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GROWTH RATE AND TEMPERATURE RESPONSES IN BRYOPHYTES

II. A COMPARATIVE STUDY OF SPECIES OF CONTRASTED ECOLOGY

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SUMMARY

(1) Forty species of bryophyte of contrasted growth-form and ecology have been grown under controlled laboratory conditions using a standardized procedure. The results allow the mean relative growth rate of the species to be compared over the temperature range 5–35 °C.

(2) The mean relative growth rate varied considerably with temperature and according to the ecology of the species. High values were recorded in the ruderal species *Funaria hygrometrica* and in perennial pleurocarpous species of fertile habitats, e.g. *Brachythecium rutabulum*. Low values typified species of continuously unproductive habitats and were particularly characteristic of lithophytes.

(3) The optimal temperature for growth in the majority of species was between 15 °C and 25 °C and in many species there was a considerable gain in dry weight at temperatures below 10 °C. With respect to growth at temperatures below 18 °C, shoots of *Brachythecium rutabulum* obtained in winter were superior to those collected in summer. All species were killed, often very rapidly, when maintained in a continuously moist condition at 35 °C and many species died eventually when kept continuously at temperatures above 30 °C.

(4) It is concluded that, for ecological investigations with bryophytes, growth studies under controlled conditions provide a desirable complement to the more conventional short-term investigations of photosynthesis, respiration and tissue viability under stress.

INTRODUCTION

Although observations have been made on the growth of bryophytes in the field (e.g. Tamm 1953; Tallis 1959a, b; Clymo 1970; Longton 1974; Pitkin 1975) very little is known concerning potential rates of growth and variation between species in this respect. Apart from casual comparisons of plants growing in culture or rare experiments, such as the one reported by Tallis (1959a), in which he grew *Funaria hygrometrica** and *Racomitrium lanuginosum* from spores and measured the length of the protonema after a period of cultivation, comparative growth experiments involving bryophytes have not been attempted.

The results of the experiments described in Furness & Grime (1982) demonstrate that it is possible to grow *Brachythecium rutabulum* under controlled conditions and to measure the mean relative growth rate, **R**. In the studies described here, the same techniques have been used with a wide range of bryophytes to determine whether differences in potential mean relative growth rate and response to temperature are related to differences in ecology.

* Nomenclature follows that of Clapham, Tutin & Warburg (1962) for angiosperms, of Smith (1978) for mosses, and of Watson (1969) for liverworts.

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MATERIALS AND METHODS

Plant material

Initially the aim of the experiment was to examine the temperature responses and growth rates of species which occurred in vegetation under investigation in concurrent field studies (Al-Mufti *et al.* 1977; Furness 1980). However, as the experiment progressed the value of examining a larger number of species was appreciated. The range of plants was therefore widened to encompass species from a variety of contrasting habitats. The selection of plants was governed to some extent by the availability of material and the limitations of the experimental procedure. For example, ephemeral mosses of arable fields are not represented as their small size and very short vegetative phase of development present practical problems especially in making accurate weighings.

All bryophytes used in the growth experiments were freshly collected from the field. At each collection site, details of topography, soil, habitat and vegetation were recorded and some of these results are presented in Table 1.

Experimental conditions

Measurements of mean relative growth rate were based upon the culture of shoot cuttings in the temperature gradient incubator described by Furness & Grime (1982). Shoots were grown at each of ten constant temperatures, between 5 °C and 35 °C, on sand soaked initially with 0·01 full-strength Rorison solution, pH 6·0 (Hewitt 1966). Warm-white fluorescent tubes gave a light flux of about 25 W m^{-2} over a daylength of 12 h.

Procedure

Plant material was brought back to the laboratory in plastic bags and stored in a cold room at 5 °C. Shoots were removed from the current year's growth and were cut into lengths which ranged from 10 mm to 25 mm according to the species. Very careful selection and matching of shoots within each species was essential. This applied particularly to the slower-growing species where initial variability in the experimental material would have obscured any differential growth responses.

