can be seen, with careful examination of his enlargements, that a similar pattern of growth is manifest on a micro-scale in that species.

Internal lobe growth in _L. oregana_ as far back as 1 to 2 cm from lobe tips is an unusual example of the capacity of the mycobiont hyphae there to undergo intercalary growth. This is probably a general rule for all lichen mycobionts. Growth in nonlichenized fungi is regarded as usually occurring only at the distal point of the hyphal tip (Burnett, 1968). The peculiar growth pattern of lichen fungi may be connected to their ability to remain viable for much longer periods of time than nonlichenized fungi. The micromorphology of the lobe tips of _L. oregana_ may give a clue as to how this growth occurs.

Once a lobe has been delimited, its growth is largely along an axis away from the point of attachment of the rest of the thallus. Other lobes are delimited (such as those between points e and h along lobe tip f in Thallus #6) which, in turn, will grow out away from the edge of the existing lobe. On a microscale, Hale's (1970) Parmelia caperata lobes appeared to grow perpendicular to the axis of growth, but on a larger scale, these delimited lobes did not continue to grow perpendicularly.

In L. oregana, growth does not completely stop along the lobe edges which are not growing outward, however. Along the internal margins of old lobes, usually from 50 to 100 mm from the actively growing tips, and along the edges of reticulations within lobes, a vast proliferation of tiny lobules is produced. It is impossible to estimate the amount of lichen biomass going into lobule production from the photographs used in this thesis. From preliminary study of weight class distribution of L. oregana in Tree #201 (Table 9), it is apparent that these lobules function in the vegetative reproduction of L. oregana. They readily break off from dry thalli, drift through the canopy habitat and continually reestablish the species. They may also form a considerable portion of mycophagous insect diets as reported above.

In conclusion, the analysis of linear growth has led to the following view of the growth strategy of L. oregana. Growth can be divided into three "phases":

1. Rapid (up to ten mm per year) growth of delimited lobes -- this growth extends the thalli along and over the substrate at maximum speed.
2. Formation of reticulations within the larger lobes of a thallus -- these reticulations may function to improve precipitation interception and holding for maximum water uptake by these thalli.
3. Lobule formation along the trailing margins of developing lobes and along reticulation ridges within lobes. These lobules provide a means of asexual dissemination and may also enter the food chain through mycophagous insects and small mammals.

Although these three "phases" occur sequentially in any single lobe, the change from one phase to another is gradual, and all three phases are occurring at once in larger lobes and entire thalli.

BIBLIOGRAPHY

Ahmadjian, V. 1967. The Lichen Symbiosis. Blaisdell Publ. Co. Waltham.

Ahmadjian, V. and M. E. Hale, eds. 1973. The Lichens. Academic Press. New York.

Andreev, V. N. 1954. Growth of forage lichens and methods of improving it. Geobotania. 9:11-74.

Anonymous. 1973. Lichenometry. Arctic and Alpine Research 5(4):291-424.

Bailey, R. H. 1970. Animals and the dispersal of soredia from *Lecanora conizaeoides* Nyl. ex Cromb. Lichenol. 4:256.

Barkman, J. J. 1958. Phytosociology and Ecology of Cryptogamic Epiphytes. Van Gorcum & Comp. N. V. Assen, Netherlands.

Beauchamp, J. J. and J. S. Olson. 1973. Corrections for bias in regression estimates after logarithmic transformation. Ecology 54(6):1403-1407.

Beschel, R. E. 1950. "Lichens as a Measure of the Age of Recent Moraines." (English translation), In: Arctic and Alpine Research 5(4):303-310.

__________ 1961. "Dating Rock Surfaces by Lichen Growth and Its Application to Glaciology and Physiography (Lichenometry." In: Geology of the Arctic (G. O. Raasch, ed.). Univ. of Toronto Press. Toronto. pp. 1044-1062.

Burnett, J. H. 1968. Fundamentals of Mycology. Edward Arnold Publ. London.

Carroll, G. 1973. Personal communication.

Degelius, G. 1964. Biological studies of the epiphytic vegetation on twigs of *Fraxinus excelsior*. Acta Horti gothoburg 27(3):11-55.

Denison, W. C. 1973. Life in Tall Trees. Sci. Am. 228(6):74-80.

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: Franklin, J. F., L. J. Dempster, and R. H. Waring, eds. Proceedings - research on coniferous forest ecosystems - a symposium. Pacific Northwest Forest and Range Experiment Station. Portland. pp. 147-158.

Edwards, R. Y., J. Roos and R. W. Ritcey. 1960. Quantitative Observations on Epidendric Lichens Used as Food by Caribou. Ecology. 41:425-431.

Fink, B. 1917. The rate of growth and ecesis in lichens. Mycologia 9:138-158.

Frey, E. 1959. Die Flechtenflora und-vegetation des National-parks im Untergardin. II. Teil: Die Entwicklung der Flechten vegetation auf photogrammetrisch kontrollierten Dauerflachen. Ergeb. der Wiss. Untersuchs. des Schweiz. Nationalpark. N. F. 6:241-320.

