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Age Estimation of Antarctic Macrolichens by Radiocarbon Measurements[#]

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Summary: By the nuclear bomb tests during the 1950s and early 1960s, the radiocarbon content of the atmospheric CO₂ on the Southern Hemisphere Summary: By the fucted both tests during the 1930s and early 1900s, the radiocarobic content of the antospheric CO, on the southern remissioned to reserving a few years from 98 to 162% of the standard recent value and then dropped to 122% (at the end of 1984). This rapid fluctuation was used to determine the lifetime of five species of lichens collected in the beginning of 1985 in the maritime Antarctic. Under the assumption that lichens assimilate each year carbon at the same rate and that carbon once fixed at least in main branches never will be exchanged later on, the age of mature thall in *Caloplaca regalis. Ramalina terebrata* and *Usinea antarctica* was determined to 32 years, while *U. aurantiaco-atra* and *Himantormia lugubris* gave an age of ca. 38 years and ca. 60 years, respectively.

Zusammenfassung: Durch die Atombombenversuche in den 50er und 60er Jahren dieses Jahrhunderts stieg der Radiokohlenstoffgehalt des atmo-Zusammernassung: Durch erköntbomberversuche in den Oder Jahre von 98% auf 162% des Standard-Rezentwertes und fiel danach auf 122% (Ende 1984). Diese rasche Änderung wurde genutzt, um die Lebensalter von Flechten zu bestimmen, die 1985 in der maritimen Antarktis gesammell wor-den waren. Unter der Annahme, daß Flechten konstante Assimilationsraten pro Jahr aufweisen und daß einmal fixierter Kohlenstoff in den Haupt-stämmen nicht wieder ausgetauscht wird, wurden Alter ausgereifter Thalli von *Caloplaca regalis. Ramalina terbrata* und *Usnea antarctica* von 36 Jahren bestimmt. *Usnea aurantiaco-atra* und *Himantornia lugubris* hatten Alter von 38 bzw. 60 Jahren.

INTRODUCTION

Among plants, lichens are known for slow growth. With this respect, lichens differ from most of the free living relatives of their symbionts the algae and fungi which pass a whole generation cycle within a few months or less. The life span particular of crustose lichens may reach several centuries (HENSSEN & JAHNS 1974) and in polar and alpine regions millennia (BESCHEL 1957, 1958, DENTON & KARLÉN 1973). It is therefore not unexpected that thalli of Rinodina frigida on the Antarctic continent were estimated to be up to 1500 years old (LINDSAY 1978).

Fruticose lichen species that exist in the comparative milder maritime Antarctic region were reported to reach up to 500 years (HOOKER 1980b, KAPPEN 1989). These records illustrate that Antarctic lichens are at least potentially longliving. However, several other studies record thalli of lichens of considerable size were found on substrates not longer exposed than a few decades in polar regions (MILLER 1973, LINDSAY 1973a,b, HAWORTH et al. 1986). SMITH (1990) states that "growth and community development may in fact be proceeding faster than has been generally accepted".

Various methods have been applied to measure the growth rates of lichens. In foliose and crustose lichens increment can be recorded by repeated photography over a period of years or decades (HOOKER & BROWN 1977, HALE 1983, PROCTOR 1983, LANGE & EVENARI 1971, SMITH 1990). In fruticose lichens which are considered in this study the annual increment of length (,,mean annual linear growth") or weight of branches or of "internodes" (Cladina) is usually measured (PEGAN 1968, KÄRENLÄMPI 1970, LINDSAY 1973, PRINCE 1974, LINDSAY 1975, HOOKER 1980a, b, HAWORTH et al. 1986). The age of lichens can be estimated if the diameter of the largest thalli is related with the age of a dated substrate on which they colonize (lichenometric method: BESCHEL 1958, LINDSAY 1973, DENTON & KARLÉN 1973).

Regarding the longevity of lichens, the radiocarbon method seems to be a useful tool for determining their lifespan. The carbon of living plants or animals has a certain content of radiocarbon (14C). In comparison to the normal carbon isotope ¹²C, the abundance of ¹⁴C is about 1 : 1.2•10⁻¹². The radioactivity of recent material gives 13.56 dpm per g of carbon (= 226 Bq per kg). This activity decreases with a half-life of 5730 years. Hence, it is possible to calculate the age of a carbonaceous sample on the basis of its actual radioactivity. The precision of a ¹⁴C

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measurement is about 0.5 to 1% corresponding to an uncertainty in age of 40 to 80 years (for details see WILL-KOMM 1976, HARKNESS 1979).