In order to provide a standardized temperature pretreatment the shoots were washed gently in distilled water and stored moist in Petri-dishes for 3 days at 5 °C. An initial harvest was taken and the remaining shoots were placed on the sand in the compartments of the temperature gradient apparatus. A minimum of ten replicates of each species was put into each of the ten compartments on the bar. The shoots were then sprayed with distilled water. Subsequently all shoots were sprayed daily with distilled water and were provided on alternate days with a standardized aliquot of inorganic nutrient solution as described by Furness & Grime (1982).

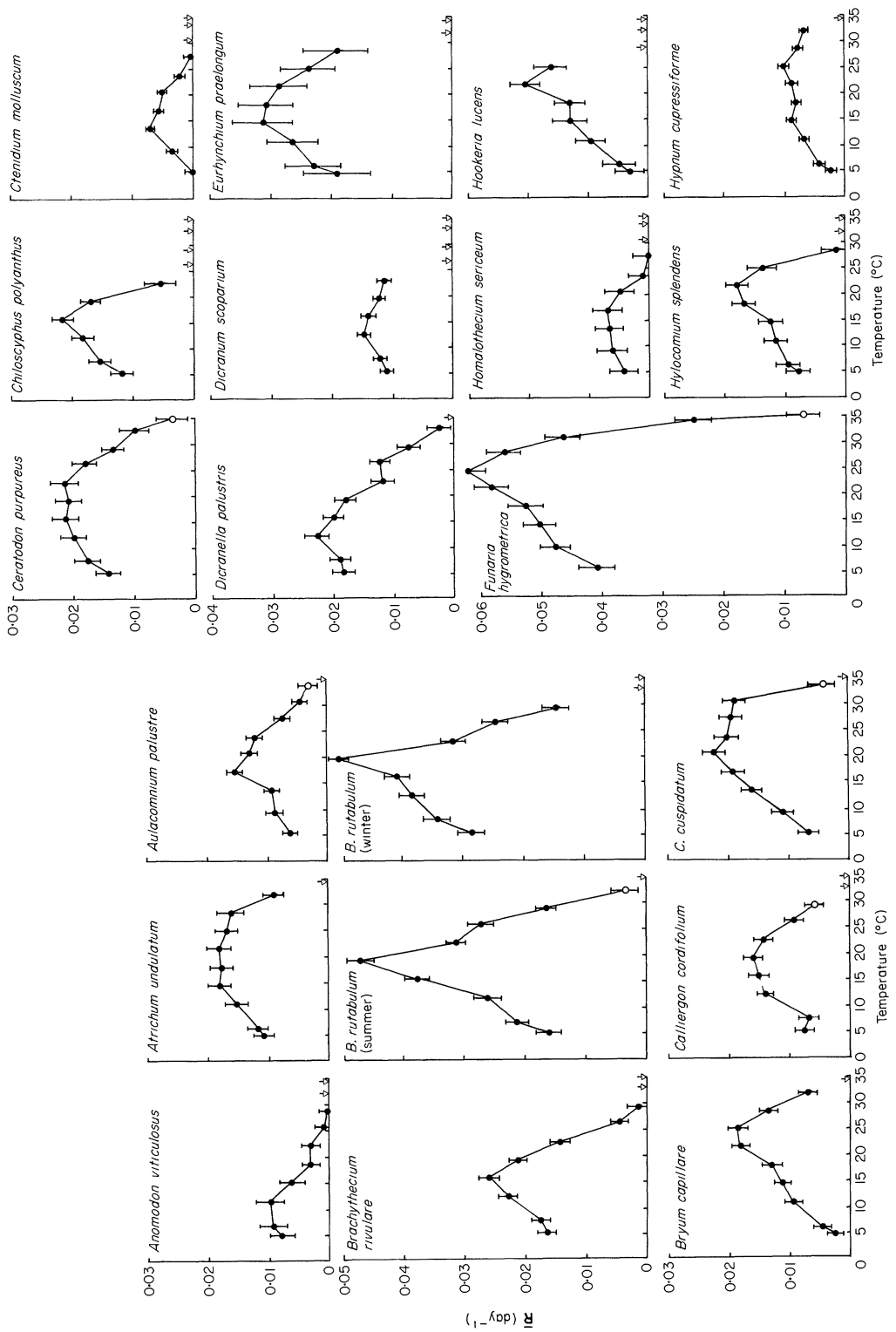
At the final harvest after 30 days (60 days in one experiment with *Racomitrium lanuginosum*) all shoots were carefully lifted from the sand and gently washed to dislodge adhering grains. Each shoot was then inspected using a binocular microscope to ensure complete removal of sand grains. The length of the main stem from cut base to apex, the length and number of laterals, and the rhizoid development of each shoot were recorded. Material from both initial and final harvests was placed between absorbent paper and oven-dried at 90 °C for 48 h. On removal from the oven, the shoots were weighed individually.

