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Morphological analysis of the growth and productivity of the lichen *Cladonia alpestris*

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Abstract

KÄRENlampi, LAURI. (Botany Dept., Univ., Turku 2, Finland) *Morphological analysis of the growth and productivity of the lichen *Cladonia alpestris**. REP KEVO SUBARCTIC RES STAT 7. 9—15. Illus 1970. — Measurements were made of the lengths and diameters of *Cladonia alpestris* thalli and the lengths of their internodes. The weight distribution in the thallus was studied by dividing thalli and weighing the different parts. The relationships between the observed values were studied and conclusions were drawn concerning growth and productivity. There are definite relationships between the length, diameter and weight of the thallus. In the Kevo area the internode seems to continue growing up to the age of eight years. The relative length growth rate of the internode is highest when it is young. A diagram was prepared which illustrates both the weight distribution and the internode lengths. This is thought to show the pattern of growth. There is a definite growth zone at the top of the older thalli. The relative length, diameter and weight growth rates were examined by means of growth analysis. The RGR values of the young individuals were found to be much higher than those of the older ones.

1. Introduction

The productivity of lichens is one of the main interests of the Kevo IBP group. Several methods for estimating their productivity are to be developed and tried. One possibility is to base productivity calculations on the age of the thallus. The age of reindeer lichens can be estimated by counting the number of nodes (see e.g. ANDREEV 1954).

This paper gives the results of a morphological analysis of the *Cladonia alpestris* thallus. The observations include measure-

ments of the lengths and diameters of the thalli, measurements of the internode lengths and data on the pattern of weight (biomass) distribution. This paper is one of a series of publications on the productivity of reindeer lichens. The synthesis, which will describe possible methods for making practical productivity measurements, will be presented later. Here only the actual analytic results are given.

2. Material

The lichen specimens were collected at the beginning of September in 1969. They were growing in dry pine forest in the vicinity of the Kevo Station. The material does not include any very old individuals, because the area is heavily grazed by reindeer. The lichens are mostly in the period of generation and some in the early part of the period of renovation (periods according to ANDREEV 1954).

According to the dry weight, the material was divided into classes, the range of each class being 10 mg between 0 and 100 mg and 25 mg between

100 and 175 mg. The measurements of the tallest individuals are not based on strictly comparable material because the taller specimens were often found in differing microhabitats (outside the heavily grazed lichen patches). The same difficulty was experienced in an earlier study (KÄRENlampi 1970).

The specimens were collected by cutting the taller ones at the point where they emerged from the dense layer of litter and moss, and the smaller ones at the point where they had started their growth.

3. Methods

The specimens were brought to the laboratory and dried for two days. When they had reached equilibrium with the air moisture, each specimen was weighed separately and subsamples were taken to be oven-dried (80°C). The water content was found to be about 11 per cent of the dry weight. The measurements were made at this water content. The length was measured from the point of cutting to the extreme tips. The diameter was measured at the thickest point, and the calculations of the average diameter were based on this value.

The specimens were classified as described in the preceding section. Each class contained 8–38 specimens. They were pressed like herbarium specimens, and divided into parts, being cut through horizontally at 2.35 mm intervals from the top of the thallus. Technical reasons decided the choice of 2.35 mm intervals. Within each class, the corresponding parts were put together and weighed.

The biomass distribution was calculated as mg per mm thallus length. The results were smoothed in the same way as in KÄRENlampi (1970). In all cases the correlation coefficient was greater than 0.95.

Several specimens were taken for the measurements of the length of the internodes. The side branches were cut off and the thick middle stems were used. They were drawn under a binocular, and the nodes marked on the drawings. The internode lengths were then measured on the drawings.

The data were processed with the aid of the electronic desk-top computer Programma 101. To bring out the relationships, the following regressions were used: logarithmic, linear and polynomial of the third degree. The RGR values (relative growth rates) were calculated using the usual formula (see e.g. BLACKMAN 1968).

4. Results

4.1. Relationships between length, diameter and weight

The results of the measurements and weighings of the thallus are shown in the Fig. 1, 2 and 3. Fig. 1 shows the relationship between the length and the dry weight of the thallus. The relationship is approximated using the logarithmic regression $\ln y = 1.278 + 0.478 \ln x$, $r = 0.993$, ($x = \text{dry weight in mg}$, $y = \text{length in mm}$).

