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*Brachythecium Rutabulum*

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## GROWTH RATE AND TEMPERATURE RESPONSES IN BRYOPHYTES

### I. AN INVESTIGATION OF *BRACHYTHECIUM RUTABULUM*

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#### SUMMARY

(1) The growth of the perennial pleurocarpous moss *Brachythecium rutabulum* under controlled conditions of temperature, irradiance, moisture and inorganic nutrient supply was analysed.

(2) Over a period of 30 days, the species maintained exponential growth and attained a relative growth rate of  $0.071 \text{ day}^{-1}$ —a value exceeding the reported maxima for seedlings of ten vascular plant species.

(3) In a temperature gradient, maxima in relative growth rate, shoot length and leaf area occurred at about  $19^\circ\text{C}$  but at  $5^\circ\text{C}$  the reduction in relative growth rate was less than 40%.

(4) The comparatively high relative growth rate of *B. rutabulum* is consistent with the large amplitude of seasonal change in biomass and rapid turnover of shoots observed under natural conditions. The capacity to grow at low temperature may be related to the tendency of the species to exploit the cool conditions of spring and autumn and may also explain the ability of the species to co-exist with productive vascular plants.

#### INTRODUCTION

Many species of bryophyte, including most of those which have been studied intensively, are confined to habitats which are so severe that vascular plants are largely excluded and the growth of mosses and liverworts appears to be intermittent and slow (Keever 1957; Tallis 1959a, b; Clymo 1970; Rastorfer 1970; Kallio & Heinonen 1973; Pitkin 1975). Considerably less information is available on the growth of bryophytes in communities dominated by vascular plants. In particular, the substantial moss component of many productive tall herb communities has received little attention. This neglect is surprising in view of the widespread interest in the vascular plants present in such vegetation. However, in an investigation conducted by Al-Mufti *et al.* (1977) seasonal sampling of the shoot material within several tall herbaceous communities revealed that *Brachythecium rutabulum*\* was the most abundant bryophyte, often forming a single-species mat which accounted for up to 25% of the above-ground biomass and showed a bimodal pattern of growth with peaks in spring and autumn. The abundance of the species raises questions concerning the role of bryophytes in nutrient recycling within the community and the large amplitude of the fluctuations in moss biomass also leads to speculation regarding the potential rate of growth of the species and the influence of temperature and other factors upon its periodicity.

To answer these questions it was necessary to analyse the growth of the moss in

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

controlled conditions. Temperature responses in the assimilation and respiration of bryophytes have been studied extensively (Stålfelt 1937; Romose 1940; Tallis 1964; Bazzaz, Paolillo & Jagels 1970; Rastorfer 1970; Kallio & Heinonen 1973; Dilks & Proctor 1975; Oechel & Collins 1976) but data relating to dry weight increment at a range of controlled temperatures or to the relative growth rate of bryophytes do not appear to have been published. Although cultural procedures suitable for bryophytes have been described (Richards 1947; Schelpe 1953; Ward 1960; Schneider, Voth & Troxler 1967) no consensus exists regarding the most suitable combinations of environmental factors for the growth of bryophytes. It was necessary therefore to identify cultural techniques and methods of study suitable for *B. rutabulum*. In this account we record the results of experiments designed to measure the relative growth rate of *B. rutabulum* at a range of temperatures under controlled laboratory conditions.

## MATERIALS AND METHODS

### *Plant material*

All of the shoot material of *B. rutabulum* used in the experiments was collected from within an extensive but fairly uniform stand of *Urtica dioica* (National Grid reference SK 316847) which in summer formed a canopy extending to 180 cm above the soil surface. Beneath this canopy *Brachythecium rutabulum* formed an almost continuous single-species mat over the soil and litter. The soil was dark brown and friable (pH 6–7) and the site was close to the entrance to a piece of waste land, where garden refuse has been deposited in the past.

Freshly-collected moss was brought back to the laboratory in plastic bags and stored, usually for not more than one day, in a cold room at 5 °C. Shoots cut to 2.5 cm in length and of approximately 3 mg dry weight were washed in distilled water and allocated at random to treatments. At harvest, shoots were washed carefully to remove sand grains, dried at 90 °C for 48 h and weighed individually.