Table 1. Species of bryophyte used and details of the sites from which they were collected.

Species	Locality	National Grid reference	Habitat	pH of 0–3 cm layer of substrate	Altitude (m)	Month of collection
Anomodon viticulosus	Bradford Dale	SK 209640	Limestone wall	7·0	150	Oct.
Atrichum undulatum	Storth Lane	SK 314854	Wooded bank	4·3	160	June
Aulacomnium palustre	Rowsley	SK 261653	Open marshy area	6·8	105	July
Brachythecium rivulare	Lathkilldale	SK 185658	Stream margin	7·2	230	Apr.
B. rutabulum	High Storrs	SK 316847	Tall herb community*	6·2	215	Aug./Jan.
Bryum capillare	Rivelin	SK 258877	Wall top	6·9	275	Mar.
Calliergon cordifolium	Catfield Fens	TG 3261	Fen	6·9	0	May
C. cuspidatum	Waterfall Farm	SK 198769	Grass verge	7·3	275	Sept.
Ceratodon purpureus	Winter Street	SK 339878	Bonfire site	7·2	90	March
Chiloscyphus polyanthus	Cressbrookdale	SK 172730	Stream side bank	7·1	185	Aug.
Ctenidium molluscum	Tansley Dale	SK 173747	Rock outcrop	7·4	230	Oct.
Dicranella palustris	Kinder	SK 111899	Moorland flush	5·3	310	July
Dicranum scoparium	Litton	SK 156733	Calcareous grassland	6·8	230	Sept.
Eurhynchium praelongum	High Storrs	SK 316847	Tall herb community*	6·3	215	Jan.
Funaria hygrometrica	Tapton Gardens	SK 331870	Greenhouse staging	6·8	200	Jan.
Homalothecium sericeum	Wardlow	SK 183745	South-facing wall	6·9	280	Nov.
Hookeria lucens	Chatsworth	SK 265705	Shaded bank	5·8	180	Dec.
Hylocomium splendens	Lathkilldale	SK 185657	Calcareous grassland*	7·0	230	Sept.
Hypnum cupressiforme	Litton	SK 156732	Rock outcrop	7·3	230	Sept.
Leptobryum pyriforme	Tapton Gardens	SK 331870	Sand tray	5·7	200	July
Lophocolea bidentata	Roughs	SK 323857	Wet flush†	6·4	160	July
Mnium hornum	Cressbrookdale	SK 172731	Woodland floor	6·3	185	June
Philonotis fontana	High Storrs	SK 323857	Wet flush	6·2	185	April
Plagiochila asplenioides var. *major*	Coombesdale	SK 232748	Tall herb community*	6·6	150	Nov.
Plagiomnium undulatum	Cressbrookdale	SK 172731	Grassy wood margin	7·1	185	Sept.
P. rostratum	Bradford Dale	SK 209639	Shaded bank	6·1	150	Oct.
Plagiothecium undulatum	Padley Wood	SK 255794	Acidic woodland	3·4	150	Nov.
Pleurozium schreberi	Cressbrookdale	SK 174745	Calcareous grassland	5·8	260	Oct.
Pohlia nutans	Seckar Wood	SE 322143	Dry heath	3·8	90	May
Polytrichum commune	Rivelin	SK 263875	Open sandy bank	4·3	244	July
Pseudoscleropodium purum	Cressbrookdale	SK 174745	Calcareous grassland	7·1	260	Sept.
Racomitrium lanuginosum	Ladybower	SK 204868	Rock outcrop	3·6	305	Aug./March
Rhizomnium punctatum	Cressbrookdale	SK 172731	Decaying log	5·8	185	June
Rhynchostegium riparioides	Cressbrookdale	SK 173729	Stream bed	7·2	215	March
Rhytidiadelphus loreus	Aber, Wales	SH 682704	Acidic moorland	—	530	May
R. squarrosus	Cressbrookdale	SK 173742	Calcareous grassland	7·0	250	March
R. triquetrus	Cressbrookdale	SK 173743	Calcareous grassland	7·0	250	March
Scorpidium scorpioides	Catfield Fens	TG 3621	Fen	6·9	0	March
Thuidium tamariscinum	Cressbrookdale	SK 173744	Shady grassy bank	7·3	260	Sept.
Tortula ruralis spp. *ruraliformis*	Newbrough Warren	SH 419644	Sand dune	—	0	Jan.