The nearly stable concentration of ¹⁴C in the atmospheric CO₂ was heavily disturbed by the great atmospheric nuclear tests in the early 1960s (VOGEL 1972). Within few years, the ¹⁴C content rose up to nearly 200% of the normal value in the air. Due to the bomb moratorium in 1963, the tests in the atmosphere and on the earth's surface were stopped and the atmospheric ¹⁴C content began to decrease (NYDAL et al. 1980). This nearly exponential falling off with a time constant of approximately 17 years, however, is independent of the radioactive decay which would cause a reduction of only 1% within 80 years, but depends on the exchange of atmospheric CO₂ with the bicarbonate of the ocean.

The rapid variation in ¹⁴C concentration allows the investigation of short events and even the exact determination of a single year. Examples for this are checking the year of vintage for wine or whisky (BAXTER et al. 1969, ZIMEN 1972, BURCHULADZE et al. 1989), the growth rate determination of mussel shells (WILLKOMM 1976) or measuring the velocity of transport resp. diffusion of CO_2 within the ground (O'BRIEN & STOUT 1978). This high resolution of time spans suggests also to apply the method to living and inactive plant material such as lichens.

MATERIAL AND METHODS

For ¹⁴C measurement, mature thalli (wet weight 6-10 g) of several lichen species (*Usnea antarctica* Du Rietz, *Caloplaca regalis* Hook et Tayl., *Ramalina terebrata* Hook et Tayl., *Usnea aurantiaco-atra* (Jaqc.) Bory, and *Himantormia lugubris* (Hue) Lamb were collected during an expedition on King George Island (near Arctowski Station, 62°10' S, 58°30' W) in December/January 1984/85 (Tab. 1). All species grew on basaltic rocks in the coastal region of the Admiralty Bay.

After collection, the samples were deep-frozen and kept in the dark, in order to stop any further metabolism. In the laboratory in Kiel, the material was first purified with diluted (1n) chloric acid from adherent carbonates which might have secondarily precipitated on the lichen surface. The remaining purely organic material is supposed to belong truly to the sample. It is combusted to CO_2 and after further steps of purification the gas is filled into proportional counters where its ¹⁴C content is measured during two to seven days. A more detailed methodical description is given by WILLKOMM (1976).

For comparison, the ¹⁴C content is measured in CO_2 produced from standard material which has the ¹⁴C activity of ,,ideal wood of AD 1950" (13.56 dpm/g). This means that the activity of wood was not disturbed by human influences like the industry effect or atomic bomb effects. The ratio of the counting rates of sample material and of standard material is the ¹⁴C content q of the sample given in percent of the standard recent value.

Normally, the age (before 1950) is calculated simply by

	species	δ ¹³ C (‰)	¹⁴ C-activity ±1 s (%)
ł	Caloplaca regalis	-21.4	(131.1 ±0.9)
į	Ramalina terebrata	-23.2	(132.3 ±1.0)
ł	Usnea antarctica	-24.0	(132.3 ±1.8)
1	Himantormia lugubris	-27.9	(116.1 ±2.2)
1		-27.9	

Tab. 1: ¹⁴C activity relative to standard recent value of Antarctic lichens, coll. Jan. 1985 (activity corr. for $\partial^{13}C = -25\%$, cf. eq. 2).

Tab. 1: 12 C-Aktivitäten antarktischer Flechten in Beziehung zum Standardrezentwert, gesammelt Jan. 1985 (Aktivitätskorrektur für ∂^{12} C = -25%, vgl. Gleichung 2).

$T = -\tau \cdot \ln q$,

where t = 8267 yrs is the mean life time of radiocarbon. The formula is valid under the assumption that when originating (e.g. growing of a plant, a tree ring, a layer of peat) the sample had an activity of 100%. When it is measured later on, the activity will be less than 100% and ln q is negative. Therefore, the formula will give a positive value for T, the age BP (before present = before AD 1950).

The lichens, however, had activity values higher than 100%. Therefore the simple way of age calculation cannot be used. Instead of this, we will try to explain the measured activities with the real atmospheric activity caused by the atomic bomb effect (NYDAL et al. 1980).

