

# THE RATE OF PRODUCTION AND DECOMPOSITION OF *Chorisodontium aciphyllum* (Hook. f. & Wils.) Broth.

By J. H. BAKER

**ABSTRACT.** Net annual production of a peat-forming moss, *Chorisodontium aciphyllum*, on Signy Island has been calculated to be 436 g./m.<sup>2</sup>/yr. The method involved the use of crank-shaped markers from which vertical growth was measured. Three methods have been used to determine the rate of decomposition of the same moss. The decomposition rate appears to have been approximately linear for a number of years, averaging only 2 per cent each year. Several hypotheses are advanced concerning the low rate of decomposition and consequent development of peat.

A NUMBER of studies has been made on the productivity of higher plants and the results of many of these studies, covering a wide range of ecosystems extending from Arctic tundra to tropical rain forest, have been collected by Rodin and Basilevič (1968). In contrast, very few investigations have been made on the productivity of bryophytes in either temperate regions or the less hospitable parts of the world, and the need for more work in this field has been stressed by Holdgate (1967). So far, only one set of figures is available for Antarctic regions (Longton, 1970). Consequently, with the stimulus of the International Biological Programme, a project was undertaken to determine the rate of production of the moss *Chorisodontium aciphyllum* (Hook. f. & Wils.) Broth., formerly known as *Dicranum aciphyllum* Hook. f. & Wils. Although there is some knowledge of the decay rate of the remains of higher plants, particularly forest litter (e.g. Witkamp, 1966), little is known about the decomposition rate of mosses. A concurrent study was therefore conducted with the object of ascertaining the rate of loss of dry matter by recently dead *C. aciphyllum*. In the Antarctic, where there are no macro-herbivores, when the rate of production exceeds the rate of decomposition, organic matter accumulates, sometimes forming peat. Conversely, when the rate of decomposition is greater than the rate of production, the organisms (mainly micro-organisms) responsible for the decomposition are starved.

## SITE

The work was carried out on Signy Island (lat. 60°43'S., long 45°38'W.), South Orkney Islands, from late 1965 to early 1968. Signy Island is in the maritime Antarctic as defined by Holdgate (1964) and its climate is typical of that zone, i.e. the maximum mean monthly temperature is approximately 0° C and the minimum mean monthly temperature is about -12° C. The climate has been described in more detail by Holdgate and others (1967), and the vegetation communities have been classified by Gimingham and Smith (1970).

*C. aciphyllum* occurs extensively throughout the maritime Antarctic and on Signy Island it forms peat banks near the coast, particularly on gently sloping ground. Such banks have been described as a sociation within the "moss turf subformation" (Gimingham and Smith, 1970). The peat is superficially similar to the palsas of northern Scandinavia in that both formations have a perennially frozen core. However, the bog surrounding the palsas lacks permafrost (Salmi, 1970), whereas the Signy Island peat is part of a region of continuous permafrost, although the active layer tends to be shallower (approximately 25 cm.) in the peat than in the surrounding ground.

The peat bank chosen for this study was on the west coast of Signy Island north of Spindrift Rocks. It is the same site as that on which microbiological investigations have been carried out (Baker, 1970a, b). The species cover of the bank was >99 per cent *C. aciphyllum* (personal communication from R. I. L. Smith), although occasional clumps of *Pohlia nutans* occurred and the leafy liverwort, *Cephaloziella varians*, was abundantly distributed throughout. The almost pure nature of the vegetation greatly facilitated the estimation of total production per unit area. The site sloped gently west towards the sea and its area was 110 m.<sup>2</sup>; it has been illustrated by Baker (1970a, fig. 1).

