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NATURAL HISTORY OF PLUMMERS ISLAND, MARYLAND[1]
XXIII. STUDIES ON LICHEN GROWTH RATE AT PLUMMERS ISLAND, MARYLAND

James T. Lawrey, and Mason E. Hale, Jr.

Introduction

In 1965 the junior author started photographing a series of lichen quadrats on rock exposures at Plummers Island, Maryland. The main goal was to determine as accurately as possible how fast the lichens grow and how this growth is affected by weather conditions. In the past 12 years a file of hundreds of photographs has accumulated along with detailed weather data taken on the island from 1966 to 1970. One article, a study of single-lobe growth rates (Hale, 1970), has already appeared. The present article attempts to summarize some of the data over the period 1965–1970, when photographs were taken at intervals of 7–58 days, and to present a statistical analysis of some of the factors that we consider important in determining growth rate as well as related biological phenomena of thallus size and age, growth phases, and the effects of predation. We hope to continue photographing the lichen quadrats over a long period of time, to start new experiments to answer specific questions, and publish on these and other aspects as the opportunity arises.

Methods

There are numerous difficulties in studying lichen growth and the environmental factors which affect it. These difficulties can hamper precise planning and implementation of growth rate studies, resulting in published reports that contain noncompatible data of questionable value. For example, whole lichen thalli cannot yet be studied with reliability under controlled conditions; growth measurements must be taken in the field. Therefore, since weather conditions fluctuate considerably from year to year, lichen thalli must be observed over long periods of time to determine how variations in growth rate reflect variations in environmental factors. Armstrong (1973) attempted to avoid wide variations in growth due to microclimatological variability by placing saxicolous lichen thalli attached to loose pieces of slate on flat boards in one area. Thus, all thalli were under approximately the same environmental conditions. Most studies, however, are conducted in situ. For this reason, observations must be made more often than once or twice a year in order for them to contain sufficient information. Most long-term studies involve one to a few observations per

year, whereas intensive studies in which measurements are taken at frequent intervals (weekly or monthly) are rarely long enough in duration.

Difficulties also arise because lichens exhibit widely variable growth rates not only from thallus to thallus, but from lobe to lobe on the same thallus (Hale, 1970). Therefore, numerous samples must be taken to account for this variability in observed growth rates.

Colonies of saxicolous foliose lichens, primarily *Pseudoparmelia baltimorensis* (Gyel. & For.) Hale and *Xanthoparmelia conspersa* (Ach.) Hale, and crustose lichens *(Graphis, Huilia, Lecidea,* etc.) were photographed from 1965 to 1976 at intervals ranging from several days early in the study to several months near the end of the study, depending on weather conditions, access to the island during floods, and scheduling of time for photography. Holes were usually drilled into the rocks on which lichen colonies were found to facilitate location and orientation of the colonies in the field. To avoid obvious errors in lobe measurement due to thallus expansion, photographs were taken at least 48 hours after periods of precipitation so that air-dry equilibrium was reached. During the 12-year study period, over fifty colonies were photographed, many of which disappeared at some time during the study. Figure 1 illustrates the camera set-up used throughout the study. Prints of each colony were enlarged about 2× and measurements taken from the prints.

Weather data were collected from the island during a four-year period (1966–1969) early in the study. Precipitation, minimum and maximum temperatures, and relative humidity were monitored on the island using standard meteorological equipment, located within 2–150 m of the quadrats. Percent cloud cover data for the area were compiled from weather summaries collected at National Airport, 18.5 km SSE away. During this time, growth data were collected at as close to monthly intervals as possible to insure maximum precision in detecting correlations with weather data.

Using the photographic raw data, we measured the cumulative growth and annual growth in mm of selected lichen lobes (approximately five per thallus), and calculated average growth in mm per day for each sampling interval (Hale, 1970). After scanning a series of photographs, we selected only those lobes which exhibited obvious growth over long intervals. Some lobes exhibited either periods of little growth or no growth at all. The method of computing lichen growth by sampling period allowed a direct interpretation of relationships with climatic variables, which were also arranged and summarized by sampling period. Annual growth rates were averaged from growth rate data collected for all thalli of each species throughout the entire study period, in order to reduce the error associated with annual differences in growth rates. In an attempt to identify the climatological factor or factors most closely related to lichen growth, step-

Fig. 1.   Positioning of camera for close-up photography of saxicolous lichen colonies from Plummers Island, Maryland.

wise multiple regressions were run with lichen growth the dependent variable and weather factors the independent variables. We also compared lichen growth rates of the major lichen species studied, and the growth rates of juvenile and mature thalli of *P. baltimorensis* and *X. conspersa* in order to determine whether species-related or age-related differences in growth rates are detectable.

All growth rate data, including photographs of all quadrats, are on file in the Department of Botany, National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Results and Discussion

Annual Growth Rates

Lichens are notoriously slow-growing and long-lived organisms. Of the numerous studies dealing with lichen growth in the literature (see recent reviews by Hale, 1973; Armstrong, 1976), few have reported annual radial

Table 1. Annual lichen single-lobe growth rates observed at the Plummers Island, Maryland study site for numerous thalli sampled from 1965 to 1976.

Species	Annual growth rate (mm/yr)
Parmelia rudecta	5.29 ± 1.41[a]
Pseudoparmelia baltimorensis	5.09 ± 0.25
Parmelina aurulenta	4.80 ± 0.39
Xanthoparmelia conspersa	3.28 ± 0.32
Pseudoparmelia baltimorensis (juvenile)[b]	2.63 ± 0.31
Xanthoparmelia conspersa (juvenile)	2.15 ± 0.48
Physcia millegrana	1.72 ± 0.39
Graphis scripta[c]	0.85 ± 0.01
Lecanora muralis	0.84 ± 0.01
Lecidea albocaerulescens	0.70 ± 0.10

[a] Growth rates are means (mm/yr) ± S.E. N = 15 lobes or greater.
[b] Juvenile thalli are less than 1.5 cm in diameter.
[c] Corticolous.

increases greater than a few millimeters. Mean annual growth rates for all lichen species observed during our study are shown in Table 1. These growth data are means of single-lobe growth rates for numerous individual lichen thalli summarized for all sampling intervals during the twelve-year study. The Parmelias, excepting *Xanthoparmelia conspersa*, exhibited growth rates of around 5 mm/yr, significantly higher ($p < 0.05$) than any of the other species. *Xanthoparmelia conspersa* exhibited an intermediate growth rate (3.28 mm/yr), as did *Physcia millegrana* (1.72 mm/yr). The crustose species had the lowest rates. If one morphological factor is directly related to growth rate, it appears to be lobe width. Generally, the larger and wider the lichen lobes, the higher the growth rate. This relationship is also apparent from the growth data summarized by Hale (1973) for numerous other species.

Lichens are known to exhibit annual variations in growth rates. Brodo (1965) discovered relatively large variations in growth rate data for several corticolous lichens growing on Long Island, New York, and attributed this to fluctuations in climatic factors from one year to the next. Hakulinen (1966) also found that widely variable annual growth rates occurred for lichens in Finland during the three-year period from 1961 to 1964. More recently Showman (1976) recorded rates of 4.28 mm, 3.45 mm, and 4.30 mm for *Pseudoparmelia caperata* (a close relative of *P. baltimorensis*) during the years 1973, 1974, and 1975, respectively. Inasmuch as few long-term studies of lichen growth are reported in the literature, however, this phenomenon requires further documentation to determine the causes of annual variation in growth rates.

QUADRAT 6

LOBE 6

PERIOD	ENDING DATE	CUMULATIVE GROWTH IN MM.	DAYS IN PERIOD	GROWTH PER DAY IN MM.
1	5 OCT 1965	1.2	36.0	
2	30 OCT 1965	1.4	25.0	.0080
3	5 DEC 1965	1.9	36.0	.0139
4	31 DEC 1965		26.0	
5	27 FEB 1966	2.7	58.0	.0101
6	20 MAR 1966	2.8	21.0	.0048
7	4 MAY 1966	3.5	45.0	.0156
8	5 JUN 1966	3.5	32.0	.0000
9	5 JUL 1966		30.0	
10	21 AUG 1966	4.8	47.0	.0173
11	18 SEP 1966	4.8	28.0	.0000
12	15 OCT 1966	4.9	27.0	.0037
13	30 OCT 1966	4.9	15.0	.0000
14	13 NOV 1966	5.0	13.0	.0077
15	4 DEC 1966	5.0	21.0	.0000
16	6 JAN 1967	5.6	33.0	.0182
17	26 FEB 1967	5.8	51.0	.0039
18	26 MAR 1967	5.8	28.0	.0000
19	23 APR 1967	6.2	28.0	.0143
20	25 MAY 1967	6.8	32.0	.0187
21	4 JUN 1967	7.2	10.0	.0400
22	20 JUN 1967	7.2	16.0	.0000
23	24 JUL 1967	7.5	34.0	.0088
24	13 AUG 1967	7.9	20.0	.0200
25	31 AUG 1967	7.9	18.0	.0000

Fig. 2. Example of output from lichen single-lobe daily growth rate computer program. Data shown are for quadrat 6, which is a colony of *Pseudoparmelia baltimorensis* illustrated in Figs. 5–12. Growth data are collected approximately monthly, and increment increases are expressed in mm per day.

Daily Growth Rates

In addition to determining annual rates for the lichens observed during this study, we plotted average daily growth rates of dominant species at around monthly intervals to determine seasonal changes in growth. Figure 2 shows an example of output generated by the single-lobe lichen growth rate computer program on file in the Department of Botany, Smithsonian Institution. Daily growth rates of several lobes of *Pseudoparmelia baltimorensis* (quadrat 6) are printed by sampling period. These data can then be summarized by year, or can be punched on another set of computer cards containing weather data for each sampling period for use in regression analyses. Figures 3 and 4 show average daily growth summaries for *P. baltimorensis* and *X. conspersa* during 1966 and 1967, and for *Parmelia rudecta* during 1967.

Lichen growth rates have been shown to vary seasonally, suggesting a correlation between climate and growth rate (Rydzak, 1961; Phillips, 1963; Brodo, 1965; Hale, 1970; Armstrong, 1973; Showman, 1976). Decrease or cessation of growth during winter months has been shown for various species growing in Poland (Rydzak, 1961), Long Island, New York (Brodo, 1965), Plummers Island, Maryland (Hale, 1970), and Ohio (Showman, 1976). All species in our study exhibit similar general patterns of growth, with the highest growth occurring in the spring and summer months, and the
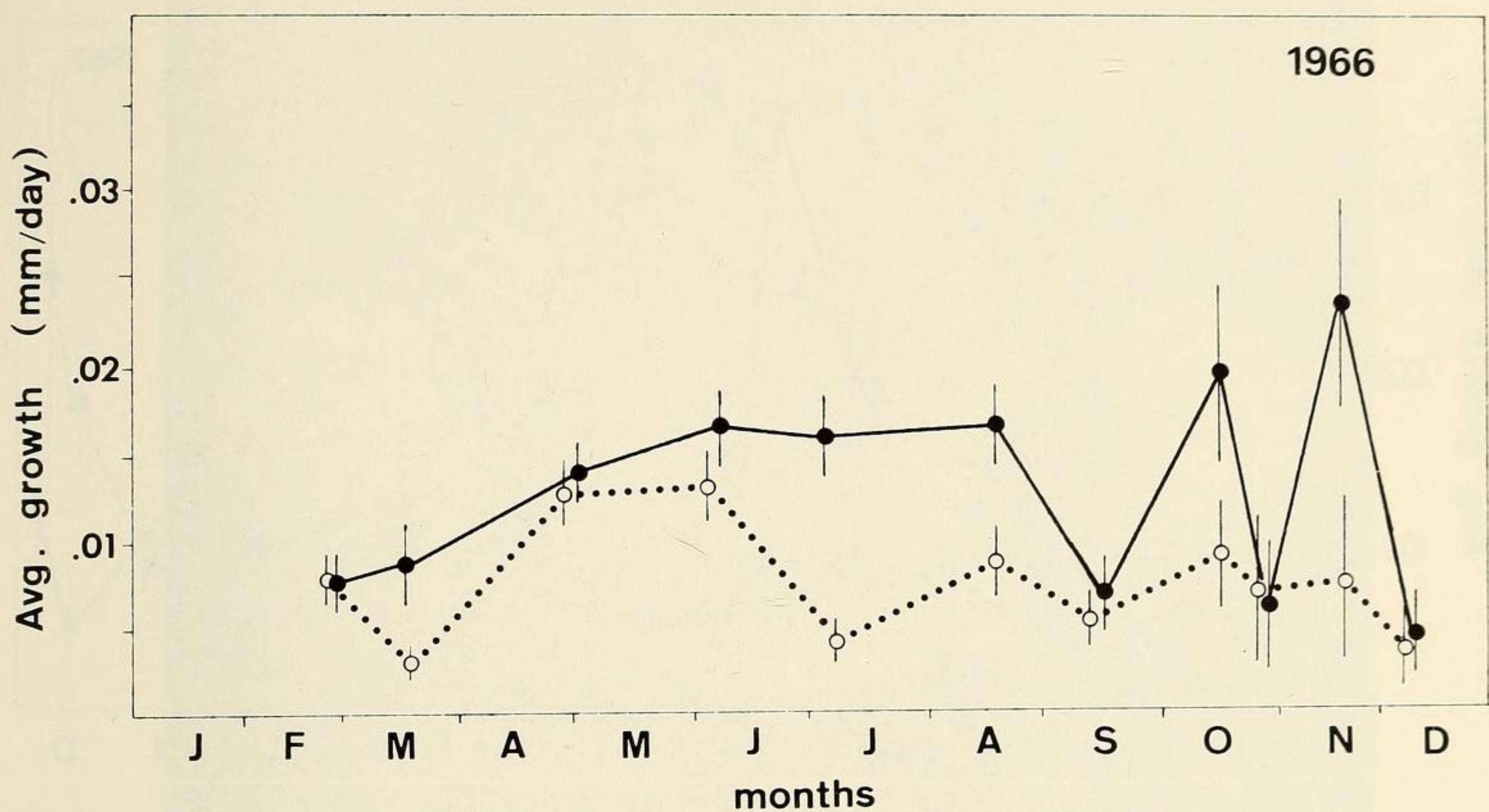
Fig. 3. Growth rates during 1966 for mature thalli (over 1.5 cm diameter) of *Pseudo-parmelia baltimorensis* (closed circles) and *Xanthoparmelia conspersa* (open circles). Data points are means ± S.E. N = 15 lobes or greater.