Fig. 2 shows the relationship between the

diameter and the dry weight of the thallus. The relationship is approximated using the logarithmic regression $\ln y = 1.176 + 0.374 \ln x$, $r = 0.997$, ($x = \text{dry weight in mg}$, $y = \text{diameter in mm}$). The similar form of the curves in Fig. 1 and 2 suggests, that the length and the diameter may be in linear correlation within the measured range. This is shown in the Fig. 3: linear regression $y = 2.242 + 0.495 x$, $r = 0.987$, ($x = \text{length in mm}$, $y = \text{diameter in mm}$).

The conclusion to be drawn from the

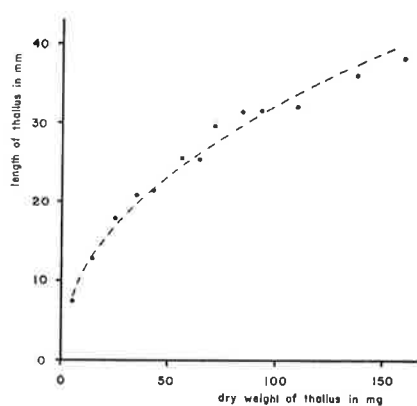


Fig. 1. Length plotted against dry weight of the thallus. Each dot represents the mean of several (8–38) measurements. The dashed line gives the logarithmic regression.

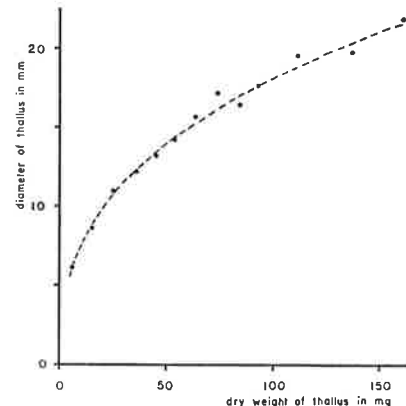


Fig. 2. Diameter plotted against dry weight of the thallus. Each dot represents the mean of several (8–38) measurements. The dashed line gives the logarithmic regression.

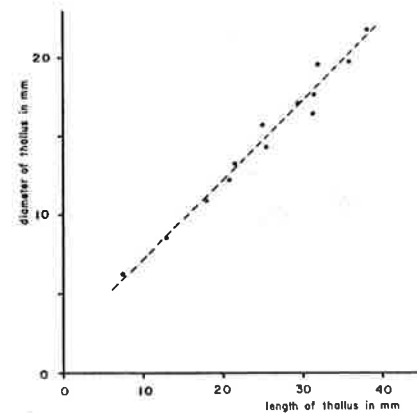


Fig. 3. Diameter plotted against length of the thallus. Each dot represents the mean of several (8–38) measurements. The dashed line gives the linear regression.

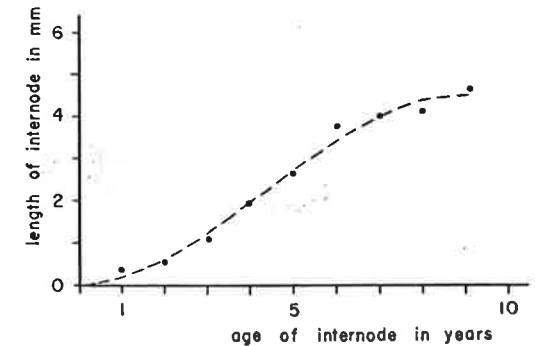


Fig. 4. Length plotted against the age of the internode. Each dot represents the mean of several (4–26) measurements. The dashed line gives the polynomial of third degree regression.

above results is that the thallus of *Cladonia alpestris* has a well-defined form; in other words, it develops regularly. Therefore, there are good reasons to study the relationships between age, productivity and the size and weight of the thallus.

The standard error of length is about 8–14 per cent of the mean, except in the class of the lightest specimens, where it is 32 per cent. The standard error of diameter is about 8–10 per cent of the mean, except in the class of the lightest specimens, where it is 24 per cent. The standard error of weight is about 3–8 per cent of the mean, except in the three lightest classes, where it rises to 12, 22 and 46 per cent.