## METHODS

The net annual production, i.e. gross production minus that part respired by the plant, was estimated by first determining the annual average extension growth of the moss shoots. In some mosses, e.g. *Polytrichum alpestre*, there are distinct bands along the stem which clearly demarcate 1 year's growth from the next (Longton, 1970). In *Chorisodontium aciphyllum*, although the current year's growth does not appear to have as many rhizoids as the older parts of the plant and the leaves are more adpressed to the stem in the young growth, such differentiation is not sufficiently clear to enable an accurate assessment of annual growth. Therefore, growth was measured by positioning markers level with the tips of the leaves in January 1966 and measuring the height of the stems above the markers 2 years later. The markers used initially were cranks (Clymo, 1970) made from anodized garden labels as shown diagrammatically in Fig. 1 and 50 were randomly distributed over the site. Measurement was made vertically from

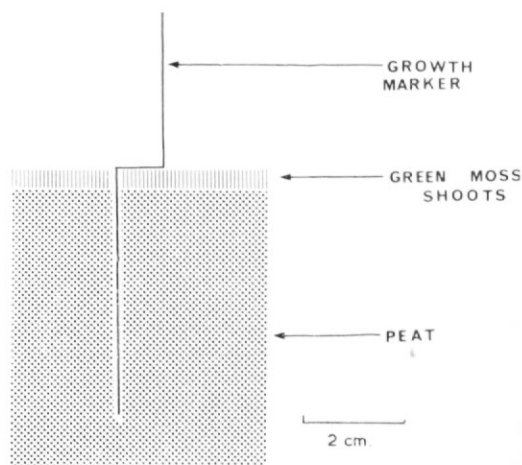


Fig. 1. Diagrammatic vertical section through the peat showing a cranked marker at the beginning of the growth experiment.

the horizontal part of the crank (1 cm. long) to the tips of the uppermost leaves using a pair of dividers. Unfortunately these markers were found to be unsatisfactory in the field since they were easily and frequently removed by skuas nesting in the area. The small cranks were therefore supplemented by 25 much larger markers made from galvanized wire 4.8 mm. in diameter and 40 cm. long. The density of the *Chorisodontium* stems was found by counting the number of stems in 30 random quadrats of area 1.61 cm.<sup>2</sup> (0.25 sq. in.). To determine annual production per unit area the mean extension growth as measured above was then cut separately off 100 stems from each of five random samples (Fig. 2). This operation was performed under a microscope and the measurement was made from the stem apex rather than the top of the uppermost leaf. Each set of 100 stem apices was dried at 105° C for 24 hr. and weighed.

The rate of decomposition of the moss has been estimated by three methods: first, 45 samples of peat were taken with a soil corer. A transverse section, 1 cm. deep, was cut from the entire width of each core, air dried for 1 week in the laboratory and weighed. Each section was then enclosed in a terylene netting bag and tied to an anodized marker with nylon string. The netting was 1 mm. mesh size, sufficient to allow the free entry of all the possible decomposing organisms (Edwards and Heath, 1963). The bags were sealed by welding the opening together with a soldering iron using a cellophane barrier film. The bagged sections were then put back in the cores from which they were taken and the reconstructed cores replaced in their original positions in the field. After 2 years the sections were exhumed, air dried for 1 week and re-weighed. The above procedure will give a valid rate for decomposition only if the sections consist entirely of dead moss. However, it is not easy to decide when *Chorisodontium aciphyllum* is dead; the top 1 cm. of stem is capable of an apparently normal growth without any of the underlying peat

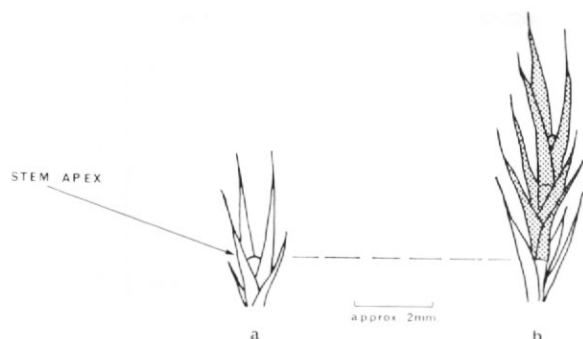


Fig. 2. a. Diagrammatic representation of a *Chorisodontium aciphyllum* stem at the beginning of the production measurement.  
 b. The same plant after 1 year's growth; the shaded area is the part used for the production experiment. The size of the leaves varied greatly from plant to plant on the sample site.

being present; conversely, sections from the 6–7 cm. depth, when left in the warmth of the laboratory produced an occasional green moss shoot. Thus all the moss is not dead even at this depth. An arbitrary depth of 2–3 cm. was chosen as a reasonable estimate of the depth at which decomposition might be expected to occur.