RESULTS AND DISCUSSION

According to the longevity of lichens particularly in the Antarctic region, we expected that only a small portion of their carbon content was assimilated during the period of the atomic bomb tests, i.e. within the last 30 years since 1955. In this time, the mean ¹⁴C activity of the atmospheric CO₂ in the Southern Hemisphere was about 134%. The major portion of the carbon was expected to be assimilated during the time before, with a recent activity of $\approx 100\%$ (compared to the standard recent value). Therefore, the mean ¹⁴C activity of the lichens should be slightly above 100%, and perhaps, considering the radioactive decay, even below 100%.

In contrast to these expectations, the measured activities of three species were between 131 and 132%, and the fourth species gave a value of 116% (Tab. 1; Fig. 1). All samples are greatly influenced by the atomic bomb effect and the assumption that the main part of the carbon came from the "pre-bomb time" must be abandoned.

For a more precise interpretation, a concept about the carbon metabolism of lichens is needed. In principle, there are two possibilities:

(i) In the first case, the carbon (or any other chemical element) remains only a finite time in the plant (or animal) because a small fraction of carbon per time is continuously exchanged resulting in a sort of half-life in the

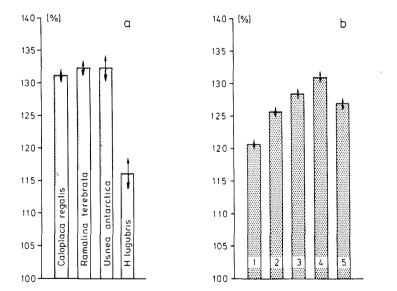


Fig. 1: ¹⁴C activity ($\frac{1}{2}$) in various lichen species (a) and in different sections of *Lsnea aurannaco-atra* (b). The arrows indicate the uncertainty of ± 1 $\frac{3}{2}$ 1 = main stem, 2 = branching of 1st order, 3 = branches of 2nd and 3rd order, 4 = tips, 5 = apothecia.

Abb. 1: ^μC-Aktivitäten verschiedener Flechten (a) und verschiedener Abschnitte von Usnea aurantiaco-atra (b). Die Pfeile verweisen auf die ± 1 σ-Fehlerbreiten. 1 = Hauptstamm, 2 = Verzweigung 1. Ordnung, 3 = Verzweigung 2. und 3. Ordnung, 4 = Spitzen, 5 = Apothecien. organism, the so called ,,biological half-life". For humans e.g., potassium is rather quickly exchanged with a biological half-life of only 100 days, while calcium once fixed in bone, remains there for an infinite time.

MCKAY et al. (1986) assumed that such a biotic system originates with a carbon activity of 100%. In the following time, the incorporated carbon is continuously exchanged by fresh carbon. Therefore, the ¹⁴C content in the biotic system follows with a certain delay to the changing ¹⁴C content of the atmosphere. Regarding the atomic bomb effect, the authors calculate the ¹⁴C content of the reservoirs in the Northern Hemisphere with exchange times between 0.2 and 200 years. Erraneously, the exchange times of 10 to 10,000 years given by MCKAY et al. (1986, Fig. 3) are overestimated by a factor of 50 compared to eq. 11 of this paper. Consequently, the discrepancy between true and apparent ¹⁴C age with bomb effect (in their Fig. 4) is also overestimated. Besides, the curve with apparent age of –8000 years has no physical sense, because an activity of 264% never existed. Until 1970, this hemisphere had a clearly higher bomb effect than the southern one.

For small exchange periods, i.e. small biological half-lives, the ${}^{14}C$ content of a system follows exactly the activity of the atmosphere. In this case, it is impossible to determine the age of the system, i.e. the date when the system originated.

(ii) In the second case, the carbon once fixed remains definitely in the plant tissue. Typical examples are the rings of trees: In stems or branches, the carbon transport occurs only in the fibre layer, and there is no exchange into lignified tree rings. Even the conversion of sapwood to heartwood (in oaks typically after 30 years) needs no additional carbon from outer parts of the tree. This was examined in trees that started growth in the pre-bomb time (activity 98% with respect to standard activity) and continued under the influence of the bomb effect with activity temporarily 150 - 200% (WILSON 1961).

For modelling the assimilation of carbon, we assume according to (ii) that the lichen thalli fix their carbon only during growth and that the carbon never has been exchanged or supplemented by younger carbon at later times. Further, we assume a linear growth rate (HALE 1983) and neglect a relatively short juvenile period. This means that each year, the same amount of carbon was assimilated. Linear growth rates exist at least in mature thalli. Such model has been applied to fruticose lichens by LINDSAY (1973, 1975, HOOKER 1980). Therfore, the mean ¹⁴C content of a lichen or a part of it should be equal to the mean ¹⁴C content of the atmosphere during its growth.