lowest growth occurring in February. These patterns are similar to those calculated for other years during the study for which less growth information was available.

The seasonal variability in growth rate for *P. baltimorensis* is much greater than for *X. conspersa* (Figs. 3 and 4). *Xanthoparmelia conspersa* exhibits a relatively flat growth curve during 1966 and 1967, with low peaks and little variation; *P. baltimorensis*, however, has a modulating growth curve with high peaks and more obvious differences in seasonal growth from one year to the next, giving more discernible growth patterns than *X. conspersa*. We believe this characteristic of *P. baltimorensis* (and other broad-lobed species) makes it more amenable to correlations between growth and environmental factors than species which grow less rapidly.

There is a great deal of lobe-to-lobe variation among all lichen thalli photographed, which would be most clearly seen if lobes were sampled randomly. However, we took measurements from only those lobes which exhibited obvious measurable growth. More work needs to be done to determine the proportion of lobes which show measurable growth relative to lobes which stop growing and the causes for this cessation of growth. We compared lobes for each thallus of *P. baltimorensis* which exhibited growth and found that the lobe-to-lobe variation in radial growth was up to 50%. Thus, even thallus lobes which exhibited active growth show widely variable increments with time. This observation emphasizes the need to sample numerous lobes from many thalli over long time intervals before acurate generalizations regarding growth can be made.
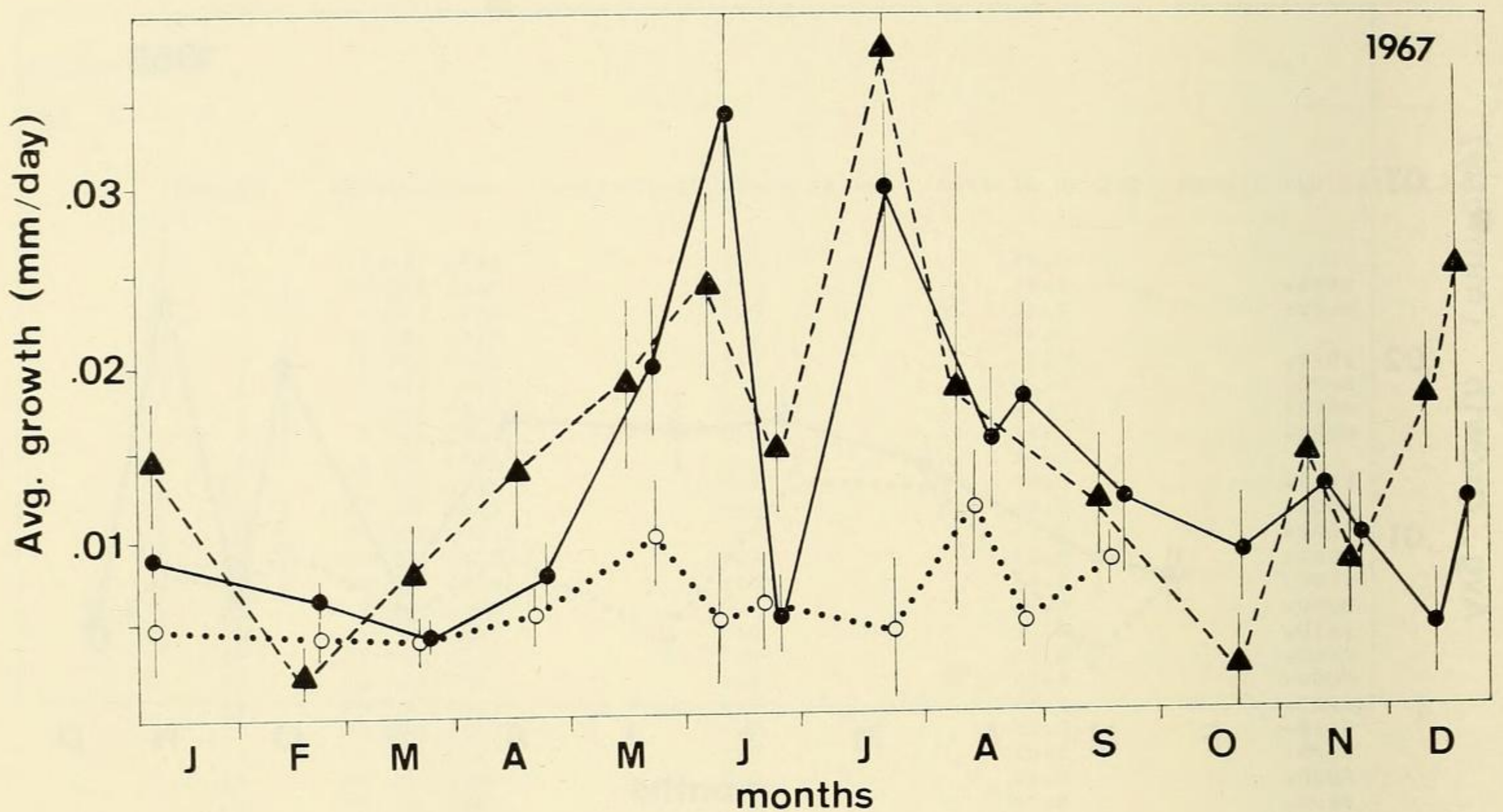
Fig. 4.   Growth rates during 1967 for mature thalli (over 1.5 cm diameter) of *Pseudoparmelia baltimorensis* (closed circles), *Xanthoparmelia conspersa* (open circles), and *Parmelia rudecta* (triangles). Data points are means ± S.E. N = 15 lobes or greater.

Growth Phases in Lichens

Lichen growth studies have shown that many species pass through various growth phases throughout life. These are presumed to be as follows: (a) a juvenile growth phase characterized by small thalli (usually less than 1.5 cm diameter) which grow at reduced rates; (b) a "great" period (Beschel, 1958) during which time thalli grow at maximum rates; (c) a maturation period during which time thalli approach maximum size and growth is linear; (d) a senescence period characterized by mature thalli which exhibit decreased growth rates and varying degrees of disintegration. Because there are very few complete life history studies available for lichens, these growth phases should be considered tentative. However, the existing information supports the notion that lichen growth is not uniform, and that most species exhibit one or more of the above growth phases. For example, Armstrong (1974) found that for *Parmelia glabratula* ssp. *fuliginosa* there was a distinct prelinear juvenile growth phase and a linear growth phase, but found no evidence of reduced growth at the time of thallus disintegration (fragmentation). Hale (1967), however, showed that the radial growth rate of *Parmelia (Xanthoparmelia) conspersa* is reduced as a thallus diameter of 13 cm is reached, corresponding to the senescence growth phase. Kärenlampi (1970, 1971) found that as thalli of *Cladina stellaris* (*Cladonia alpestris*) aged, relative growth rate decreased. More studies of lichen growth and thallus age are required for a wider variety of species before the concept of growth in phases can be more firmly established.
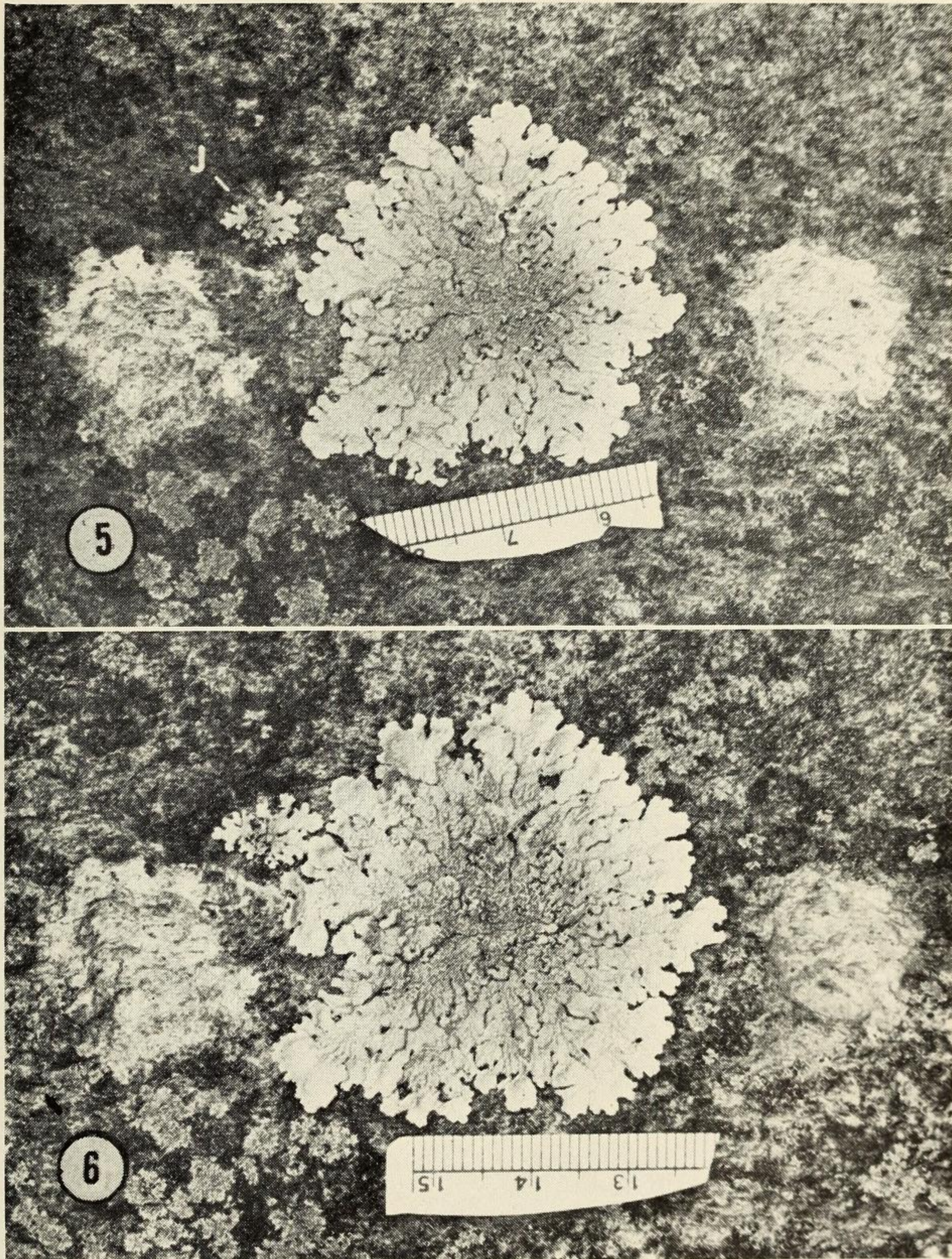
Figs. 5–12. Successive photographs of *Pseudoparmelia baltimorensis* taken at Plummers Island. Note juvenile thallus (J). Main thallus is flanked by two drill holes in the rock surface used for relocation of the colony. Scale in mm. Fig. 5. 20 March, 1966. Fig. 6. 21 August, 1966.