* Dominant tall herb *Urtica dioica*.

† Dominant tall herb *Epilobium hirsutum*.



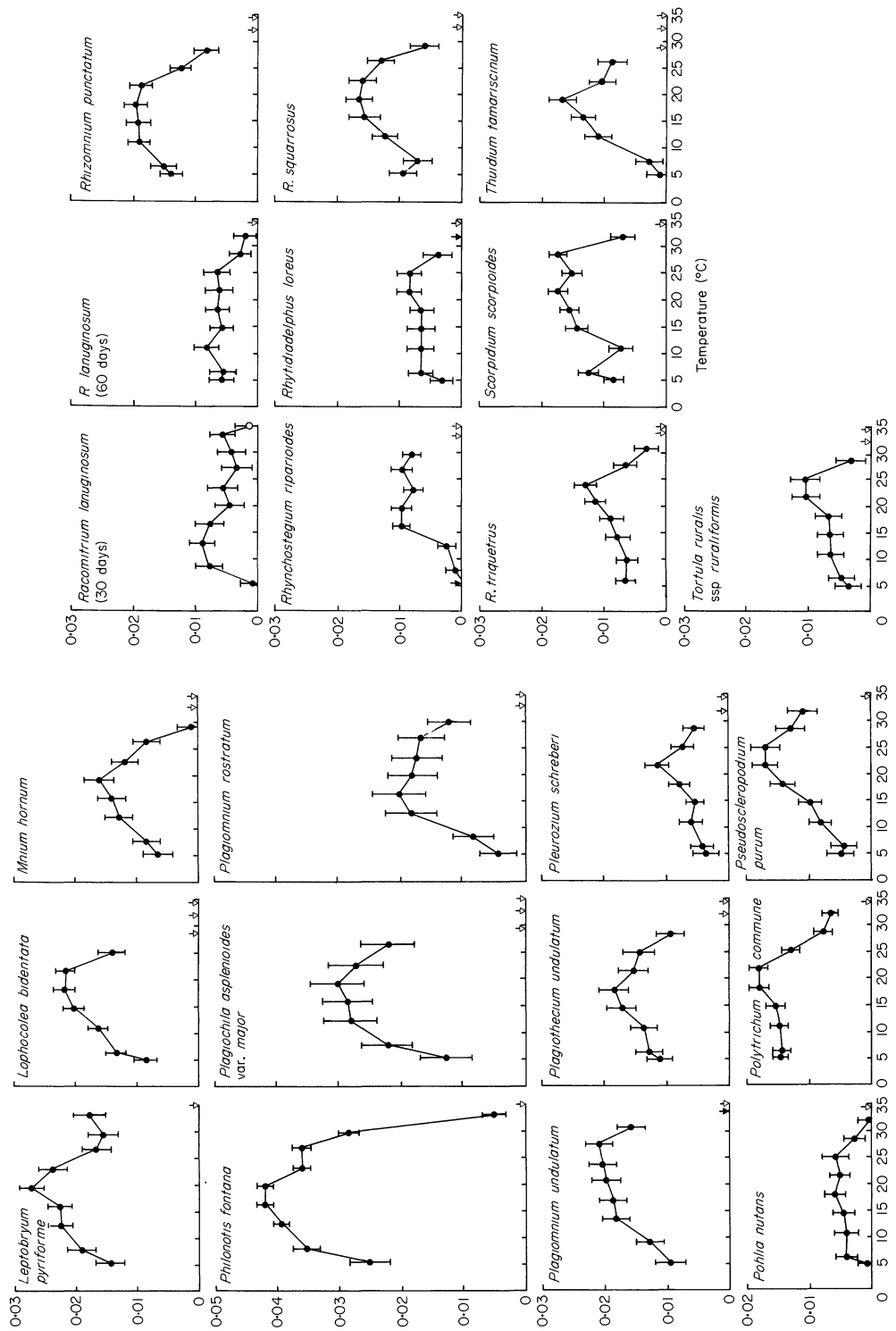


FIG. 1. The effect of temperature upon the mean relative growth rate, $\bar{R}$, of the forty species of bryophyte investigated. The spacing of points along the temperature axis differs slightly according to species; this corresponds to variation in the position of plants within compartments of the incubator. Unfilled circles indicate treatments in which there was a net gain in weight but where all the plants died eventually. Vertical arrows indicate net loss in weight in living (filled) or dead (unfilled) material. Vertical lines indicate 1 S.E. $n \geqslant 10$.

Mean relative growth rate, $\bar{\mathbf{R}}$, over the 30 day period was calculated assuming exponential growth, i.e. a linear regression of log dry weight against time. This is known to be true for *Brachythecium rutabulum* (Furness & Grime 1982) but would be inaccurate with any species which did not display exponential growth during the experimental period. It was impracticable to determine the time course of growth for the forty species used in this survey, and the results must be interpreted cautiously. It is reassuring however to note the close similarity of the values obtained in the 30 day and 60 day experiments on *Racomitrium lanuginosum* (Fig. 1).

These techniques were found to be less suitable for extremely slow-growing or ephemeral species. It is likely that the growth rates achieved by slow-growing species will be affected by the size of the cutting used and by the age-structure of its component parts at the beginning of the experiment. In ephemeral species the foliar gametophyte is usually too small to manipulate and weigh and when larger it includes shoots which are near the end of their life and are unlikely to be growing exponentially.

RESULTS

Vigorous healthy shoot growth, not unlike that observed in the natural environment, was apparent in most species particularly at and below the optimum temperature. Etiolation was evident after prolonged exposure to supra-optimal temperatures especially in some of the rapid-growing pleurocarpous species.