For better calculation, we also have to simplify slightly the description of the atmospheric ${}^{14}C$ content (see Fig. 2):

(i) Suess effect: With the beginning of this century burning of fossil fuel increased drastically and caused a linear decline of the atmospheric radiocarbon content from 99.7% (1900) to 97.8% (1954) (cf. e.g. STUIVER & PEARSON 1986).

(ii) Rapid increase of ¹⁴C in the atmosphere by bomb effect: Between 1955 and 1970, the bomb-produced activity changed rapidly and irregularly as shown in Table 2. The samples from Antarctica are determined by the ¹⁴C content of the Southern Hemisphere, which was lower than in that of the Northern Hemisphere because nearly all atomic bomb tests occured in the north. Differences in concentration within one hemisphere vanish within a few months; therefore also values from lower latitudes may be compared with the activity of the lichens from 62° S. The Southern Hemisphere values given by NYDAL et al. (1980) were measured in Madagascar (21° S) after 1962. Further values are reported by RAFTER & O'BRIEN (1970). They describe the ¹⁴C content in New Zealand (41° S) between 1956 and 1964. Other data were gained from measurements near Melbourne (38° S), Scott-Base in the Antarctic (78° S), Pretoria (26° S), and other regions in the Southern Hemisphere (RAFTER & O'BRIEN 1970, VOGEL 1972). All figures are very similar and demonstrate that there is no local variation in radioactivity within the Southern Hemisphere.

(iii) Exponential decreasing due to exchange with the ocean: In the years after 1970, the radioactivity decreased nearly exponentially according to

$$A_{atm}[\%] = 100 + 54.7 \cdot \exp\{-(T - 1970.0)/16.7\}; \quad T \ge 1970$$
(1)

Fig. 2 illustrates the radiocarbon activity during the atomic bomb effect. All values are corrected for $\partial^{13}C = -25\%c$ according to

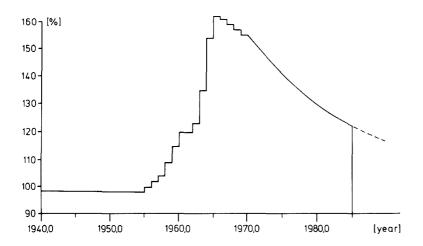


Fig. 2: Approximation of atmospheric ¹⁴C contents: 1900..1955.5: linear decline (Suess effect), 1955.0..1970.0: step function (atomic bomb effect, Southern Hemisphere), after 1970.0: exponential decay (exchange with sea water, cf. eq. 1).

Abb. 2: Näherung des ¹⁴C-Gehaltes der Atmosphäre: 1900..1950.0: linearer Abfall (Suess-Effekt), 1955.0..1970.0 : Stufenfunktion (Atombombeneffekt, südliche Hemisphäre), nach 1970.0: exponentieller Abfall (Austausch mit Seewasser, vgl. Gleichung 1).

Year	activity	year	activity
1900	99.7 %	1960	120 %
1920	99.0 %	1961	120 %
1940	98.3 %	1962	123 %
1954	97.8 %	1963	135 %
		1964	154 %
1955	100 %	1965	162 %
1956	102 %	1966	161 %
1957	104 %	1967	159 %
1958	109 %	1968	157 %
1959	115 %	1969	155 %

Tab. 2: Annual mean ¹⁴C content of atmospheric carbon dioxide for the southern hemisphere (values corr. for $\partial^{13}C = -25\%$, NYDAL et al. 1980). **Tab. 2:** Mittlerer jährlicher ¹⁴C-Gehalt des atmosphärischen Kohlendioxids für die südliche Hemisphäre (Werte korrigiert für $\partial^{13}C = -25\%$, NYDAL et al. 1980)

$$A_{korr} = A \cdot 0.975^2 / (1 + d^{13}C)^2.$$
⁽²⁾

By this way, atmospheric carbon ($\partial^{13}C = -7\%$) and the carbon of plants ($\partial^{13}C \approx -25\%$) are directly comparable. Otherwise without this correction, the atmospheric ¹⁴C content would be 3.6% (= 2 • 18\%) higher than in plant tissue.