In our study it was possible to attack this problem by selecting speci-mens of various size classes from the photographs. For example, juvenile thalli of *P. baltimorensis* (defined as less than 1.5 cm diameter) grow at significantly lower rates ($p < 0.001$) than do mature thalli (Table 1). This relationship is true at a lower significance level ($p < 0.05$) for *X. conspersa*. Figures 5–12 illustrate the difference in growth rates between mature and juvenile thalli of *P. baltimorensis* in one quadrat. The juvenile
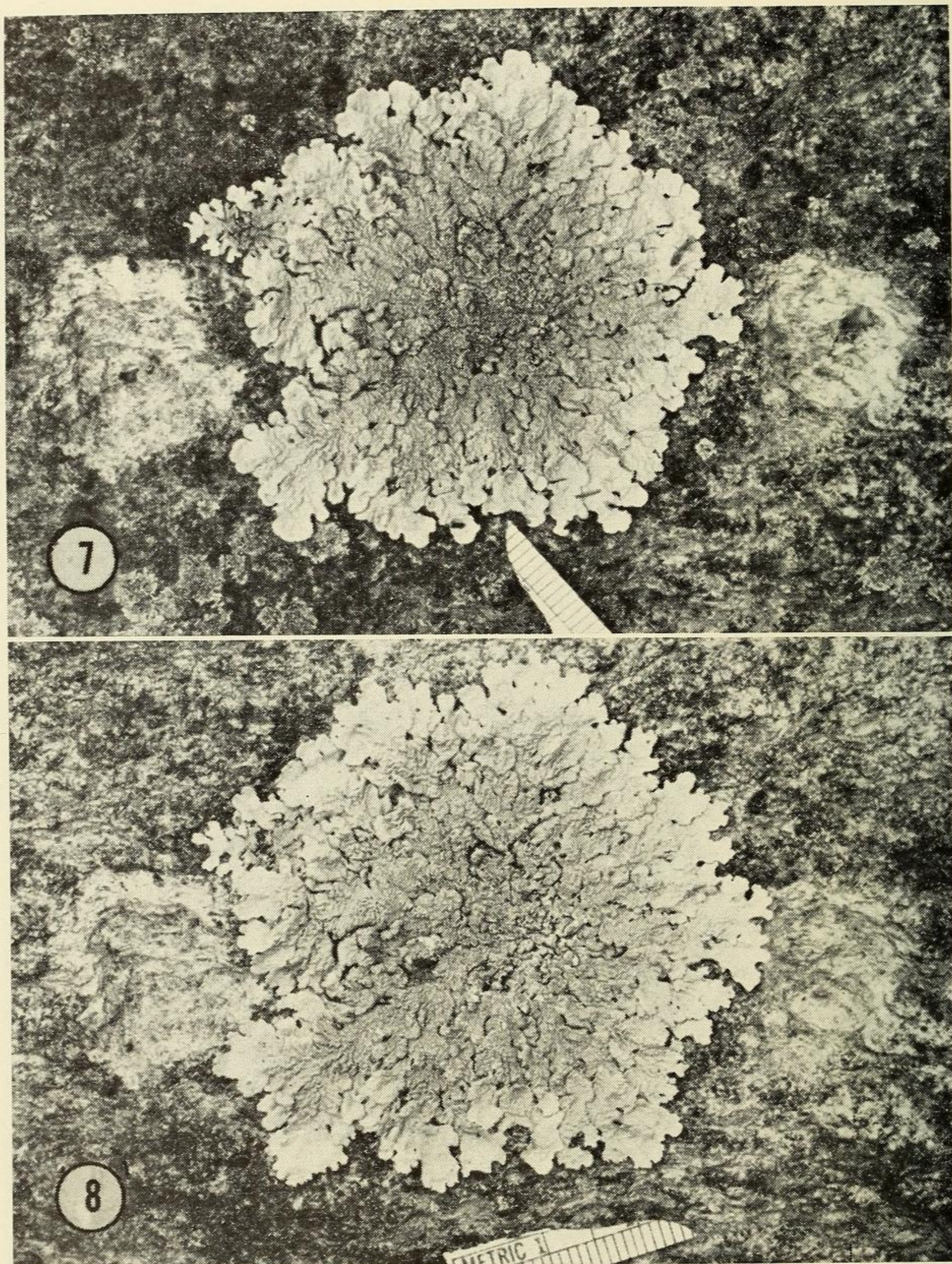
Fig. 7.   23 April, 1967. Fig. 8. 22 October. (See legend for Figs. 5–12.)

thallus is engulfed by the more rapidly-growing lobes of the mature thallus (Figs. 7–9), causing its death and disintegration (Fig. 10).

Armstrong (1976) reported that as thallus diameter increased, growth rate for *Parmelia glabratula* ssp. *fuliginosa* tended also to increase. Our data confirm this kind of relationship for *P. baltimorensis* and *X. conspersa*. Other species were not tested due to an insufficient number of thalli photographed; however, we expect that the juvenile thalli of most species would consistently grow at lower rates than mature thalli, the question being how small a thallus should be to be considered juvenile. Figures 13–18 show a growth sequence of a very tiny (less than 1.0 mm) thallus of *P. baltimoren-*
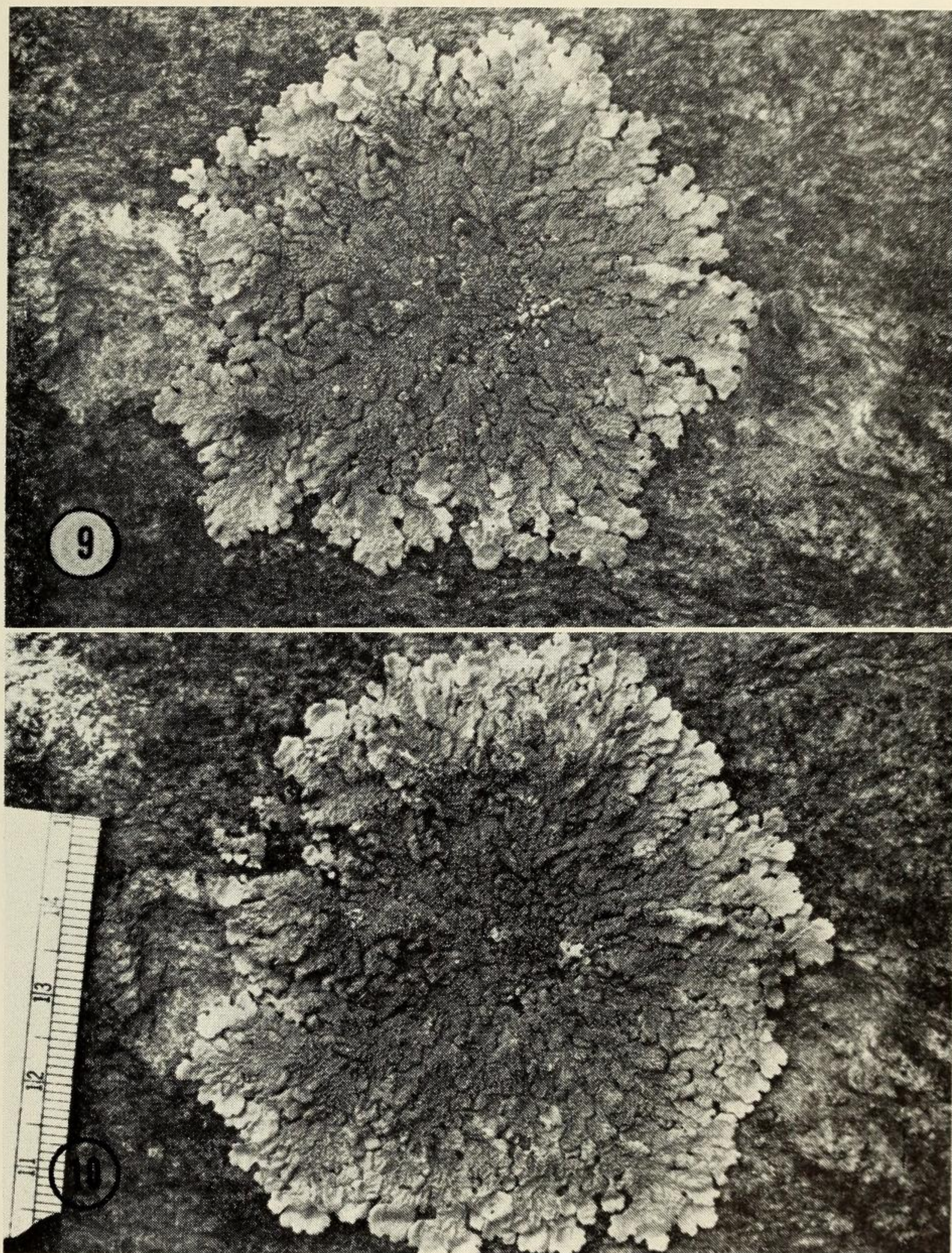
Fig. 9. 12 April, 1968. Fig. 10. 17 June, 1969. (See legend for Figs. 5–12.)

sis. This thallus increases in surface area by more than 200% in less than one year, yet, the maximum annual radial increase is only 0.7 mm, far from the approximately 5 mm for a mature thallus. Armstrong (1974) recognized the logarithmic increase in relative growth rates ($cm^2/cm^2/yr$) of small thalli (2–3 mm) of *Parmelia* (*Xanthoparmelia*) *conspersa* and *Parmelia glabratula* ssp. *fuliginosa.*

To our knowledge, there have been no quantitative studies of small lichen thalli which attempt to discover the mortality rates during the pre-linear juvenile growth phase. Most growth studies make use of measurements of mature thalli. Inasmuch as mortality statistics are basic to all
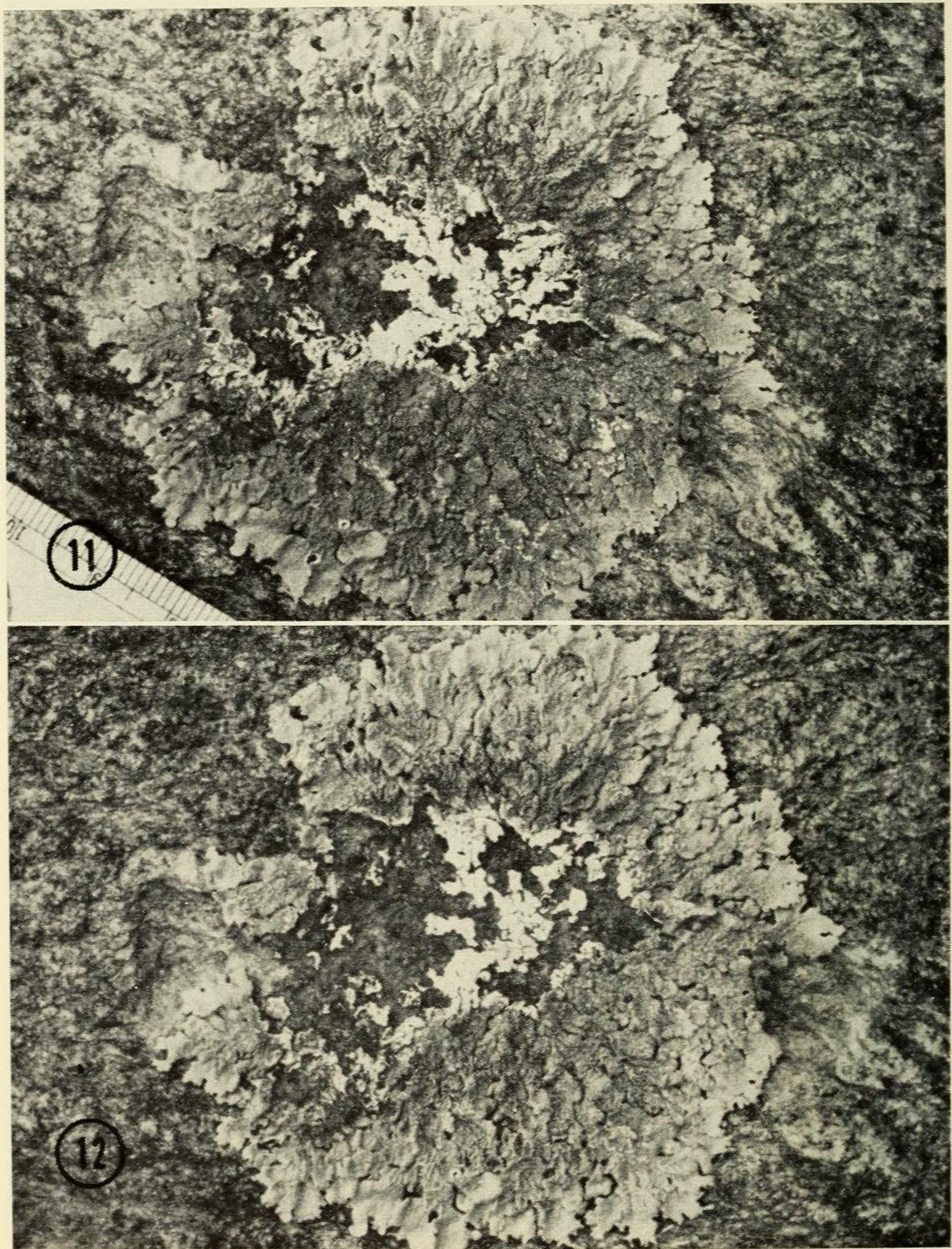
Fig. 11. 7 October, 1969. Fig. 12. 17 November, 1969. (See legend for Figs. 5–12.)