4.2. Internode length growth

Fig. 4 shows the results of the measurements of the internode length. It is seen that in the Kevo area the period during which an internode grows in length is about eight years. The relationship is approximated using the polynomial regression $y = 0.0392 + 1.709 \left(\frac{x}{10}\right)^2 - 0.128 \left(\frac{x}{10}\right)^3$, ($x = \text{age in years}$, $y = \text{length in mm}$). The observed value of the length at 1 year's age seems to be much higher than the predicted value. This might be the effect of the inconspicuous young pycnidia in the tips.

It should be noted that the age is not known exactly, because the time of branching is not known. Probably the age of every internode given in the diagram is a little too high. This should not make the form of the curve wrong, but just move it to the right. In spite of its limitations, the curve is thought to approximate the relationship well enough for use in computing the RGR.

Fig. 5 shows the relative length growth rate (RGR) of the internode at different ages. In 8–9-year-old internodes the RGR approaches zero, while it is higher in younger internodes. The very high predicted values of the youngest parts may be greater than in reality owing to the probable energy transfer from the lower internodes. The RGR values are computed per day, and the annual number of growing days is taken to be 140. The length of the growing season of the lichens in the Kevo area will be dealt with in a later paper.

If the lengths of the internodes are added together, the sum obtained is not the true length of the lichen. The true length is smaller, because the internodes tend to diverge from the length axis of the thallus. In this study the lengths of the thalli were obtained by measuring the true (lesser) length.

In future studies, diagrams like those in Figs. 4 and 5 may prove to be more reliable, if the material on which they are based is divided into different age classes. The ma-

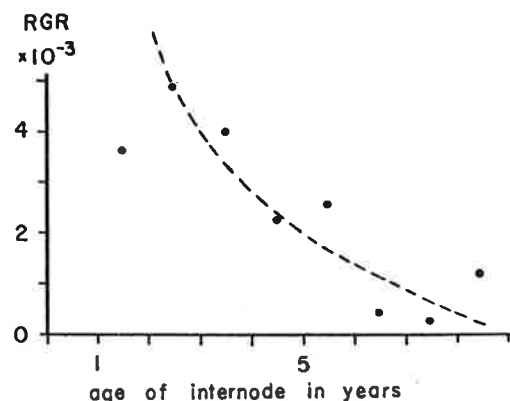


Fig. 5. RGR (relative length growth rate) of the internodes. The dashed line shows the RGR computed from the values predicted with the polynomial regression (shown in Fig. 4).

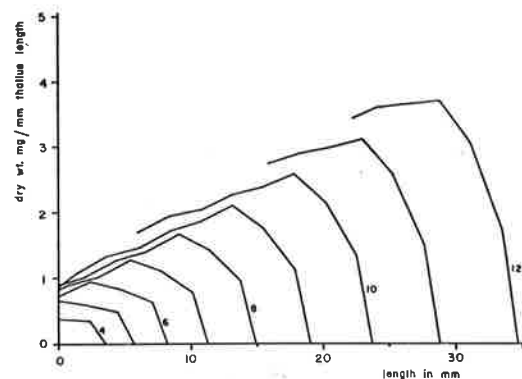


Fig. 6. Weight distribution in the thallus of *Cladonia alpestris*. The numbers beside the curves refer to the age. The results are slightly smoothed (the smoothing method is given in the text).

terial of the present study comprised specimens whose age ranged from 4 to 9 years, and the measurements were united in one diagram.

The standard errors of internode lengths are high: 30–50 per cent of the mean. Thus the number of samples must be increased and suitable sampling methods must be evolved if reliable results are to be obtained. The standard error of the length from the top of the thallus to the lower end of the n th internode (Fig. 8) is also high (about 20–50 per cent).

4.3. Weight distribution in the thallus

Fig. 6 is based on the results obtained when the different parts of the thalli were weighed. The observed average ages of the weight classes were not used in the figure because the numbers of years were not integers. The results were smoothed with logarithmic regressions and the curves shown are those predicted for integral numbers of years. The curves relating to the oldest individuals are not drawn completely, because there were some weaknesses, probably due to the heterogeneity of the material and the low number of samples of the basal parts.

It is seen (Fig. 6) that the youngest individuals grow in 'thickness' as well as in

length. In the older individuals the basal parts have ceased to increase in thickness.