A further correction is generally necessary because the measured ¹⁴C content is normally calculated for the year 1950, while the values given for the atmospheric CO_2 refer to the year in question. For the period 1920 to 1985 this correction is negligible.

The ¹⁴C contents of the measured lichens range between 116 and 132%. Assuming equal increment of biomass each year, this radioactivity should be equal to the mean atmospheric radioactivity during the lifetime of the lichen. For determining this lifetime, the measured activity (e.g. 132%) is depicted by a horizontal line in Figure 3. This line ends at 1985.0, the date of collection. The "line of life" has to be extended to the point where the rectangle under the line (in percent • years) has the same extension as the corresponding area under the curve representing the atmospheric radioactivity.

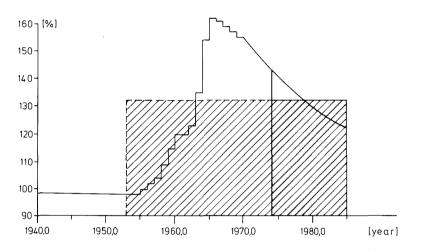


Fig. 3: Fitting a mean activity of 132% to the atmospheric ¹⁴C content. Total hatched area: ..Long-term model": small area (right): "short-term model". Abb. 3: Anpassung der mittleren Aktivität von 132% an den atmosphärischen ¹⁴C-Gehalt. Gesamte schraffierte Fläche: "Langzeitmodell"; rechte Teilfläche: "Kurzzeitmodell".

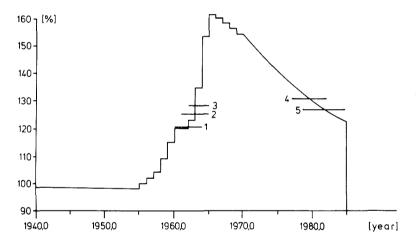


Fig. 4: Fitting of parts of U. aurantiaco-atra. 1 = stems, 2 = branches of 1st order, 3 = branches of 2nd and 3rd order, 4 = tips. 5 = apothecia (cf. Tab. 3).

Abb. 4: Anpassung der Abschnitte von *Usnea aurantiaco-atra*. 1 = Hauptstamm, 2 = Verzweigungen 1. Ordnung, 3 = Verzweigungen 2. und 3. Ordnung, 4 = Spitzen, 5 = Apothecien (vgl. Tab. 3).

The measured activity of 132%, can be interpreted in two ways: it represents either a) a short-term model, lasting from about 1974-1985, or b) a long-term model, covering 1950-1985.

In the first case, the lichen lived only when the atomic bomb effect was decreasing and when the higher radioactivity of the first years was compensated by the lower activity during the last ones. In the other case, the lichen existed already during the whole period with the bomb effect, and the lower mean value results from several years before the great bomb tests.

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Short-term model

The excess activity E(T) % is the excess of the atmospheric activity A(T) % over the standard activity of 100%: E(T) = A(T) - 100

The lichen existed from T_1 until present ($T_2 = 1985.0$). During this period, the atmosphere had the total excess value:

$$S[\% yrs] = \int E(T) dt$$
$$T_1$$

Regarding

$$E(T) = E(T_0) \cdot \exp\{-(T - T_0) / \tau^*\}$$
(3)

with $\tau^* = 16.7$ years, $T_0 = 1970.0$, $E(T_0) = 54.7\%$, cf. eq. (1) follows

$$S = E(T_0) \cdot \int \exp \{ -(T - T_0)/\tau^* \}$$

$$T_1$$

$$S = \tau^* \cdot E(T_2) [\exp \{ \Delta T/\tau^* \} - 1]$$
(4)

Dividing S by the number of years $\Delta T = T_1 - T_2$, we get the mean excess value:

$$\mathbf{E}_{\mathrm{m}} = \mathbf{S}/\Delta \mathbf{T} = (\tau^*/\Delta \mathbf{T}) \cdot \mathbf{E}(\mathbf{T}_2) \cdot [\exp \{\Delta \mathbf{T}/\tau^*\} - 1]$$

For $T_2 = 1985.0$: follows from (6) $E(T_2) = 22.3\%$. With different values for T_1 , we get:

$T_1 = 1973.0$:	$\Delta T = 12$ years;	->	$E_{m} = 32.6\%$
$T_1 = 1974.0$:	$\Delta T = 11$ years;	->	$E_{m} = 31.5\%$
$T_1 = 1975.0$:	$\Delta T = 10$ years;	->	$E_{m} = 30.5\%$

Therefore, the activity of *C. regalis*, *R. terebrata* and *U. antarctica* were estimated to start with the carbon assimilation within a period of 1973 and 1975. As for *H. lugubris*, apparently a short term model does not apply because the CO_2 -activity of the atmosphere was higher than the activity in the thallus, suggesting a longer life span of the lichen.