population studies and lichen growth studies are typically lacking in basic demographic functions, this kind of study would provide a new point of view of considerable utility. We are designing experiments which will involve sampling of large numbers of tiny thalli (1 mm diameter) and determining rates of juvenile mortality as a function of substrate surface area, predation, age, and environmental factors. We also hope other studies of this type will be forthcoming in the literature. In this connection we might add that lichen growth studies have rarely examined the relationship between growth and predation upon lichens. The impact of predators
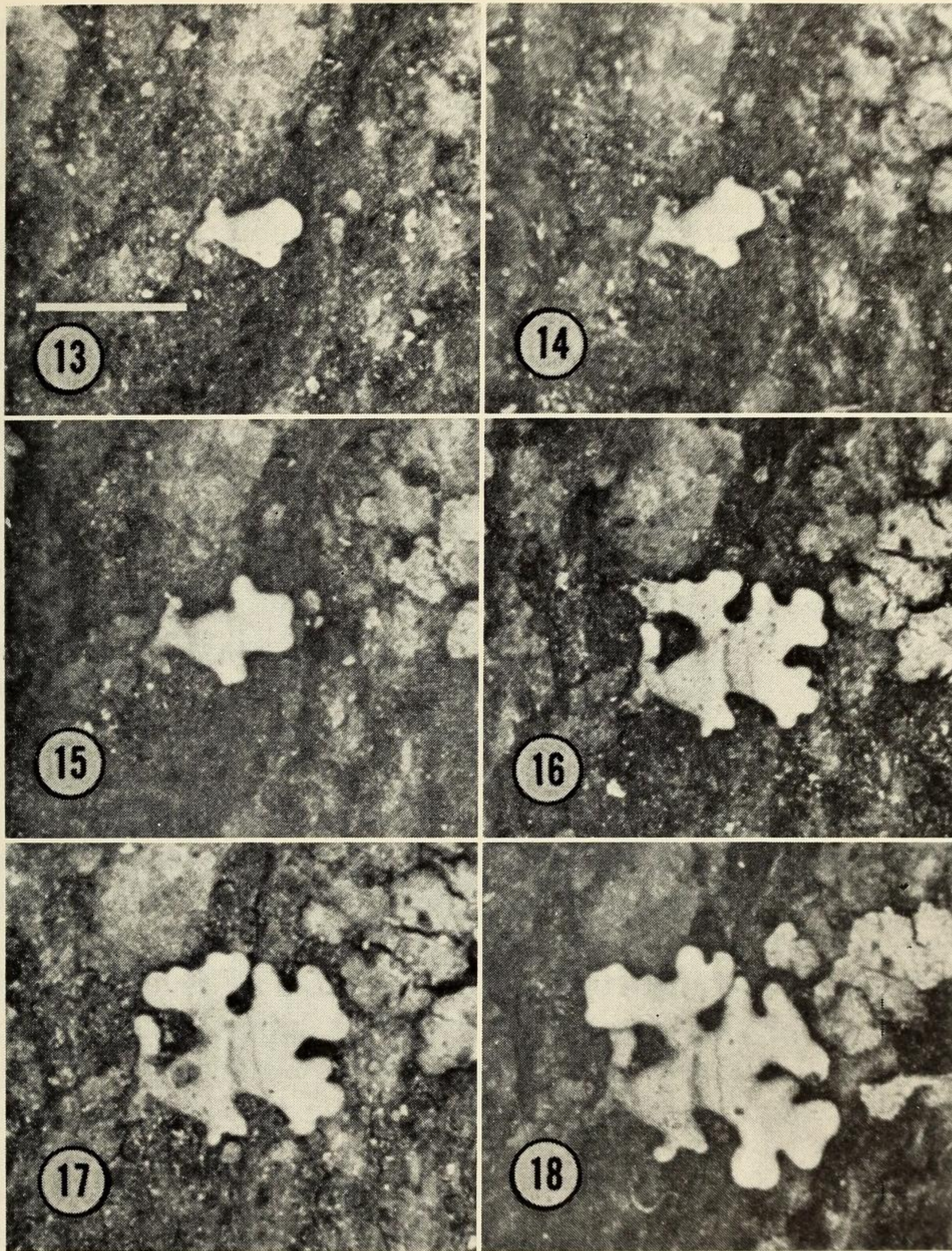
Figs. 13–18. Successive photographs of a minute thallus of *Pseudoparmelia balti-morensis* taken at Plummers Island. All photographs same scale; horizontal line in Fig. 13 = 1 mm. Fig. 13. 15 March, 1969. Fig. 14. 15 May, 1969. Fig. 15. 17 June, 1969. Fig. 16. 1 February, 1970. Fig. 17. 12 April, 1970. Fig. 18. 21 June, 1970.

upon lichens is well documented (Broadhead and Thornton, 1955; Coker, 1967; Peake and James, 1967; Laundon, 1971; Sowter, 1971), and there is a need to determine how this impact influences growth patterns. Hale (1972) reported a case of infestation by a population of collembolids upon the saxicolous lichen *Pseudoparmelia baltimorensis* on Plummers Island, Maryland. These insects fed on the upper cortex and algal layer of the thalli, resulting in widespread loss of juvenile thalli and severe damage

to larger thalli. Many thalli subsequently regenerated, but at least half of the colonies were lost. Although this is an example of extreme predation, it illustrates the need to consider predation as a factor influencing lichen growth and demography.

Figures 11 and 12 illustrate the senescence and disintegration of the center portion of a *P. baltimorensis* thallus, in this case initiated at least in part by slug and collembolid damage. Even without predator damage, however, this pattern of disintegration appears to occur consistently soon after thalli attain a certain maximum diameter. No thalli of *P. baltimorensis* occur on Plummers Island at diameters larger than about 15 cm. *Xanthoparmelia conspersa* also exhibits a period of senescence and thallus disintegration (Figs. 23–28). Hale (1967) calculated growth rates for *X. conspersa* immediately before and during disintegration of the thallus and detected growth rates significantly reduced from normal. However, Armstrong (1974) found no significant differences in radial growth rates between "fragmenting" and "nonfragmenting" thalli of *Parmelia glabratula* ssp. *fuliginosa*. Also, he found no particular relationship between percent fragmentation (surface area disintegration/total thallus surface area $\times$ 100) and growth rate for the same species.

We calculated sequential annual growth rates of six thalli for which many years growth data were available (Table 2) and detected significant differences in growth rates for three *P. baltimorensis* thalli before and after disintegration. One *P. baltimorensis* thallus (Quadrat 22) showed no significant changes in growth rate after initiation of senescence. Neither thallus of *X. conspersa* (Quadrats 12 and 14) exhibited significant changes in annual growth rate after disintegration. Our tentative conclusion is that the onset of senescence probably results in reduced growth rate. Senescence in lichens is perhaps more a rejuvenation process than a true senescence. Centers of old thalli disintegrate and fall away, leaving new, essentially juvenile thalli derived from lobe tips to continue growing. Armstrong (1974, 1976) described an increasing relative growth rate ($cm^2/cm^2/yr$) for *Parmelia glabratula* ssp. *fuliginosa* after fragmentation, which supports this point of view. The reason *X. conspersa* thalli exhibit no significant differences in radial growth rate between old thalli and non-senescent thalli is probably due to the slower rate of growth characteristic of this species. As explained in the previous section on growth phases, *Pseudoparmelia baltimorensis* grows faster than *X. conspersa* and should therefore exhibit more discernible changes in growth rate when these changes occur. We would expect, then, that lichens which exhibit the most rapid measurable growth rates will be most likely to exhibit detectable changes in growth rate as a function of both thallus age and climate. Lichen growth studies should be critically evaluated with this in mind.

There is very little published information relating lichen growth patterns

Table 2. Changes in annual single-lobe growth rates for the lichens *Pseudoparmelia baltimorensis* and *Xanthoparmelia conspersa* as thalli approach senescence. The last growth rate listed in each array is that calculated for disintegrating thalli.

	Growth rates (mm/yr)					
	Pseudoparmelia baltimorensis				*Xanthoparmelia conspersa*	
Year	Quadrat 6	Quadrat 9	Quadrat 11	Quadrat 22	Quadrat 12	Quadrat 14
1965–1966	5.52 ± 0.26[a]	5.15 ± 0.37				
1966			6.88 ± 0.52		1.99 ± 0.18	
1966–1967	5.30 ± 0.40	4.66 ± 0.25				3.19 ± 0.33
1967			3.99 ± 0.25**		1.85 ± 0.24	
1967–1968	4.86 ± 0.24	3.40 ± 0.28*		5.69 ± 0.33		
1968–1969	3.73 ± 0.54*	2.82 ± 0.26**				3.33 ± 0.26
1969–1970						3.70 ± 0.20
1970				5.52 ± 1.37		

[a] Growth rates are means (mm/yr) ± S.E. N = 15 lobes or greater.

* Significantly less than initial growth rate at $p < 0.05$.

** Significantly less than initial growth rate at $p < 0.001$.
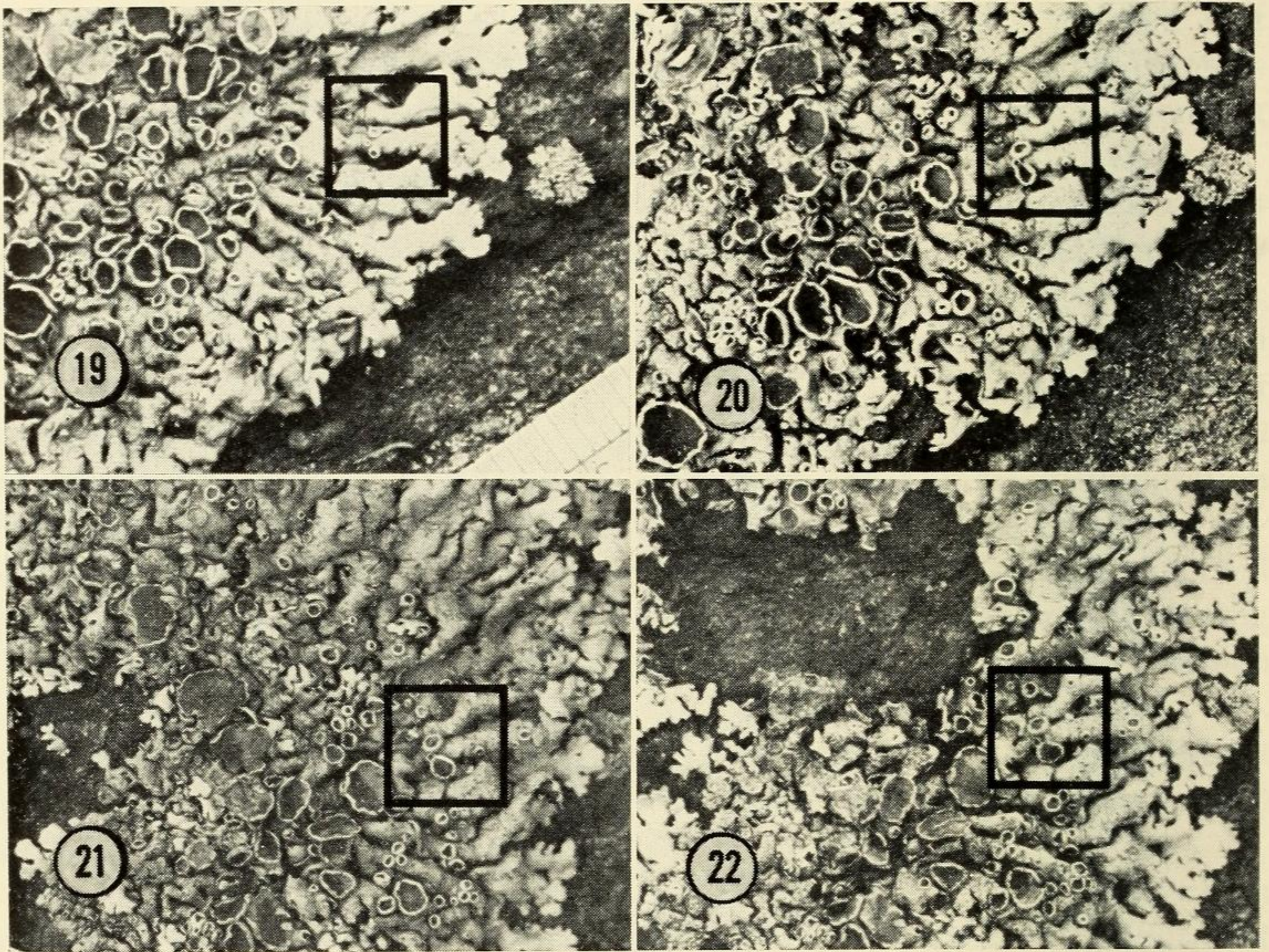
Figs. 19–22. Apothecia development in a growth series for *Xanthoparmelia conspersa*. Some apothecia grow faster than others, but the largest apothecia do not change in size. Scale in Fig. 17 for all photos in mm. Fig. 19. 4 December, 1965. Fig. 20. 6 January, 1967. Fig. 21. 16 February, 1968. Fig. 22. 15 November, 1968.