Fig. 7 shows in detail, where the growth takes place. The stepped upper line shows the weight distribution in a 9-year-old thallus. Verticals divide it into parts. The first part from the right represents the four uppermost internodes. The following parts represent one internode only. The shaded portions represent the parts of the 8-year-old thallus, from which the corresponding 9th year parts have grown. The number of internodes comprised by the shaded portions is 1 less than the number of the 9-year-old thallus. The proportion of the white area represents the proportion of the new biomass.

The diagram in Fig. 7 demonstrates clearly that the relative growth rate is much higher in the top than in the more basal parts. In addition, it demonstrates that the actively growing zone is differentiated from the remainder of the thallus. The length of the zone may be estimated to be about 6 mm in this case, and it extends to the middle of the highest part of the stepped line.

The diagram in Fig. 7 is by no means exact. The growth of a lichen is never so schematic, and curves and other irregularities always occur. Nevertheless, the author thinks that the scheme fits the pattern of growth very well.

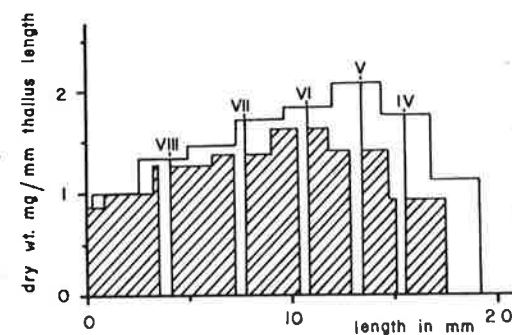


Fig. 7. The growth of the *Cladonia alpestris* thallus from 8 to 9 years old. The stepped upper line gives the weight distribution of a 9-year-old thallus. It is divided by verticals that coincide with the nodes. The numbers of the nodes are given in Roman numerals. The shaded portion gives the part of the 8-year-old thallus from which the corresponding part has grown. The white part represents the new biomass. The diagram is intended to show where the growth occurs, and to distinguish between growth in length and growth in thickness.

4.4. Relative growth rates of thalli of different age

Fig. 8, 9 and 10 show the lengths, diameters and weights of the thalli plotted against their age, and, in addition, the corresponding values for the relative growth rate. Here, too, the RGR values are computed per day, and the growing period is assumed to be 140 days.

Fig. 8 gives the relationship between the

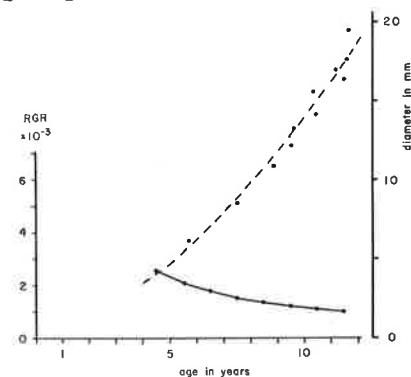


Fig. 9. Diameter (right-hand y -axis, dots and dashed line) plotted against the age of the thallus. The dashed line gives the logarithmic regression. The relative diameter growth rate curve (left-hand y -axis, solid line) is computed from the values predicted with the regression.

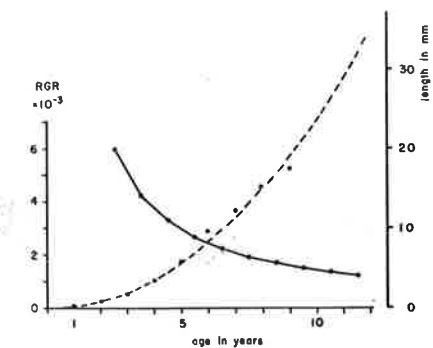


Fig. 8. Length (right-hand y -axis, dots and dashed line) plotted against the age of the thallus. The dashed line gives the logarithmic regression. The relative length growth rate curve (left-hand y -axis, solid line) is computed from the values predicted with the regression.

age and the length of the thallus. The relationship is approximated using the logarithmic regression $\ln y = -1.6058 + 2.0728 \ln x$, $r = 0.996$, ($x =$ age in years, $y =$ length in mm). The RGR values are computed using the predicted length values (shown with the dashed line). It is seen that the RGR values become very low in the older specimens because they are much longer and grow only at the top.