Severing the main stem did not appear to have an adverse or disruptive effect on the growth processes in the shoots. This is hardly surprising as establishment from detached shoots may be an important form of regeneration in many species (Keever 1957; Tallis 1959a; Bayfield 1976; Miller & Ambrose 1976). New growth was visible within a few days in most species; indeed many acrocarpous species developed rhizoids extremely rapidly at the cut surface (cf. La Rue 1942).

Figure 1 shows estimates of $\bar{\mathbf{R}}$ for each species at each of the experimental temperatures. Growth rate showed great variation with respect to temperature and species. In Fig. 2 are the frequency distributions of species in relation to $\bar{\mathbf{R}}$ at the optimum temperature. The distribution of groups of species from selected habitats is also shown. Lithophytes (such as *Homalothecium sericeum* and *Ctenidium molluscum*) ocur only in the slowest growth rate classes, grassland species occur near the modal class and species from tall herb communities on fertile soils are concentrated in the higher growth rate classes.

The shape and position of the temperature response curve differed widely among species; the distribution of temperature optima in all the species examined is shown in Fig. 3. Optimal temperature for the growth of most species was in the range 15–25 °C. Most plants grew at temperatures between 5 °C and 30 °C, with many showing fairly rapid growth at the lowest temperature (5 °C). All species were killed, usually within a week, at the highest temperature (35 °C) and most shoots died eventually at temperatures above 30 °C.

The shoots of *Funaria hygrometrica*, *Ceratodon purpureus* and *Racomitrium lanuginosum* were exceptional in that growth was observed at high temperatures but even in these species prolonged exposure resulted in death. From Fig. 1 it is apparent that the responses of *Brachythecium rutabulum* samples collected in summer (1 August 1977) and winter (19 January 1978) were almost identical with respect to temperature optimum, maximum $\bar{\mathbf{R}}$ and high temperature death. At 35 °C the plants died after 4–5 days in each case. However, differences were apparent at low temperature in that winter-collected material showed more rapid growth below 18 °C.