Hakulinen, R. 1966. Uber die Wachstumgeschwindigkeit einiger Laubflechten. Ann. Bot. Fenn. 3:167-179.

Hale, M. E., Jr. 1959. Studies on lichen growth rate and succession. Bull. Torrey Bot. Club. 86:126-129.

________ 1967. The Biology of Lichens. Edward Arnold. London.

________ 1970. Single lobe growth-rate patterns in the lichen Parmelia caperata. Bryol. 73:72-81.

________ 1973. "Growth" In: Ahmadjian, V. and M. E. Hale, eds. The Lichens. Academic Press. New York.

Henriksson, E. and B. Simu. 1971. Nitrogen fixation by lichens. Oikos. 22:119-121.

Herre, A. W. 1904. The Growth of Ramalina reticulata Kremplh. Bot. Gaz. 38:218-219.

Jochimsen, M. 1966. Ist die Grosse des Flechtenthallus wirklich ein brauchbarer Masstab zur Datierung bon glazialmorphologischen Relikten. Geographiska Ann. 48A:157-164.

Jones, K. 1970. Nitrogen fixation in the phyllosphere of the Douglas fir, Pseudotsuga douglasii. Ann. Bot. 34:239-244.

Jordan, W. P. 1970. The Internal Cephalodia of the Genus Lobaria. Bryol. 73(4):669-681.

__________ 1973. The Genus Lobaria in North America North of Mexico. Bryol. 76:225-251.

Karenlampi, L. 1970. Morphological analysis of the growth and productivity of the lichen Cladonia alpestris. Rep. Kevo Subartic Res. Stat. 7:9-15.

__________ 1971. Studies in the relative growth rate of some fruticose lichens. Rep. Kevo Subartic Res. Stat. 7:33-39.

Linkola, K. 1918. Messungen uber den jahrlichen Langenzuwachs einiger Parmelia- und Parmeliopsis-Arten. Societes Pro Fauna et Flora Fennica, Meddelanden. 44:153-158.

Millbank, J. W. and K. A. Kershaw. 1970. Nitrogen metabolism in lichens. III. Nitrogen fixation by internal cephalodia in Lobaria pulmonaria. New Phytol. 69:595-597.

Nienburg, W. 1919. Studien zur Biologie der Flechten. I. II. III. Z. Bot. 11:1-38.

Ozenda, P. and G. Clauzade. 1970. Les Lichens. Masson et Cire. Paris.

Phillips, H. C. 1969. Annual growth rate of three species of foliose lichens determined photographically. Bull. Torrey Bot. Club. 96:202-206.

Pike, L. H. 1971a. A method for Estimating Productivity of Twig Epiphytes. (Abstract) Proc. of the Ore. Acad. of Sci. 7:66.

__________ 1971b. The Role of Epiphytic Lichens and Mosses in Production and Nutrient Cycling of an Oak Forest. Ph. D. Thesis. Univ. of Oregon, Eugene.

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: Franklin, J. F., L. J. Dempster, and R. H. Waring, eds. Proceedings - research on coniferous forest ecosystems - a symposium. Pacific Northwest Forest and Range Experiment Station. Portland. pp. 177-187.

Pike, L. H., W. C. Denison, F. M. Rhoades and M. Sherwood. 1974. Floristic Survey of Epiphytic Lichens and Bryophytes Growing on Trunks and Branches of Living, Old-growth Conifers in Western Oregon. Submitted to the Bryol.

Platt, R. B. and F. P. Amsler. 1955. A Basic Method for the Immediate Study of Lichen Growth Rates and Succession. J. Tenn. Acad. Sci. 30:177-183.

Porter, L. 1927. The rate of growth of lichens. Trans. Brit. Mycol. Soc. 12:149-152.

Prince, C. R. 1974. Growth rates and productivity of Cladonia arbuscula and Cladonia impexa on the sand of Forvie, Scotland. Can. J. Bot. 52:431-433.

Reid, A. 1960. Thallusbau und Assimilationshaushalt von Laub und Krustenflechten. Biol. Zentralbl. 79:129-151.

Rossman, A. 1972. Unpublished data.

Rydzak, J. 1961. Investigations on the Growth Rate of Lichens. Ann. Univ. Marie Curie-Skłodowska. C16:1-13.

__________ 1966. Investigations on the Growth Rate of Lichens. Part II. Ann. Univ. Marie Curie-Skłodowska. 21:167-182. (Polish with English summary)

Scott, G. D. 1956. Further investigations of some lichens for fixation of nitrogen. New Phytol. 55:111-116.

Scotter, G. W. 1963. Growth Rates of Cladonia alpestris, C. mitis and C. rangiferina in the Taltson River Regions, N. W. T. Can. J. Bot. 41:1199-1202.

Steel, R. G. D. and J. H. Torrie. 1960. Principles and Procedures of Statistics. McGraw-Hill. New York.

Tracy, D. M. and D. Nielsen. 1971. Northwest Science.

Woolhouse, H. W. 1968. The measurement of growth rates in lichens. Lichenol. 4:32-33.