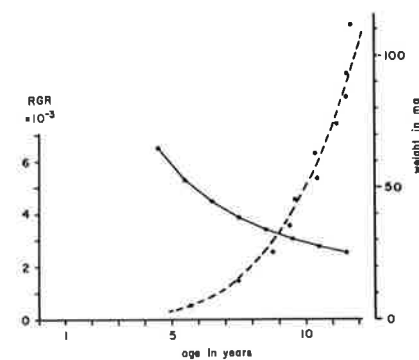


Fig. 10. Weight (right-hand y -axis, dots and dashed line) plotted against the age of the thallus. The dashed line gives the logarithmic regression. The relative weight growth rate curve (left-hand y -axis, solid line) is computed from the values predicted with the regression.

Fig. 9 gives the relationship between the age and the diameter of the thallus. The logarithmic regression is $\ln y = -0.9599 + 1.5644 \ln x$, $r = 0.987$, ($x =$ age in years, $y =$ diameter in mm). The RGR values are computed using the predicted diameter values (shown with the dashed line). It is seen that within the studied range the RGR changes in the same way as in the preceding figure.

Fig. 10 gives the relationship between the age and the weight of the thallus. The logarithmic approximation is $\ln y = -5.4533 +$

$4.0697 \ln x$, $r = 0.993$, ($x =$ age in years, $y =$ dry weight in mg). The RGR values are computed using the predicted weight values (shown with the dashed line). The RGR of a 5-year-old *Cladonia alpestris* thallus is about twice that of a 10-year-old thallus. This must be remembered when the effects of grazing are considered. In a heavily grazed area the lichens tend to be very young, and relatively very productive, but the producing biomass is low. In older lichen stands the biomass is higher but not as productive in terms of RGR.

5. Discussion

There are two widely used methods for estimating the length growth of lichen thalli from the node numbers and the length. One, described by ANDREEV (1954), is to divide the length of the living part of the podetium by its number of nodes. Mature podetia must be used, and the result is the so-called average annual linear growth rate. The method is not very useful in an overgrazed area, where no tall podetia are found, or if one wants to know the growth of different ages separately. The other method, mentioned by SALAZKIN (1937), is to measure the length of the oldest living internode. Mainly for the same reasons, this method is unsatisfactory in detailed analysis. These methods are of course easy to employ and have given results, which are suitable for use in various comparisons. However, for more detailed analysis the following method is suggested.

Numerous specimens are collected in the area to be studied. The material should represent all possible ages of specimens. The cutting should be made at the base of the individual, or in the case of the older ones, at the point where the individual rises above the moss and litter layer. The lengths of the individuals are measured and the number of internodes counted. The results are plotted in a diagram (age on x — axis, length on y — axis), and a curve is fitted to them by eye or using some kind of computation. On this curve is seen the length at each age and the yearly length growth at each age. The results obtained will not be valid in respect of the very young specimens, because of the

effect of variations in climatological factors from one year to another.

The results given in this paper indicate that there is a definite growth zone in the top parts of *Cladonia alpestris*. It seems to be about 6 mm long in 8-year-old individuals. KÄRENlampi (1970) has shown that the chlorophyll content per unit dry weight is highest in the same top part. The importance of this top biomass is emphasized by the observations of AKSENOVA (1937), whose studies show that chemically the top part is different, and more suitable as reindeer forage.

ANDREEV (1954) presented many detailed analyses of the thalli of *Cladonia* species. He showed how in many species the length growth is concentrated in the top parts (1954: 23) and how the length growth of an internode is distributed in relationship to its age in *Cladonia silvatica* (1954: 21). If these results of his are interpreted in terms of growth analysis, they seem to lead to the conclusions given in the present paper. ANDREEV (1954: 31, 32) also presented data on the relationships between age, length (wet) and weight (air-dry). Though the curves seem to be based on a few measured points only, their form tends to be similar to that of the curves given in the present study.

KÄRENlampi (1970) concluded that the net photosynthesis of the *Cladonia alpestris* thallus was correlated with the chlorophyll content. A comparison of the RGR curve with the net photosynthesis and chlorophyll distributions shows that the RGR values seem

to be correlated with them. This stresses the value of chlorophyll determinations.

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