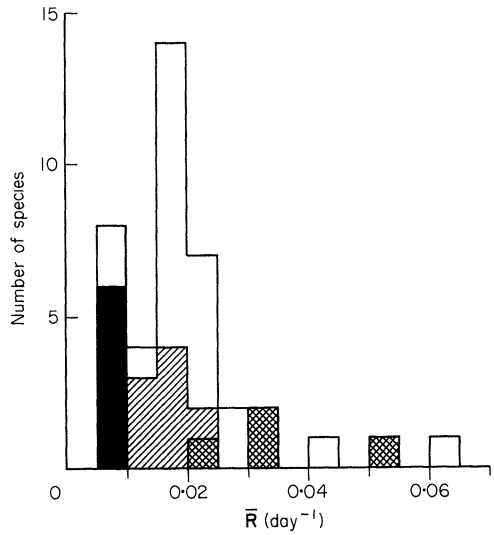


FIG. 2. Frequency distribution of mean relative growth rate, $\bar{R}$, of forty species of bryophyte at the optimum temperature. Species collected from a rock substrate are shown black; species from tall herbaceous vegetation are cross-hatched; species from grassland habitats are hatched; other species white.

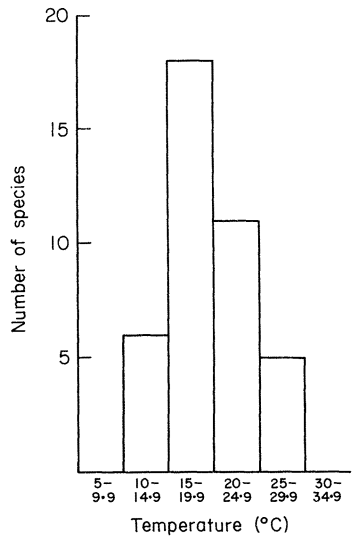


FIG. 3. Frequency distribution of forty species of bryophyte in the relative growth rate temperature optimum classes.

In each of the two experiments conducted on *Racomitrium lanuginosum* slow growth was observed over a wide range of temperatures and the optimum, although difficult to discern, appeared to lie between 10 °C and 15 °C.

DISCUSSION

Maximum relative growth rates of *Brachythecium rutabulum* and *Eurhynchium praelongum* attained in this study were 0·050 day^{-1} and 0·032 day^{-1} whereas in similar

experiments with higher nutrient concentrations (Furness 1980) growth rates of 0·071 day^{-1} and 0·039 day^{-1} respectively have been measured. Nutrient limitation, particularly of the more vigorous species, must be taken into consideration therefore in interpreting the results.

As it was not possible to grow all the species simultaneously, the results may be affected also by the time of year at which the plants were collected It is known that prevailing climatic conditions may modify the temperature response of assimilation (Harder 1925; Stålfelt 1937; Kallio & Kärenlampi 1975; Hicklenton & Oechel 1976; Collins & Callaghan 1977) and that acclimation may occur in as little as 48 h in *Dicranum fuscescens* (Hicklenton & Oechel 1976). The effect of acclimation on long-term growth of bryophytes is unknown, but the data for *Brachythecium rutabulum* in the present study suggest that the season of collection may have affected growth at low temperature, but that the temperature optimum, the rate of growth at the optimum and the high temperature tolerance were not affected. The present studies involved a 3 day cold pretreatment and a relatively long period of culture, so acclimation is unlikely to have dramatically affected the results presented here.

Temperature optima

In earlier studies of temperature-related processes in bryophytes and in higher plants much emphasis has been placed on the thermal optimum. The present study demonstrates that although there is great variation with respect to the temperature optimum for growth, from low (12–13 °C) in *Dicranella palustris* and *Racomitrium lanuginosum* to relatively high (23–26 °C) in *Bryum capillare*, *Funaria hygrometrica* and *Tortula muralis* ssp. *ruraliformis*, the optimum for the majority of species investigated occurred between 15 °C and 25 °C. A consistent feature of the results in Fig. 1 is the broad plateau of response to temperature observed in most species; over the range 10–25 °C, $\bar{\mathbf{R}}$ differs by no more than a factor of 2·0 in thirty of the forty species examined.