### *Culture conditions*

Growth media used in previous bryophyte studies have included potting compost (Newton 1972; Longton & Greene 1979), agar (Robbins 1918; Patterson 1957; Burkholder 1959; Benson-Evans 1964), filter paper (Gemmell 1953; Oliver 1971; Longton & Greene 1979) and sand (Pfeffer 1874; Schelpe 1953; Furness & Gilbert 1980). In preliminary experiments *B. rutabulum* was grown on all four of these substrates. As explained in Furness (1980), sand was found to present few problems as a growth medium; grains adhered to the rhizoids but were easily removed by immersing the shoots in water and rubbing gently. For each experiment Silica Sand (Double Arches Pit. no. 21, Messrs. Arnold Quarries Limited, Leighton Buzzard, Bedfordshire) was:

- (1) washed through a 2 mm sieve with tap water;
- (2) treated with hydrochloric acid (Hewitt 1966);
- (3) washed with distilled water, until all traces of acid were removed; and
- (4) oven-dried at 90 °C.

The sand was distributed evenly as a 1 cm layer in Petri-dishes or in the growth chambers of a temperature gradient incubator (described later). Aliquots of inorganic nutrients were applied to the shoots at intervals of 48 h in the form of a very fine spray of dilute nutrient solution 0.01 or 0.1 full-strength Rorison nitrate solution, pH 6.0 (Hewitt 1966) delivered from a hypodermic syringe connected to an atomiser (Furness 1980). On

alternate days distilled water was applied as a fine spray until moisture was visible at the sand surface and the shoots were in capillary contact with the water. The air space above the sand was minimal (5–10 mm) in order to maintain a high relative humidity.

In preliminary experiments photobleaching was evident in the leaves of *B. rutabulum* grown at an irradiance of  $30 \text{ W m}^{-2}$ , and in experiments with *Thuidium tamariscinum* and *Eurhynchium praelongum* the effect was even more pronounced. At low irradiances ( $0.8$  and  $5.5 \text{ W m}^{-2}$ ) growth was reduced and etiolation of the stems occurred. It was decided therefore in subsequent experiments to provide irradiance of  $25 \text{ W m}^{-2}$  using warm-white fluorescent tubes.

#### *Growth-rate experiment*

In this experiment shoots were grown in Petri-dishes (five shoots per dish) in a growth cabinet providing an 18 h day at  $20^\circ\text{C}$  and a night temperature of  $15^\circ\text{C}$ . Each dish was sprayed daily to provide an aliquot of  $0.5 \text{ ml}$  of  $0.1$  full-strength Rorison nutrient solution. Initial measurements were on twenty shoots matched in size with those placed in the dishes. At intervals of 3 days further harvests were made each involving the removal of eight randomly-selected shoots from the dishes.

#### *Temperature experiment*

In order to avoid the expense and inconvenience of a series of simultaneous experiments in conventional growth rooms at different temperatures, a temperature gradient incubator was constructed. This apparatus is based upon the principle which has been used for culture of algae (Halldall & French 1958). The same apparatus has already been used in seed germination studies (Elliot & French 1959; Chatterton & Kadish 1969; Thompson & Fox 1971; Mason 1976; Grime *et al.* 1981). A similar piece of equipment was used to examine germination and shoot extension in *Tetraphis pellucida* (Forman 1964).

A diagram of the apparatus is shown in Fig. 1. The basal aluminium plate was  $100 \times 30 \times 1 \text{ cm}$ . Two reservoirs were milled from aluminium blocks ( $30 \times 10 \times 4 \text{ cm}$ ). Each had inlet and outlet nozzles attached and was bolted laterally across one end of the plate. Aluminium sides ( $100 \times 3 \times 0.4 \text{ cm}$ ) were fixed around the plate converting the upper surface into a shallow tray in which plants could be placed to grow. All internal joints were sealed with silicone rubber. Nine equidistant vertical grooves milled into the longitudinal side pieces accepted  $5 \text{ mm}$  thick Perspex partitions which effectively divided the bar laterally into ten separate growth chambers. A glass lid covered the whole apparatus. On it was placed a 'Perspex' tank filled to a depth of  $7 \text{ cm}$  with distilled water which acted as a filter for the low flux of infra-red radiation from the lights above. The water was changed once a week to prevent the accumulation of algae.

To minimize the possible effects of fluctuations in ambient air temperature the base and sides of the apparatus were insulated with  $5 \text{ cm}$  layers of expanded polystyrene and the inlet and outlet pipes with sponge rubber hose.

A gradient was maintained by circulating water through the two reservoirs by means of independent circulating units equipped with integral contact thermostats. To achieve the required  $5^\circ\text{C}$  to  $35^\circ\text{C}$  gradient at the substrate surface it was necessary to circulate water at  $4^\circ\text{C}$  and  $37^\circ\text{C}$  respectively. The circulating equipment was housed beneath the bar which stood within an enclosed reflective box. Overhead lighting was provided by a bank of fluorescent tubes controlled by a time-clock. A chart recorder connected to thermistors inserted into holes drilled into the aluminium base plate constantly monitored the thermal gradient.