to development of specific lichen structures, the kind of information that would be of value in recognizing growth phases in lichens and interpreting life history data in terms of population dynamics. Sernander-Du Rietz (1957) conducted a study on the factors influencing apothecia initiation and development in *Parmelia tiliacea* in Fennoscandia, and found that climatological factors, particularly high temperatures and precipitation, correlated well with apothecia development. She found also that severe cold temperatures often killed microapothecia. Figures 19–22 illustrate the superficial development over a 3-year period of several selected apothecia on a mature thallus of *X. conspersa* from Plummers Island. Most apothecia grow slowly and consistently to a specific maximum size, but the growth of some apothecia appears to be halted shortly after initiation. This is particularly true of microapothecia located close to larger apothecia. Additional studies of this nature should be done to learn how apothecial development correlates with thallus age and size and how growth rate of the thallus is influenced by the initiation of apothecia development during the life history of a lichen thallus.
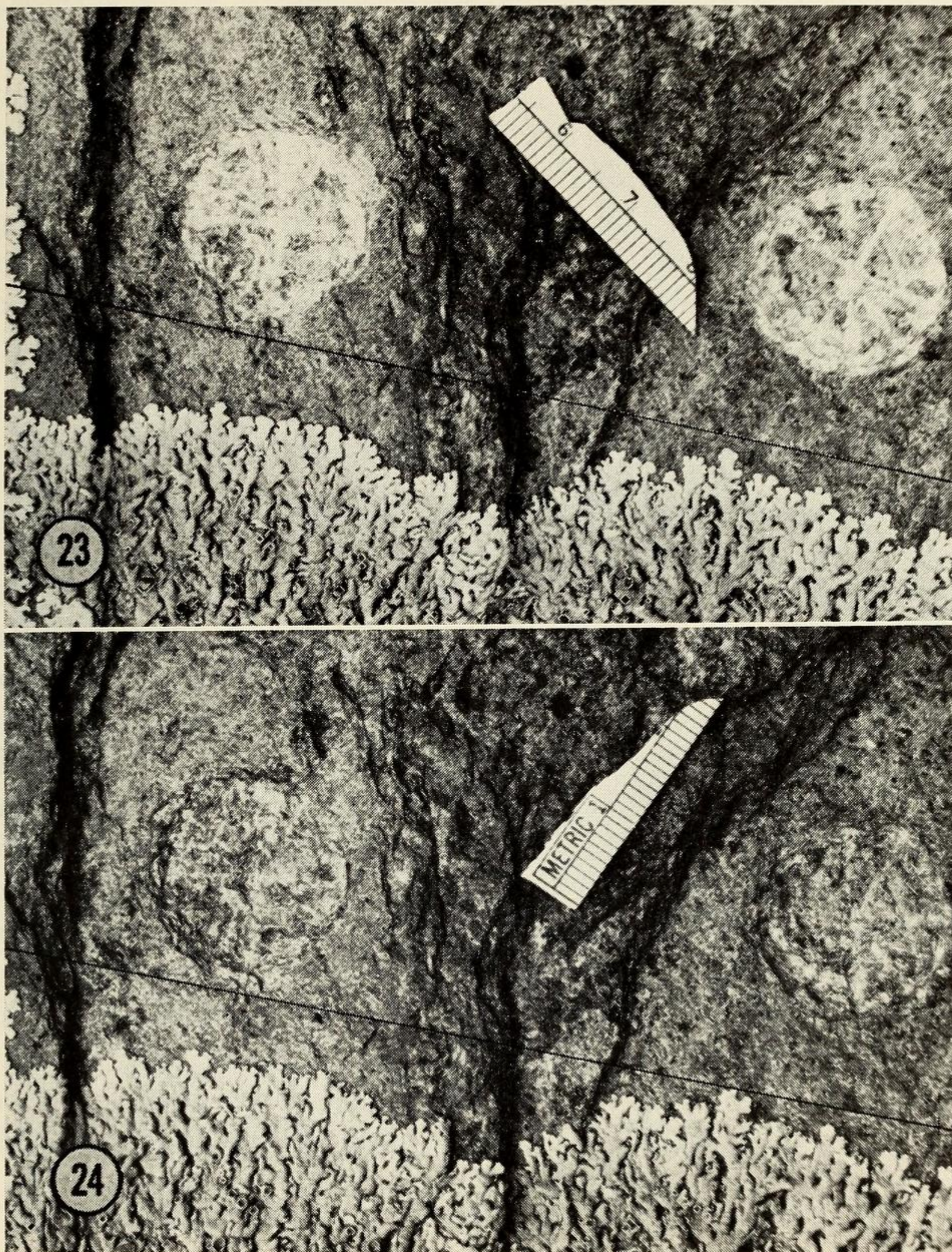
Figs. 23–28.   Successive photographs of *Xanthoparmelia conspersa* taken at Plummers Island. The two light circles are drill holes used for relocation of the colony. Line drawn for viewer orientation. Scale in mm. Fig. 23. 20 March, 1966. Fig. 24. 18 September, 1966.

Our studies of growth phases have uncovered significant life cycle patterns among the lichens observed on Plummers Island. We believe that additional studies are required, particularly in view of the increasing number of studies of lichen distribution in relation to long-term, chronic air pollution (e.g., automobile exhaust). If lichen growth studies continue to show determinant life cycles for many species of lichens, many of the conclusions of lichen-air pollution studies which show gradual changes

in lichen distribution over long periods of time will have to be reinterpreted. Since so little is known about the "typical" responses of lichens to environmental factors over long periods of time, we suggest that it is unwise to read too much into uncritical short-term lichen distribution studies which make use of presence-absence data or growth rate data without adequate controls. We would hope that lichenologists will feel compelled to provide answers to basic questions concerning life cycle patterns of lichens, including demographic patterns. Until these questions are answered more critically, it is hazardous to make too many assumptions regarding lichens as "indicators" of low-level air pollution.

Growth Rates and Environmental Factors

The influence of microclimatological factors (e.g., light, relative humidity, cloud cover, wind, etc.) on lichen growth is not well documented. Hausman (1948) claimed that high growth rates for *Parmelia centrifuga* in New England correlated with high cloud cover. Kärenlampi (1971) investigated the influence of several climatic factors on growth of various *Cladonia* ssp. during a summer in Finland. He found that lichen growth was influenced mostly by rainfall and to a lesser degree by temperature and light. Nienburg (1919) reported that heavy rains in Germany in 1899 may have been responsible for high growth rates there. Also, Andreev (1954) and Barashkova (1961) have stated that areas of high humidity will support high growth, and Showman (1976) found that *Parmelia caperata* grew better on more consistently moist sides of a tree than on exposures which dried out quickly. Miller's (1966) study of lichen growth and thallus wetness and Kärenlampi's (1971) study of fruticose lichen growth rates are among the few which make use of microclimatological data collected at the level of the plants themselves. Weather summaries collected many miles from the study site are not sufficiently exact to be used in lichen growth studies without more precise corroborating evidence. There is also a need for statistical analysis of growth data which allows broad inferences to be drawn from large amounts of data. Consequently, the use of computers to calculate growth rates and to determine statistically significant relationships between growth and various environmental variables is becoming more frequent (Kärenlampi, 1971).

A summary of Plummers Island weather variables for the years 1966–1969 (Fig. 29) shows maximum-minimum temperatures and total precipitation data collected at the growth study sites. We computed average precipitation (total precipitation in period/days of precipitation in period) and percent cloudy days (number days in period with 60% of greater cloud cover/total number days in period × 100) for each period from National Airport weather summaries. During the four years of weather sampling, temperature patterns were relatively predictable with maximum
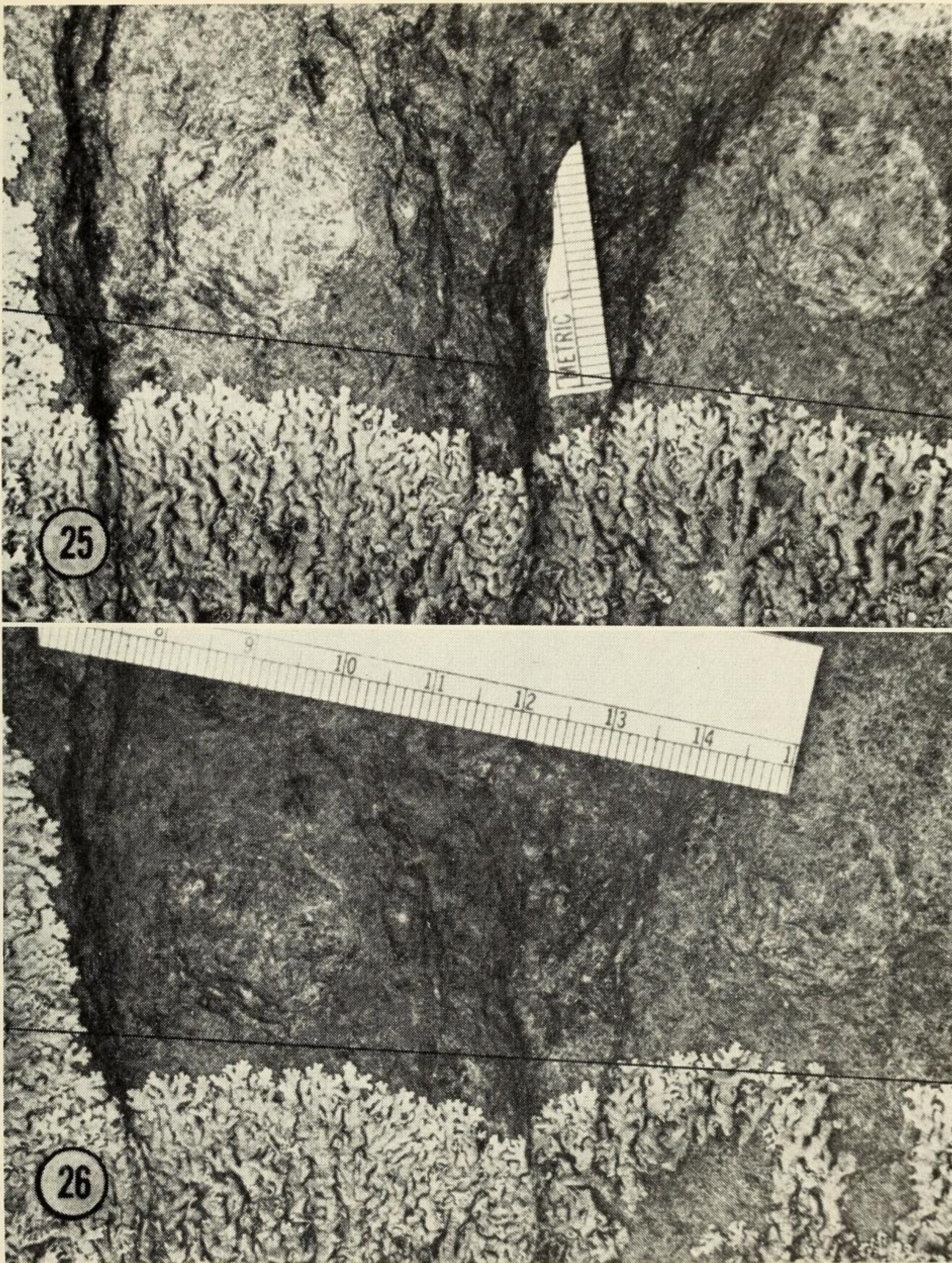
Fig. 25. 13 August, 1967. Fig. 26. 15 November, 1968. (See legend for Figs. 23–28.)

temperatures approching 40°C in the summer and minimum temperatures often –15°C in the winter. Precipitation, however, was not constant. Total precipitation in 1968, for example, was much lower than in 1969. Analysis of cloud cover data revealed no seasonal pattern of cloud cover from 1966–1969.