Although no previous estimates of growth rate are available for bryophytes grown at controlled temperatures, comparisons can be drawn with the results of short-term physiological studies of the temperature responses of photosynthesis and respiration. Optima between 15 °C and 25 °C for temperate species are in general agreement with the data of Stålfelt (1937) but are at variance with the values published by Dilks & Proctor (1975) who, in an investigation of twenty-eight species of British bryophyte, found optima for net assimilation in most species between 25 °C and 35 °C.

Rastorfer & Higinbotham (1968) and Rastorfer (1970) published similarly high temperature optima for temperate and antarctic mosses; Oechel & Collins (1976) suggested that these may be attributable to the high concentrations of carbon dioxide used during the experimental procedure. Lundegardh (1966) showed that in vascular plant species high CO_2 concentration (1·22%) raised the temperature optimum for photosynthesis 10 °C above that determined at more realistic CO_2 values (0·03%); this effect has also been reported by Bjorkman, Badger & Armond (1978).

Variations in CO_2 concentration and acclimation are just two of the factors which make temperature optima obtained by short-term measurements of assimilation difficult to interpret. Long-term growth experiments appear to present fewer problems and may provide ecologically meaningful estimations of the temperature optima and responses in bryophytes.

In general, the optima are noticeably lower than those published for vascular plant species of the Sheffield region (cf. Mahmoud 1973; Al-Mufti 1978), and are consistent

with the hypothesis that the bryophytes of temperate habitats tend to exploit the cooler conditions of spring, autumn and winter.

The effects of extreme temperature

A feature common to many of the bryophytes investigated was their ability to grow at low temperature. More than half the species investigated showed a reduction of less than 50% in $\bar{R}$ (at the optimum temperature) at 5 °C. These results suggest that growth in many bryophytes would occur at even lower temperatures, and appear to be consistent with reports of assimilation and respiration below 0 °C (Stålfelt 1937; Rastorfer & Higinbotham 1968; Ahmadjian 1970: Atanasiu 1971; Kallio & Heinonen 1973).

At the other extreme all species died at the highest temperature (35 °C) and most shoots died eventually at temperatures above 30 °C. Particularly sensitive species were *Thuidium tamariscinum*, which died after about 20 days at 29 °C, and *Chiloscyphus polyanthus*, which died within 5 days at 27 °C. Some bryophytes survive high temperatures (60–100 °C) when desiccated (Ewart 1896; Lange 1955; Norr 1974), but hydrated tissue of the same species has been shown to die at much lower temperatures (Ewart 1896; Norr 1974).

These results are consistent with the fact that, in the British Isles, bryophytes experience hot and humid conditions only briefly because high temperatures are usually associated with low relative humidity. Species living in open situations, such as exposed mountain habitats, may be subject to high temperature but under such conditions the tissues are unlikely to remain for long in the continuously hydrated state enforced in this study.

Temperature adaptation

The thermal regime of the habitats occupied by bryophytes differs with location, with season and from day to day. Environments such as tropical forests and polar regions display dramatic differences with respect to seasonal temperature range and degree of diel fluctuation. It might be expected therefore that plants from contrasting environments would demonstrate thermal adaptations. Published work seems to confirm this view; species from polar regions have low temperature optima for photosynthesis and respiration (Oechel & Collins 1976; N. J. Collins personal communication) and species from temperate regions have higher optima (Stålfelt 1937). Differences in the temperature responses of photosynthesis and respiration between alpine and forest populations of *Polytrichum juniperinum* have been reported by Bazzaz, Paolillo & Jagels (1970). Conversely, however, Kallio & Heinonen (1973) discovered little variation among populations of *Racomitrium lanuginosum* collected over a wide geographical range.

The temperature optima for growth recorded in the present study are rather lower than those described for temperate vascular plant species. This appears to be associated with the tendency for bryophytes of temperate regions to grow during seasons (spring and autumn) when moisture is most readily available, and when, coincidentally, the temperature is relatively low. It may be significant also that many species occupy microhabitats which are not exposed to direct sunlight. Many of the species collected from open habitats (e.g. *Bryum capillare*, *Ceratodon purpureus*, *Funaria hygrometrica*) do in fact have high temperature optima.