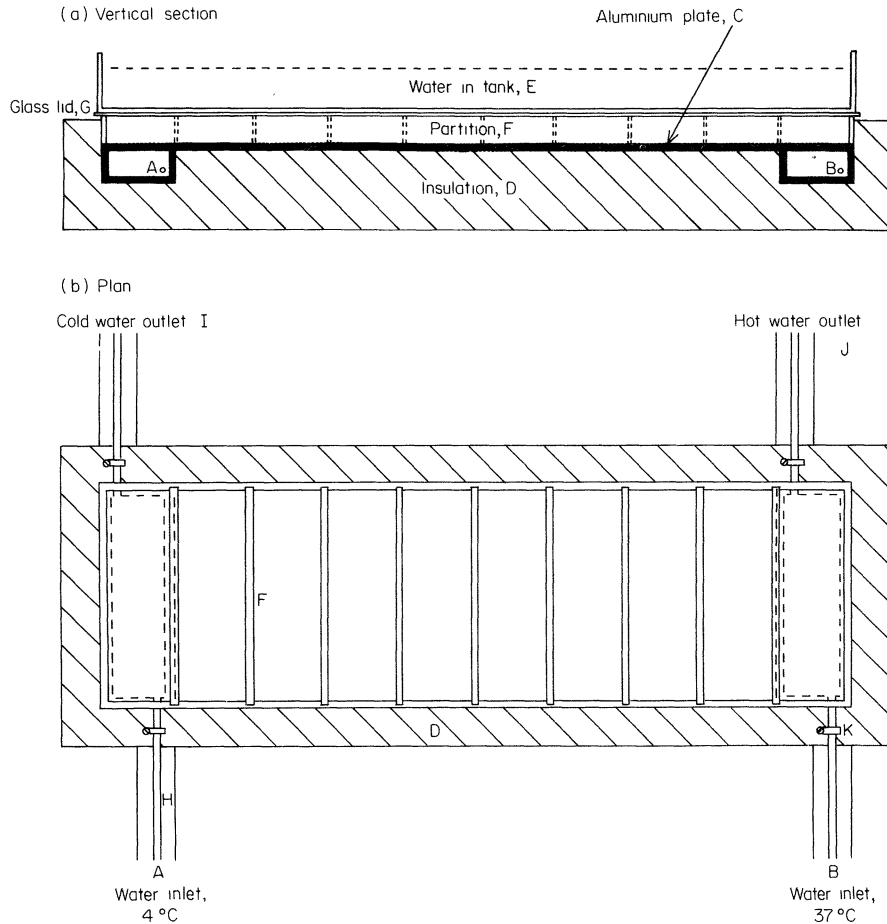


FIG. 1. Longitudinal vertical section (a) and plan (b) of the temperature-gradient bar: A, cold water (4 °C) inlet to cold reservoir; B, hot water (37 °C) inlet to heat exchange reservoir; C, aluminium plate; D, expanded polystyrene; E, Perspex tank, with 7 cm depth of water; F, Perspex partitions; G, glass lid; H, pipe insulation; I, cold water outlet; J, hot water outlet; K, pipe clamp.

Stability and accuracy of the temperature at the substrate surface was checked at intervals throughout the experimental period. These tests were conducted under normal running conditions, with temperature probes lying on the moist sand surface, and with the glass plate and water bath in position. Temperatures at three positions within each of the ten compartments were monitored throughout a full diel cycle. For most of the length there was a linear relationship between distance and temperature. Variation from the mean temperature at each position was small, particularly near the extremities. The greatest diel fluctuations (0.5 °C) occurred at approximately 15 °C.

Prior to each experiment, a 1 cm layer of silica sand was distributed evenly over the plate.

Before use in the temperature gradient apparatus, shoots of *Brachythecium rutabulum* were stored moist in sealed Petri-dishes for 3 days at 5 °C. This procedure was adopted to give the plants a standard pre-treatment.

After this, an initial harvest of twenty shoots was taken and the remaining shoots were grown for 30 days in the bryophyte compartments of the temperature gradient apparatus which at the mid-points of the ten compartments provided the following temperatures ( $^{\circ}\text{C}$ ): 5.2, 7.6, 12.2, 15.8, 19.2, 22.7, 26.5, 29.2, 32.8, 35.0. Each shoot was laid on the surface of the sand which had been previously moistened with nutrient solution. Ten replicates were planted within each of the ten compartments on the bar. After the shoots were planted they were sprayed with distilled water and the glass lid and water bath were replaced. All shoots were sprayed daily with distilled water and with nutrients on alternate days.