Scatter plots of daily lichen single-lobe growth rates vs. various weather variables were computer-generated for *Pseudoparmelia baltimorensis* and *Xanthoparmelia conspersa*. Because growth rates of *X. conspersa* exhibited little seasonal or annual variation, no weather-related growth
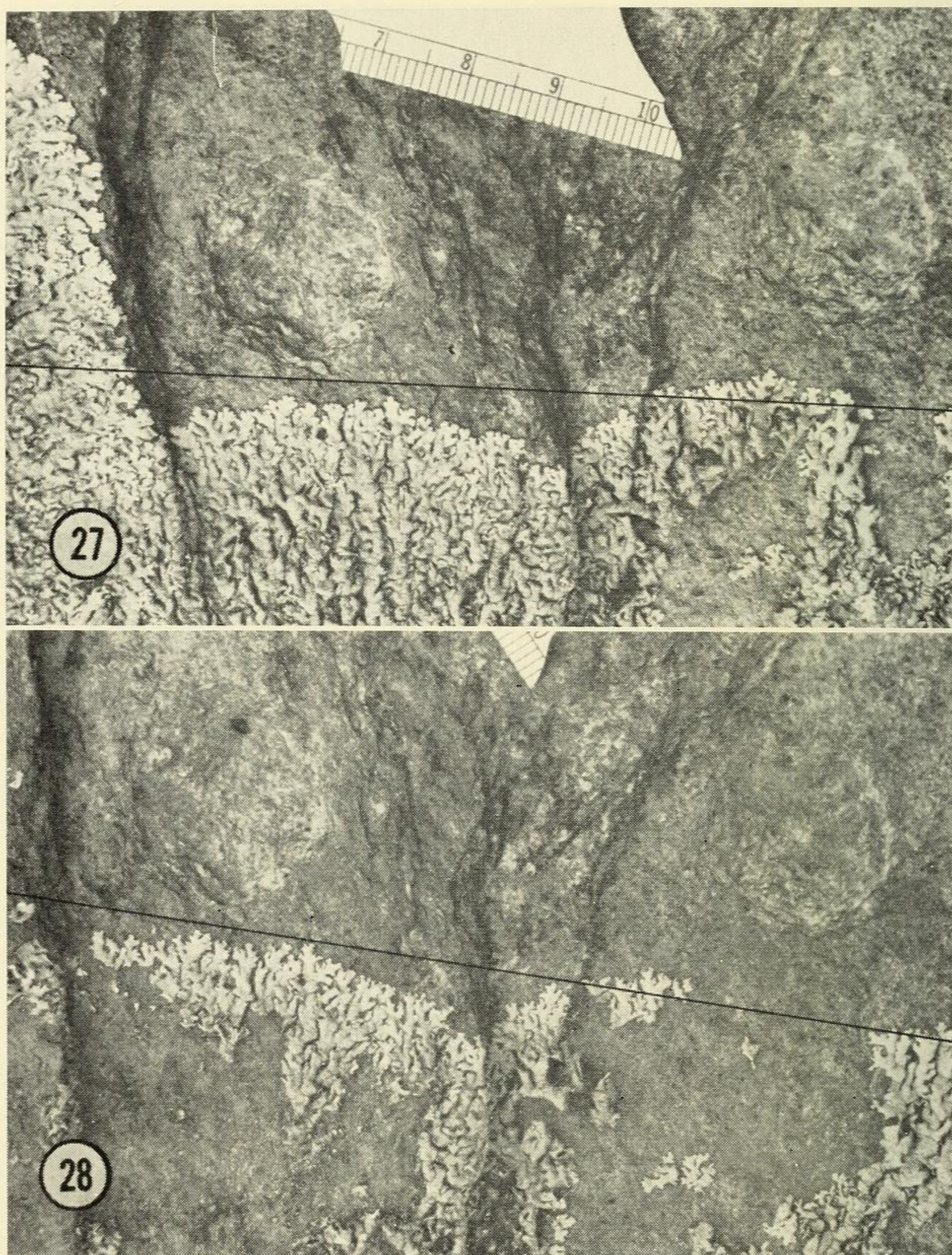
Fig. 27. 9 April, 1969. Fig. 28. 17 November, 1969. (See legend for Figs. 23–28.)

patterns were discernible for this species. However, relationships were apparent between growth rates of *P. baltimorensis* and certain weather variables. Scatter diagrams of radial growth vs. high temperature (Fig. 30) and low temperature (Fig. 31) in each sampling period show that optimum growth for *P. baltimorensis* occurs during periods in which the maximum temperature is 25–30°C and the minimum temperature is around 0°C. A glance at Fig. 29 shows that these temperature conditions occur on Plummers Island in the early spring. It is possible that during this time, increasing irradiation coupled with minimum canopy cover produce relatively high temperatures during the day and low temperatures at
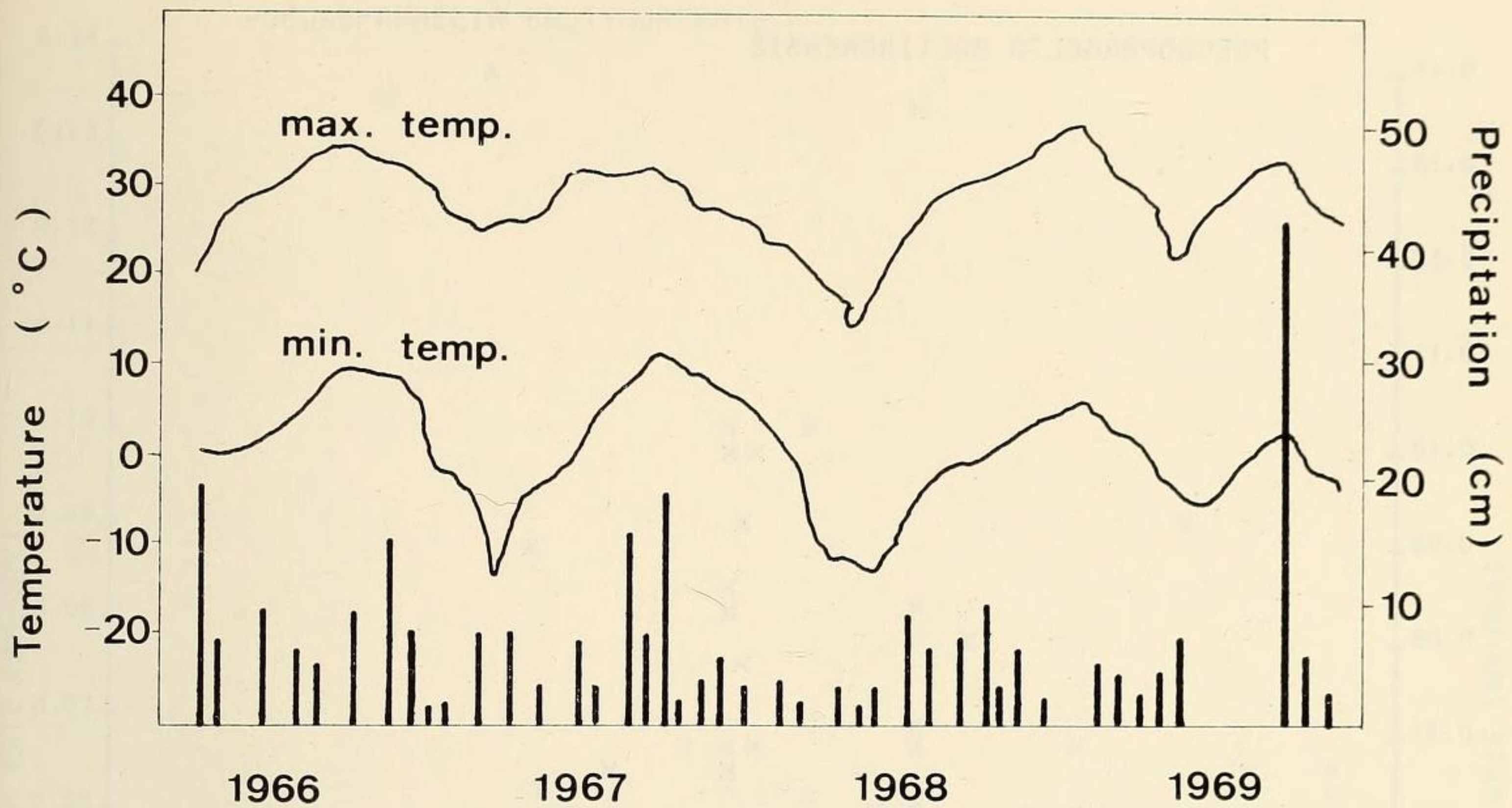
Fig. 29. Precipitation (vertical lines) and maximum-minimum temperatures (horizontal lines) recorded at Plummers Island for each sampling interval from 1966 to 1969.

night because of radiation loss. As both maximum and minimum temperatures increase during the summer, lichen growth rate decreases. It appears from the curves of lichen growth vs. temperature (Figs. 30 and 31) that temperatures rarely exceed critical limits for growth of *P. baltimorensis*. Growth of this lichen species, therefore, is possible at varying rates throughout the year on Plummers Island.

Scatter diagrams of *P. baltimorensis* growth vs. total precipitation (Fig. 32) and average precipitation (Fig. 33) in each sampling period indicate that lichen growth can actually be inhibited in periods of high precipitation. High growth of *P. baltimorensis* may conversely occur under conditions of low precipitation; optimum growth takes place when average precipitation (total precipitation/days of precipitation in period) is between 0.5–1.0 cm/day. Kärenlampi (1971) detected high levels of linear correlation between growth of fruticose lichens and rainfall (mm/day) in Finland, although rainfall data used in his study appeared to range from only 0–4 mm/day, considerably less than the maximum rainfall observed on Plummers Island. Within this narrow range of rainfall values, our growth data also show a high correlation. However, there is a considerable decline in growth once optimum rainfall is exceeded.