It is interesting to consider whether the results obtained in these experiments provide any evidence of a correlation between the distribution of bryophytes in Britain and their response to temperature. Dilks & Proctor (1975), in their comparative study, found 'no simple relationship between physiological temperature response and geographical

distribution'. In the present investigation two of the three species collected from sites above 300 m altitude, *Dicranella palustris* and *Racomitrium lanuginosum*, had the lowest temperature optima for growth, but the results as a whole reveal no convincing evidence of a relationship between temperature response and altitude of origin. Difficulty in relating temperature optima and field distribution is not unexpected and may be due to: (1) the microclimate experienced by a bryophyte may be very different from the gross climatic characteristics of a region and for this reason correlations based upon standard meteorological data may be misleading (Dilks & Proctor 1975); (2) success in the field may be related to effects which are relatively independent of the temperature optimum for growth, e.g. the capacity to survive or to grow rapidly (or to do both) at low temperatures; and (3) because bryophytes respond to temperature in different ways according to their degree of hydration, relationships between temperature and bryophyte growth and survival in the field are subject to the modifying effects of moisture supply.

From the present studies it would appear that plants from thermally extreme habitats, such as *Hypnum cupressiforme* and *Racomitrium lanuginosum*, exhibit growth over a wide range of temperature and are tolerant of high temperature. Conversely, species from more thermally stable habitats, e.g. *Chiloscyphus polyanthus* and *Hookeria lucens*, display narrow response curves and lower tolerance of high temperatures. There are exceptions to these generalizations, however. *Ctenidium molluscum*, for example, appears to grow over a limited range of temperature only.

Relative growth rate

No previously published accounts include mean relative growth rate data with which to compare the present work. From the limited information available in the literature it is possible to calculate the relative growth rate of only one bryophyte. A maximum for $\bar{\mathbf{R}}$ of about 0·043 day^{-1} for *Marchantia polymorpha* is calculable from the data of Schneider, Voth & Troxler (1967). Unfortunately this species was not included in the present study. The highest value of $\bar{\mathbf{R}}$ reported here (0·063 day^{-1}) for *Funaria hygrometrica*, is greater than the values published for some vascular plant species (Jarvis & Jarvis 1964; Loach 1970; Grime & Hunt 1975). However, the values attained at optimal temperature by mosses such as *Ctenidium molluscum*, *Homalothecium sericeum* and *Racomitrium lanuginosum* are considerably below the rates reported for other plants growing under controlled conditions (cf. Hunt 1978), although on the basis of their field distribution we may suspect that some lichens will have lower potential growth rates.

Bryophyte morphology and relative growth rate do not appear to be correlated; acrocarpous species included both the most rapid and the slowest-growing of the plants examined. Attempts to compare the rates of growth under an artificial controlled environment with field growth would be unwise because bryophyte growth is intermittent and highly dependent on prevailing climatic conditions; nevertheless relationships are apparent between inherent growth rates and habitat and these parallel those observed in vascular plant species (Grime & Hunt 1975). Inherently low rates of growth are associated with species from severely stressed habitats, rock outcrops and walls (*Ctenidium molluscum*, *Homalothecium sericeum*, *Hypnum cupressiforme* var. *cupressiforme*, *Racomitrium lanuginosum*). Species from relatively fertile habitats (*Brachythecium rutabulum*, *Eurhynchium praelongum*, *Plagiochila asplenioides* var. *major*) are prominent in the higher growth-rate classes.

The potential for rapid growth in bryophytes seems, therefore, to be associated with exploitation of fertile habitats. However, the two fastest growing species are quite

dissimilar in their ecology. *Brachythecium rutabulum* is a robust perennial pleurocarpous species regenerating mostly by vegetative expansion. *Funaria hygrometrica*, in contrast, is a small short-lived, often annual (Joenje & During 1977) acrocarpous species which regenerates primarily by spores. Although insufficient species with high growth rates have been investigated, these two very different mosses provide a strong parallel with the two rapid-growing groups of vascular plants defined by Grime & Hunt (1975). The ecological and evolutionary significance of this similarity of pattern in specialization will be discussed in detail elsewhere.

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