Long-term model

Alternatively, we suppose that the lichens existed already before the bomb tests started. In this case, the total excess results from that of three different time periods in the past (Fig. 2):

(i) 1970.0 - 1985.0 (exponential decrease): according to eq. 4 with $\Delta T = 15$, we get

$$S_1 = 542$$
 % years.

(ii) 1955.0 - 1970.0 (stepwise increase and decrease): by summing up the values given in Tab. 2 we get $S_2 = 476$ % years.

Consequently, the total excess activity from 1955.0 - 1985.0 is

 $\mathrm{S_1} + \mathrm{S_2} = 1018~\% \text{ years.}$ Within these 30 years, the mean excess is

$$E_{\rm m} = (S_1 + S_2)/30 = 33.9 \%.$$

(iii) Before 1955.0, the atmospheric ¹⁴C content was 98%, i.e. the excess was

E = -2%

If lichen growth has started n yrs before 1955.0, the mean excess is

$$E_{m} = (1018 - 2n)/(30 + n),$$

or $n = (1018 - 30 E_{m})/(E_{m} + 2)$

For *C. regalis*, *R. terebrata* and *U. antarctica*, the mean excess E_m ranged between 31 and 32%. This means that n was 1 to 3 years. Consequently, 3 species started growth in 1953.0 ±1. As for *H. lugubris* with $E_m = 16\%$, we get an n of 30 ±4, which means a start in growth since 1925.0 ±4.

Short-term or long-term model

The values we have shown were derived from the homogenates of entire lichen thalli. It was therefore not analysed whether the determined ages were the sum of growth steps of the thallus. A detailed analysis of the different regions of a fruticose thallus shall therefore indicate better their subsequent development. The result may also help to decide whether the "long term" or the "short term" model is more likely to be assumed. The relatively large thalli of *U. aurantiaco-atra* yielded sufficient material for this analysis. These thalli were dissected into main stems (as the oldest parts), first order branches, second and third order branches, and tips of the branches of last order (as the youngest parts). Also the fruiting bodies formed as apothecia of 2-8 mm in diameter were taken. They are inserted laterally at branches of second and third order. Thus five fractions are considered (Tab. 3; Fig. 1b).

The results suggest the following interpretation: the apothecia with 127% match the mean atmospheric activity during 1979-1984 (short term model). The tips of the thalli with 131% correspond to the mean of the period 1974-1984. Even a shorter interval may be possible, e.g. from 1978 to 1980 or from 1977 to 1981.

The radioactivities of the other three thallus fractions decrease from top to bottom of the thallus (128.5% for the branches of 2nd and 3rd order down to 120.6% for the main stems). We suppose that these parts of lichens were formed during the phase with increasing bomb effect. The measured values correspond to 1960 and 1961 (120%), 1962 (123%), and 1963 (135%), but the real growth may have extended over several years like that of the tips (see above). The exact values of activity are not essential, it is of importance that the basal parts of the thalli have a smaller activity than the peripheral branches.

Keeping to the short term model, the lichens *C. regalis, R. terebrata* and *U. antarctica* have started growth not earlier than 1973, which means in the phase with decreasing atomic bomb effect. In this case, their basal stems

No.	Part of lichen	∂ ¹³ C (%c)	¹⁴ C-activity related to standard activity (%)
Ki-2624.01	stems (oldest part)	-19.6	120.6 ±0.7
Ki-2624.02	branches of 1st order	-19.0	125.7 ±0.7
Ki-2624.03	branches of 2nd & 3rd order	-19.7	128.5 ± 0.7
Ki-2624.04	tips	-20.2	131.0 ±0.7
Ki-2624.05	apothecia	-21.0	127.0 ±0.9

Table 3: ¹⁴C activity of thallus sections of Usnea aurantiaco-atra, corrected to $\partial^{13}C = -25\%$ (collected in Jan. 1985 on King George Island).