The graph of growth rate for *P. baltimorensis* vs. percent cloudy days (Fig. 34) shows that optimum growth occurs during sampling periods which are cloudy (60% cloud cover or more) more than half of the time. Growth rate apparently decreases after values of percent cloudy days reach 75%
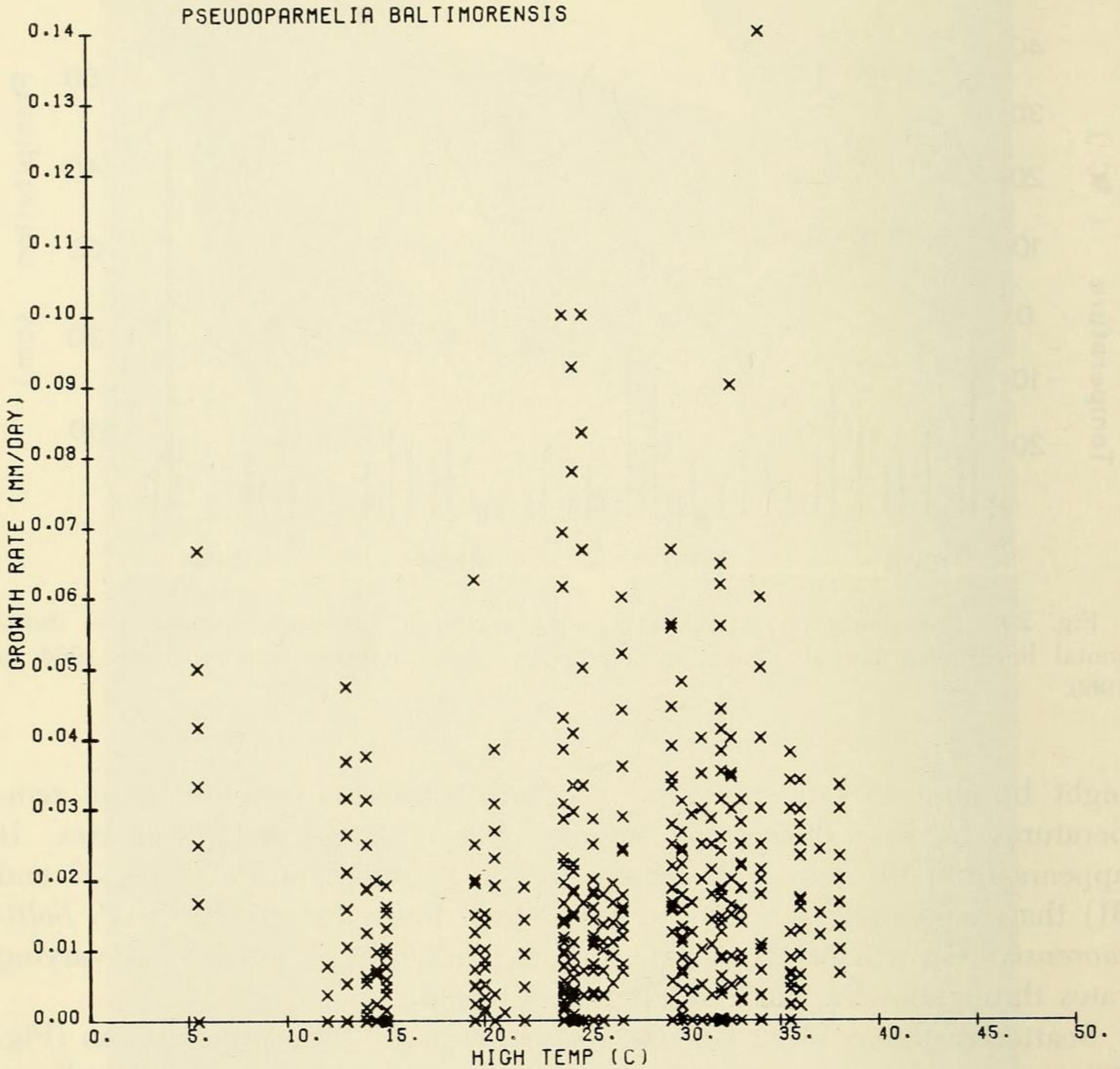
Fig. 30. Daily radial single-lobe growth rate of *Pseudoparmelia baltimorensis* vs. maximum temperature in each sampling period at Plummers Island from 1966 to 1969.

or more, although growth is active even when every day during the sampling period exhibits 60% or greater cloud cover. There is greater inhibition of *P. baltimorensis* growth during periods of little cloudiness than during periods when almost every day in the sampling period exhibits high cloud cover. This would indicate that possibly high irradiation is a more limiting environmental factor for *P. baltimorensis* than cloudiness. Hausman (1948) believed that high growth rates of *Parmelia centrifuga* in New England were due to high cloud cover. Our data would tend to support this view, with the understanding that other weather variables (temperature, relative humidity, irradiation) also change in direct proportion to the degree of cloudiness.

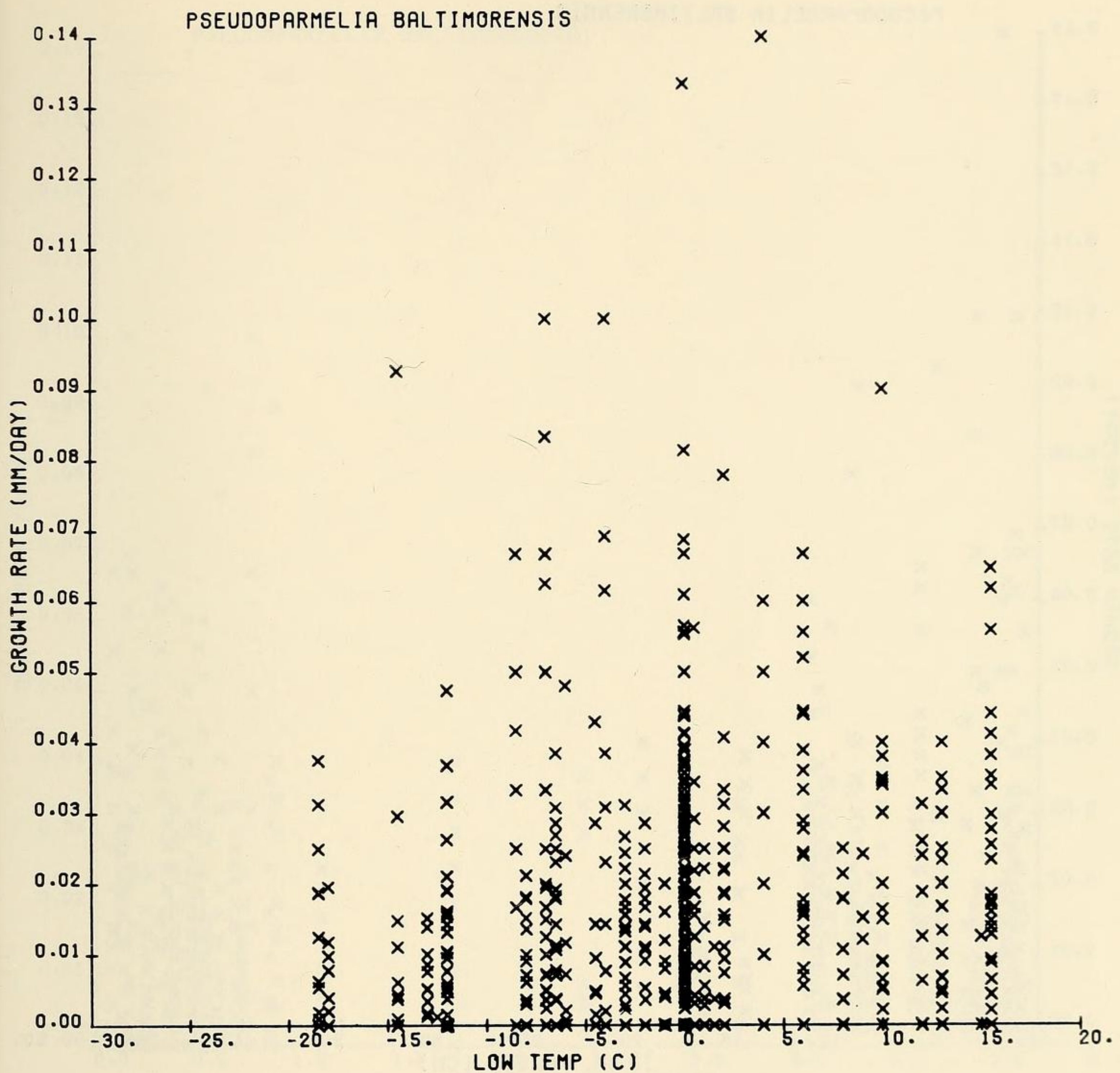Stepwise multiple regressions of mean daily growth per sampling period

Fig. 31. Daily radial single-lobe growth rate of *Pseudoparmelia baltimorensis* vs. minimum temperature in each sampling period at Plummers Island from 1966 to 1969.

on numerous weather variables were computed to determine which weather variables or combinations of weather variables explained the greatest amount of the variance in growth exhibited by *Pseudoparmelia baltimorensis*. Because we did not collect data on irradiation, aspect, or non-weather factors, we can make no determination about the relative importance of these factors even though other studies have shown they probably are important (Haukulinen, 1966; Jones and Platt, 1969; Kärenlampi, 1971). A regression equation using the variables high temperature, total precipitation and percent cloudy days was found to explain 22% of the variation in lichen growth rate for *P. baltimorensis* ($r = 0.466$, β significantly different from 0 at $p < 0.05$). Of these three weather variables, percent cloudy days explained the greatest amount of variation (14%, $r = 0.376$). The gen-
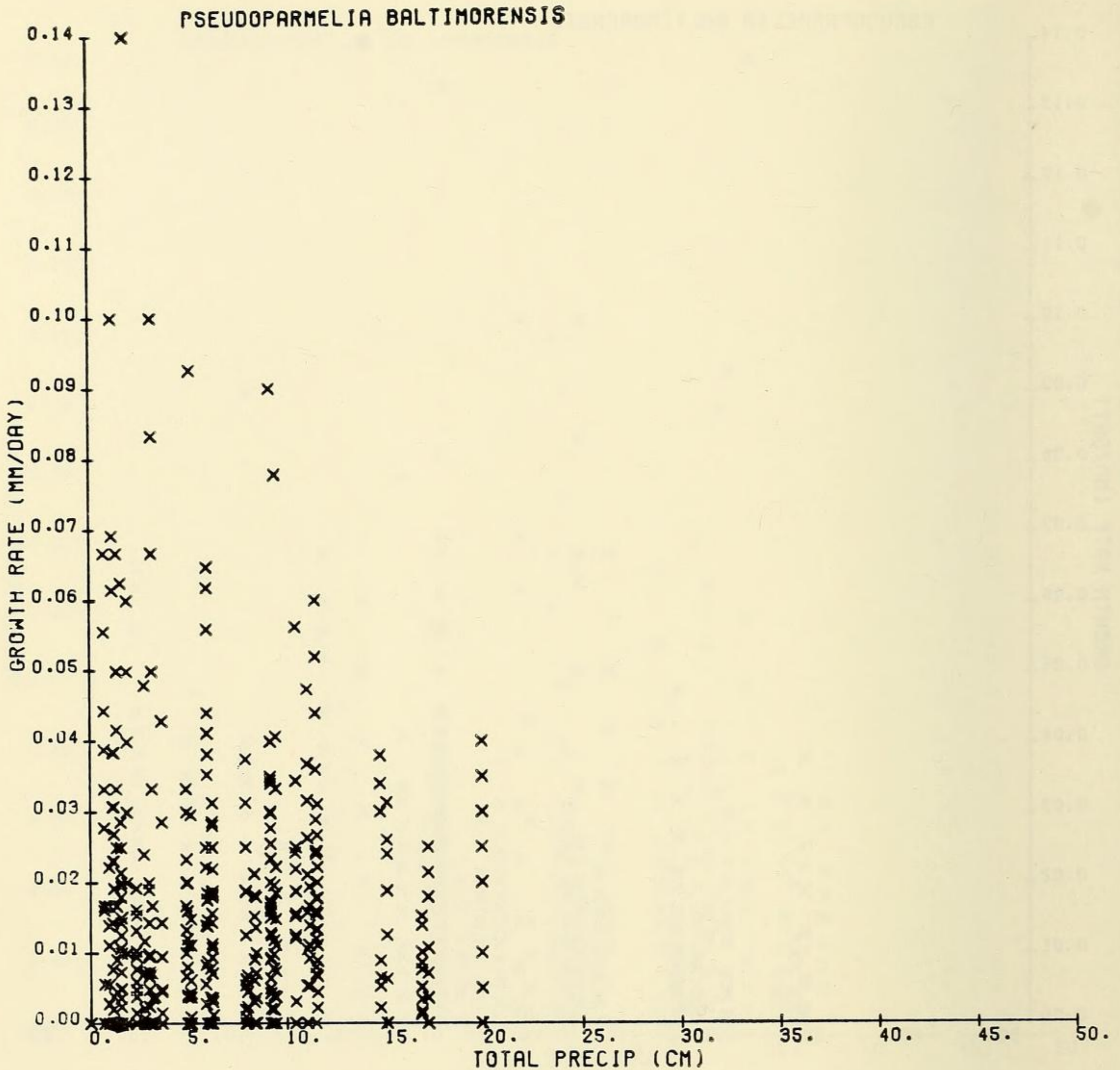
Fig. 32. Daily radial single-lobe growth rate of *Pseudoparmelia baltimorensis* vs. total precipitation in each sampling period at Plummers Island from 1966 to 1969.