The second method of measuring decomposition utilizes the fact that the moss stems are remarkably well preserved in the peat and large parts of moss stems with leaves still attached can be picked out of the Signy Island peat at depths of 50 cm. and more. In this experiment, complete unbranched *C. aciphyllum* stems were teased out of peat cores down to a maximum depth of 10 cm. and cut under the dissecting microscope into 1 cm. portions. 100 such stems were dissected from each of three separate randomly selected sets of cores and each collection of sections was dried at 105° C for 24 hr. and weighed. Assuming a uniform rate of extension growth, extrapolation from the rate measured gives a minimum age and hence the rate of loss of dry weight with time can be estimated. This method assumes that there is no vertical compression of the peat. That the assumption is likely to be valid is supported by the stems remaining vertical and not losing their leaves. Moreover, the permafrost lends considerable support to the moss stems and disturbance during sampling was prevented by taking the samples in winter when the peat was completely frozen.

The third and simplest method for determining the rate of decomposition also involves a knowledge of the growth rate. Because the peat is composed almost entirely of *C. aciphyllum*, the difference between the bulk densities at various depths is a measure of the decomposition rate. The method for determining bulk density has previously been described (Baker, 1970b).

## RESULTS

Of the 75 cranks originally placed in the field to measure growth rate, only 39 remained after 2 years. The rest, including some of the very much heavier wire cranks were pulled out by the skuas; occasionally it was possible to replace them in their rightful places but often this was not possible. In addition, the galvanized wire proved to be toxic to the moss and killed it; nonetheless, measurement was still possible from the dead surface and there was no significant difference in growth rate as measured from the two different sorts of marker. Measurement in the field using a simple pair of dividers was only possible with an accuracy of  $\pm 1$  mm. However, the mean extension growth of ten stems surrounding the same marker after 2 years was  $6.6 \pm 0.2$  mm. from 39 localities.

The density of the *Chorisodontium aciphyllum* stems was  $295 \pm 21$ /quadrat, equivalent to 183 stems/cm.<sup>2</sup> on the sample site, and the average weight of five samples of 100 stem apices 3.3 mm. long was 0.0238 g. Hence, the total net primary production of this peat bank was 436 g./m.<sup>2</sup>/yr. or approximately 4 metric tonnes/hectare/yr. Furthermore, if the growing season of *C. aciphyllum* is defined as that period during which growth of the plant can be measured rather

than in terms of meteorological conditions, on this site the production was 5.7 g./m.<sup>2</sup>/day of growing season, although of course the real value would vary from day to day depending on the micro-climatic conditions. This assumes that the growing season for the *Chorisodontium* is approximately 11 weeks, as it is for the closely associated moss, *Polytrichum alpestre* (Longton, 1970).

The skuas also removed many of the terylene netting bags despite the fact that they were buried. Of the 45 placed in the field, only 28 remained at the end of the experiment. One of the 28 was so badly damaged as to be of no value and two showed a very small gain in weight. The mean percentage loss in weight of the 27 in good condition was  $2.67 \pm 0.28$  over the 2 yr. period.

The results of the second method for assessing the rate of decomposition are shown in Fig. 3.