Tabelle 3: ¹⁴C-Aktivitäten von Thallusabschnitten von Usnea aurantiaco-atra, korrigiert für d¹²C = -25% (gesammelt im Januar 1985 auf King George

should have the highest activity, but by contrast the last measurement in *U. aurantico-atra* has shown that activity decreases when going to the basal parts of the lichen. Consequently, the short-term model is not aplicable in this case and only the long-term model is relevant. Summing up, the lifetime of the first three species must be 32 ± 1 year. As for *H. lugubris*, only the long term model gives a consistent value estimating a lifetime of 60 ± 4 years and *U. aurantiaco-atra* may have started ca 43 years ago.

CONCLUSIONS

So far, only a few attempts have been made to measure the ¹⁴C-age of plant material that is in part still active (HARKNESS 1979, BONANI et al. 1988). The high sensitivity detecting short time intervals by using the bomb effect may justify the application of the ¹⁴C-method at least for growing plants that produce a high amount of inactive material.

Similar to the wood in trees the basal stems and the 1st and 2nd order branches in fruticose lichens (particularly the subgenus *Neuropogon*) consist of sclerotic plectenchyma that strengthens the thalli enormously also against the action of wind and ice blast.

Calculations that such lichens reach an age of several centuries are consistent with the high stability of these thalli particularly under the very unproductive microclimatic conditions on the Antarctic continent. Photosynthesis rates of the continental *Neuropogon* species *Usnea sphacelata* are extremely low and the growing season is restricted to only a few weeks per year. As a consequence, growth is expected to be extremely slow (KAPPEN 1990). However, this result bases on a very rough and simplified estimate with measured photosynthesis data. Neglection of loss of biomass that reduce production and uncertainties about the real length of the annual production time period are sources of error.

On the other hand, *U. aurantiaco-atra* and *U. antarctica* were estimated to reach up to 600 years even in the mild climate of the maritime Antarctic (HOOKER 1980b). A thallus of *U. aurantiaco-atra* with a dry weight of 1 g growing on a moraine was determined to be 200 years old. This sounds convincing so far for the lichenometric method. HOOKER (1980a,b) supports these data by direct growth measurements in various fruticose lichens, he performed his experiments over a period of more than one year.

The problem of the long-term observations may be overcome if the age determination is carried out by an analysis of the biomass. The endolithic biota from the Asgard Range, McMurdo Dry Valleys, turned out to have an age ranging in thousands of years, dated by a refined method of ¹⁴C-analysis (BONANI et al. 1988).

The dating of our five lichen species from King George Island, maritime Antarctic, revealed a comparatively low individual age (32-60 years), although the thalli looked mature according to size and weight. But the data were gained in a few samples only and lack any statistical basis. An estimation of 73 years of a mature thallus (300 mg dry wt.) of *R. terebrata* (based on calculations of photosynthetic production, KAPPEN 1989) meets at least the same order of magnitude.

A relatively quick growth of fruticose lichens is also indicated by reports that *U. antarctica* formed small thalli on substrates not longer exposed than 20-46 years (LINDSAY 1973), or expanded cover over a certain area from 10-100% within 20 years, or colonized pebbles of bird nests that were abandonned only for a period of 10 years (SMITH 1990). Mature thalli (241 mg dry wt.) of *U. antarctica* from a moraine were estimated to be 120 years old (LINDSAY 1973). *Pseudephebe (Alectoria) minuscula* consisting of small intensively branched thalli has a similar growth rate (0.1-2 mm yr⁻¹ in Alaska, HAWORTH et al. 1986) as *U. antarctica* (0.5-1 mm yr⁻¹ at Signy Island, maritime Antarctic, SMITH 1984), and thalli of the former species that had not reached their maximum size were reported to be at the age of 60 to 80 years (MILLER 1973).

Other fruticose lichens such as the genera *Cladonia* and *Sphaerophorus* mostly growing on soil or moss banks obviously grow still quicker even in the maritime Antarctic region. Mature podetia of *C. rangiferina* and *Sphaerophorus* have been formed within 11-15 and 23-33 years, respectively (HOOKER 1980a).

Growth rates of Antarctic Cladonias were in the same order of magnitude as those from the Arctic (ANDREEV 1954, SCOTTER 1963, PEGAU 1968, LINDSAY 1975, SMITH 1984). But AHTI (1961) reviewing the data of ANDREEV (1954) states that podetia of *Cladonia* species (*C. rangiferina*, *C. alpestris*, *C. arbuscula*) may have a total life span of 100 to 150 years.

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