erally low correlation between weather variables and lichen growth was thought to be due to the non-linear nature of the relationship. We regressed $\log_{10}$, ln, $x^{1/2}$, and x^2 transformations of the growth data on the various weather variables in order to determine if these transformations rectified the growth data. We found that the regression of (mean lichen growth rate)^2 on percent cloud cover explained 19% of the growth variance ($r = 0.436$, significantly different from 0 at $p < 0.05$). This would indicate that possibly radial growth measurements contain less information than area measurements, but the increase in predictability was not overwhelming. Addition of the other two variables (total precipitation and high temperature) to the regression equation did not significantly increase the predictability. We concluded that percent cloudy days is most useful as a
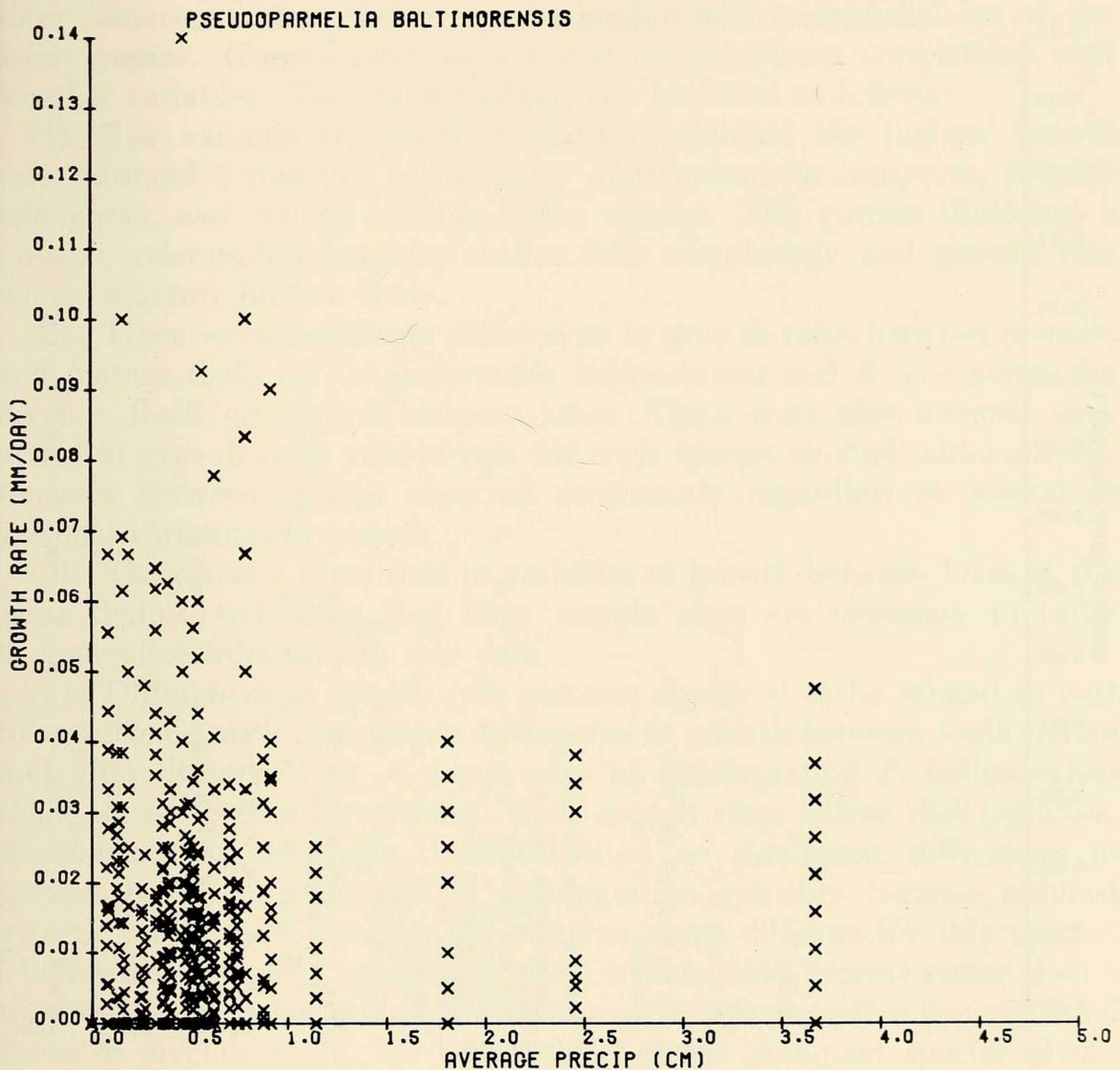
Fig. 33. Daily radial single-lobe growth rate of *Pseudoparmelia baltimorensis* vs. average precipitation (total precipitation in each sampling period/days of precipitation in each sampling period) at Plummers Island from 1966 to 1969.

predictor of lichen growth. However, none of the weather variables we measured was especially useful in this regard, since a total of only 22% of the growth rate variance is explained by any weather variable or combination of variables. Kärenlampi (1971) found high correlation between weather variables and fruticose lichen growth over short time periods. We believe this may be a result of measuring lichen growth only during favorable periods, inasmuch as lichen growth can be expected to respond more strongly to changes in weather when weather conditions are most favorable for growth. Additionally, Kärenlampi's (1971) study made use of irradiation data, which the present study does not include. This factor may contribute to lichen growth on Plummers Island as it does in Fin-
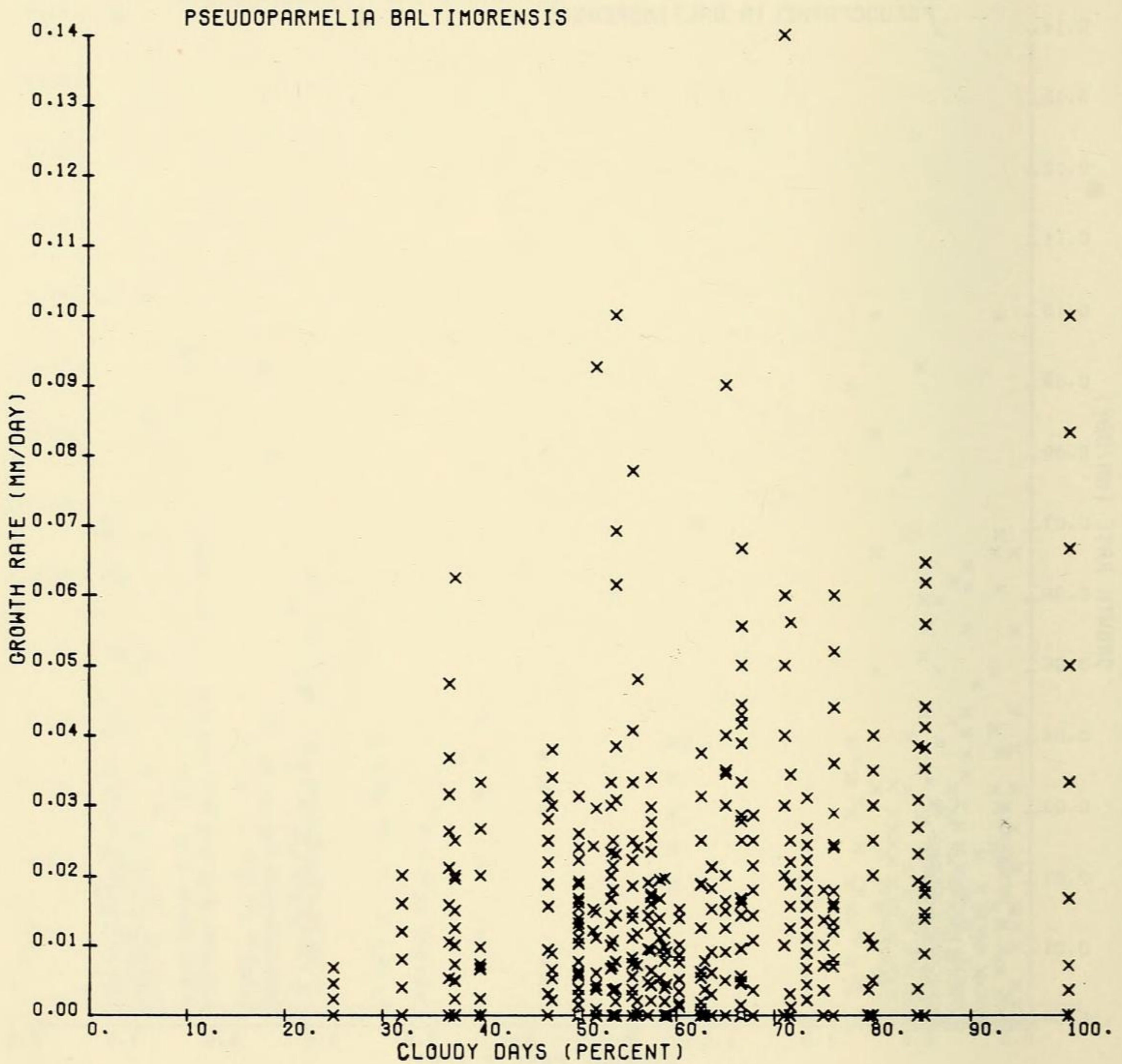
Fig. 34. Daily radial single-lobe growth rate of *Pseudoparmelia baltimorensis* vs. percent cloudy days (number days of 60% cloud cover or more/total number days in sampling period × 100) at Plummers Island from 1966 to 1969.

land, but we would expect that it would not increase correlation to the levels observed by Kärenlampi.

Additional long-term studies of the influence of weather on other lichen species in other geographic areas will allow comparisons to be made with the few studies presently available. At the present time, lichen growth appears to correlate with certain weather variables. However, we are still unable to predict changes in lichen growth over long periods of time with certainty.

Conclusions

A twelve-year growth study of saxicolous lichens from Plummers Island, Maryland, revealed numerous differences in annual and daily radial growth

rates between various lichen species and variously-aged lichens of the same species. Growth rates were tested for significant correlations with weather variables. The major findings can be listed as follows:

(1). The various large-lobed Parmelias exhibited the highest growth rates (around 5 mm/yr), followed by *Xanthoparmelia conspersa, Physcia millegrana,* and various crustose lichen species. This pattern illustrates a possible relationship between thallus lobe morphology and growth rate which requires further study.

(2). There were significant differences in growth rates between juvenile and mature thalli of *Pseudoparmelia baltimorensis* and *X. conspersa,* the juvenile thalli growing at reduced rates. There were also seasonal variations in growth from year-to-year for each species studied, although differences between species occurred consistently regardless of annual or seasonal variations in growth.

(3). There was a great deal of variation in growth between lobes of the same thallus, indicating that large sample sizes are necessary in order to generalize from growth rate data.

(4). Differences in growth rate patterns appeared to be related in part to senescence, with measurable differences in growth between thalli before and after disintegration. Growth rates of disintegrating *P. baltimorensis* thalli were significantly reduced from growth rates before disintegration. *Xanthoparmelia conspersa* thalli exhibited no significant differences in growth before or after thallus disintegration, possibly because reduced growth rates made detection of patterns more difficult for this species. Thallus disintegration appeared to be a rejuvenation process rather than a true senescence, inasmuch as growth rates after disintegration approximated those of juvenile thalli. No lichen thalli of the dominant species photographed on Plummers Island were observed at diameters much larger than 15 cm.

(5). Apothecia development was observed for *X. conspersa.* No correlations between apothecia development and other factors were possible due to a paucity of data. However, there appeared to be a maximum diameter for apothecia of *X. conspersa,* and microapothecia were observed to increase in size slowly or not at all, as if inhibited by adjacent larger apothecia.

(6). Scatter diagrams of lichen daily growth rate vs. various weather variables showed that optimum growth of *Pseudoparmelia baltimorensis* occurred on Plumers Island during sampling periods in which the maximum temperature was around 25–30°C, the minimum temperature around 0°C, the precipitation around 0.5–1.0 cm/sampling period, and the cloud cover 60% or more for at least half the sampling period. All the lichen growth vs. weather scatter plots showed lower lichen values above and below these optimum weather conditions; however, there were no weather conditions

measured on Plummers Island which consistently correlated with zero lichen growth. *Xanthoparmelia conspersa* exhibited no detectable relationships between growth rate and weather variables, a result probably due to the fact that growth rate values for this species exhibited little change from one sampling period to another.

(7). Stepwise multiple regressions of lichen growth of *P. baltimorensis* on weather variables (high temperature, total precipitation, cloud cover) revealed that a total of 22% of the lichen growth variance could be explained by any combination of weather factors. The cloud cover variable consistently explained the greatest amount of the lichen growth variance. Squaring the lichen growth dependent variable resulted in a somewhat higher correlation with weather variables, which may be due to the fact that radial growth data were used rather than area data.

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Footnote

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(JTL) Ohio State University, Columbus, Ohio 43210; and (MEH, Jr.) Smithsonian Institution, Washington, D.C. 20560.