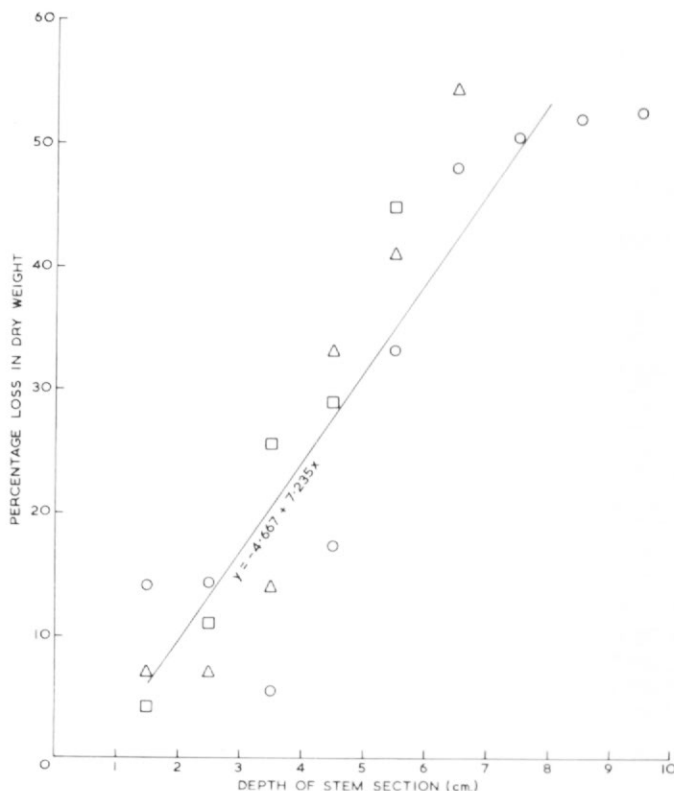


Fig. 3. Graph illustrating the percentage loss in dry weight of stem sections from increasing depths in the peat. The fitted regression line has been computed from all the points combined.

Each point represents the weight loss of 100 1 cm. long stem sections from the depth indicated, expressed as a percentage of the weight of the top centimetre from the same 100 stems. The different symbols refer to different samples. Regrettably few results were obtained for the deeper sections; nonetheless, it can be seen that the rate of decomposition is approximately linear with depth. The linear regressions from each of the three sets of data, computed separately by D. K. Lindley, are significant at the 0.1 per cent level and the linear regression for the combined data is also significant at this level.

As has been previously reported (Baker, 1970b), the bulk densities of the dried peat at 1-2 and 6-7 cm. depth are 0.123 and 0.086 g./cm.<sup>2</sup>, respectively. This is equivalent to a loss of 30.1 per cent dry weight over a depth of 5 cm. The results are summarized in Table I.

TABLE I

Density of <i>Chorisodontium</i> stems	183/cm. <sup>2</sup>
Rate of extension growth	3.3 mm./yr.
Production/annum	436 g./m. <sup>2</sup>
Production/day of growing season	5.7 g./m. <sup>2</sup>
Rate of decomposition by litter bag	1.3 per cent/yr.
Rate of decomposition by bulk density	2.0 per cent/yr.
Rate of decomposition by cut sections	2.4 per cent/yr.

## DISCUSSION AND CONCLUSIONS

Using a somewhat different technique to that described here, Longton (1970) has estimated the annual net production of *Polytrichum alpestre* on Signy Island as 342 g./m.<sup>2</sup>, rather less than the figure for *C. aciphyllum* presented here. This comparison is particularly interesting as *Polytrichum alpestre* also forms peat and is often found in close association with *C. aciphyllum*. It was noticed when the netting bags were removed that in some cases there was a considerable downward growth of rhizoids from both cut surfaces. Since there was no organic connection between the lower cut surface and the photosynthetic region of the plant, the energy for the growth of the rhizoids must have come from storage products. The storage products may accumulate either when the stem is actively photosynthesizing or, when the stem and attached leaves have ceased photosynthetic activity, the storage products may be translocated down from the younger parts of the plant. It was not ascertained whether rhizoid production in this instance was due to the stems being cut or whether it happens in the undisturbed peat. If translocation is taking place, the production figure presented here is lower than the true figure by a quantity at least as great as the weight of the material translocated. However, the production figure will not be affected by the growth of rhizoids if the energy source for such growth was produced while that same part of the stem was actively fixing carbon.

The annual production of some species of *Sphagnum* in England has been shown to be in the range 2–8 metric tonnes/hectare/yr. (Clymo, 1970). At first glance, it may seem a little surprising that the net annual production of a moss in the temperature climate of England is very similar to the production rate of a moss in the Antarctic. But it should be remembered that *Sphagnum* bogs are very poor in nutrients (Gorham, 1956), while the *Chorisodontium* is not short of any major plant nutrient (Holdgate and others, 1967). Also, in contrast to *Sphagnum* bogs, the moss turf on Signy Island covers only a very small percentage of the total land surface, as Holdgate (1967) has already pointed out. Similarly, the figure given for annual production in the Arctic, 3–242 g./m.<sup>2</sup> (Bliss, 1962), refers to the primary production of large areas and not to the rate of production by individual closed plant communities.

In a very detailed study of the production ecology of the forest moss, *Hylocomium splendens*, Tamm (1953) has shown that the maximum total annual production of the forest floor moss carpet is about 150 g./m.<sup>2</sup> in Scandinavia, but this is in addition to the production of the forest trees themselves.

The base of a peat bank adjacent to the sample site has been dated by the <sup>14</sup>C technique (Godwin and Switsur, 1966). The age given for material 150–170 cm. from the surface was 1,843 ± 96 yr., from which a growth rate of about 1 mm./yr. can be predicted (Holdgate, 1967). The prediction is based on the assumptions that the growth rate of the moss has not altered during almost 2,000 yr. and that there is no compression. Since the value found in the present study is about three times larger than Godwin and Switsur's results would indicate, it is reasonable to question these assumptions. Although no compression was apparent in the top 10 cm. on which this study was based, it may occur at greater depths. An amelioration in climate would cause an increase in growth rate, and there is some evidence that the mean annual temperature on Signy Island has risen during the last four centuries. Thus Orwell Glacier has receded leaving many moraines, and lichenometric studies suggest ages of 130 ± 15 and 390 ± 90 yr., not including colonization time, for lichens growing on the two most recently exposed moraines (personal communication from D. C. Lindsay).

The rate of decomposition of the peat calculated from Fig. 3 is about 2.4 per cent each year, compared with an average value of 1.4 per cent from the bagged sections. Moreover, as has been pointed out above, some of the bagged sections produced rhizoids, so some of the stems

in these sections were not dead or even moribund but very much alive. Therefore, the loss of weight may not be solely due to decomposition but also to the utilization of energy for rhizoid production. However, only a small percentage of the sections showed rhizoid production. The rate of decomposition calculated from the bulk density measurements was 2.0 per cent each year. Thus all three results agree reasonably well with each other. The higher value for the decomposition rate calculated from Fig. 3 may reflect a loss of leaves from the stems as they were teased from the cores, and also the other two methods include all the weight of the decomposers and their products. Since decomposition appears to be continuing at some depth in the peat, it is not easy to reach an integrated value for the total quantity of organic matter decomposed per unit area per year. Also, it is surprising that the rate of decomposition is approximately linear for so long. It might have been expected that the more easily degradable plant constituents (simple sugars, small proteins, etc.) would have been rapidly used up, whereas the tannins would have been decomposed progressively more slowly. Such a system was favoured by Olson (1963) but its validity has been questioned by Minderman (1968).

It is worth considering further why the rate of decomposition under *C. aciphyllum* is slow enough to result in an accumulation of peat whilst on the surrounding ground, dominated by species of *Brachythecium*, *Calliergon* and *Drepanocladus*, no peat forms. One possibility is that the rate of decomposition is identical under all the different bryophytes but the rate of production is greater on the *C. aciphyllum* site. Further studies on the production ecology of Antarctic mosses are necessary to resolve this possibility. Secondly, it may be that the *Chorisodontium* is more resistant to decomposition than the other mosses. Clymo (1965) has evidence to show that this mechanism is responsible for the more rapid decomposition of *Sphagnum cuspidatum* compared to *S. papillosum*. His experiment of comparing the decomposition rates of different plants in the same environment could be profitably repeated on Signy Island. Another possibility concerning the accumulation of peat under some conditions but not others is that the period of the year during which decomposition takes place may be longer for some sites than others. In the example under discussion such a situation can be envisaged for two reasons. First, snow accumulation tends to be less on the peat banks than the surrounding area, the thicker the snow cover the greater the insulation and therefore the higher the temperature of the moss, and the longer the period of decomposition. Secondly, the raised *Chorisodontium aciphyllum* banks are drier than the surrounding vegetation and they therefore have a lower thermal conductivity. Viereck (1970) has pointed out that this implies that heat penetration will be slower in summer and hence decomposition will be less. The last two arguments are circular if one says that the peat banks are raised above the ground surface because the plants have not decayed. They will hold true only if the *Chorisodontium* initially colonizes higher ground, and indeed Gimingham and Smith (1970) reported that *C. aciphyllum* is only found on well-drained substrata.

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