At final harvest the following attributes were measured: (1) length of the main stem; (2) number of lateral branches over 2 mm in length; (3) length of each lateral branch; (4) number of rhizoidal tufts; (5) shoot 'area'; and (6) total dry weight. Shoot 'area' is based upon measurements of the area of flattened shoots (i.e. silhouettes including considerable overlap of leaves) using an area meter sensing the interruption of light beams.

## RESULTS

### *Growth-rate experiment*

Shoots elongated rapidly and new branches were visible at the first harvest after 3 days. Mean dry weight per shoot increased from an initial 1.6 mg to 11.7 mg after 30 days. Growth appeared to be exponential and this was confirmed by the analysis shown in Fig. 2. A fitted linear regression (Hunt & Parsons 1974) of log dry weight on time accounted for 91% of the variability within the data. The mean relative growth rate calculated from the slope of the regression line was  $0.071 \text{ day}^{-1}$  (95% C.L.  $\pm 0.002 \text{ day}^{-1}$ ).

From Fig. 2 it is clear that over the whole period studied growth was exponential and the relative growth rate remained nearly constant. The results of this analysis suggest that a mean relative growth rate,  $\bar{R}$ , calculated from an initial and final harvest would probably represent an accurate estimate of the growth rate and we used this assumption in the temperature experiment. There is no sign that the pretreatment (cutting, washing) had a significant effect on subsequent growth. The rapid growth observed in culture is consistent with the amplitude of the fluctuations in biomass described by Al-Mufti *et al.* (1977).

### *Temperature experiment*

The main features of the results are presented in Fig. 3 (and in Furness (1980)). With the exception of shoot 'area', which was plotted as an absolute value and not as an increment, the curves showed sharp peaks. The optimum temperature for the rates of dry matter production, elongation of the main stem, total stem elongation and shoot 'area' occurred at approximately  $19^{\circ}\text{C}$ . The maximum relative growth rate attained in this experiment was  $0.050 \text{ day}^{-1}$ . The main stem increased in length six-fold, extending 120 mm in 30 days. All shoots cultured above  $30^{\circ}\text{C}$  eventually died and those at  $35^{\circ}\text{C}$  died within 5 days. At  $5^{\circ}\text{C}$ , however, there was substantial accumulation of dry weight. The maximum rate of production of lateral branches and rhizoids was at temperatures lower than those at which peaks occurred for the other variables. The greatest rate of rhizoid tuft production was found on shoots cultured at about  $12^{\circ}\text{C}$  and that of lateral branches at about  $16^{\circ}\text{C}$ .

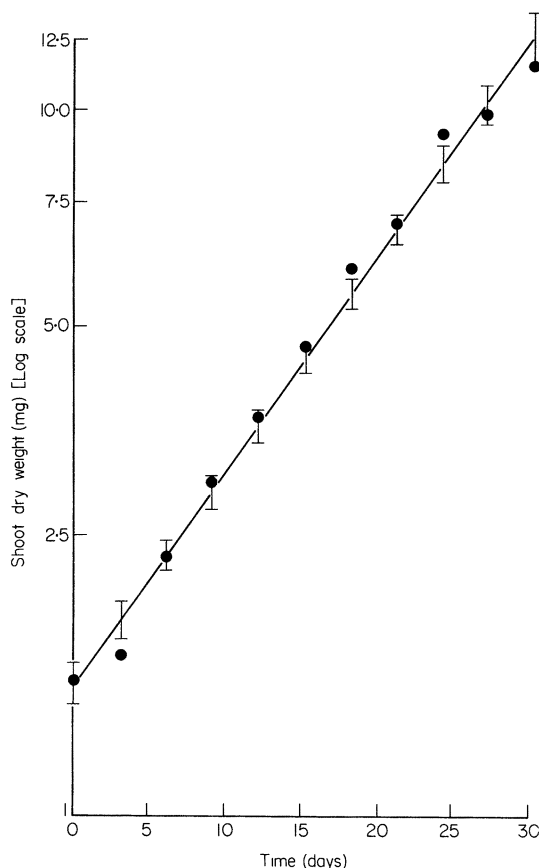


FIG. 2. Accumulation of dry-weight with time by *Brachythecium rutabulum*. The regression line is that fitted using the Hunt & Parsons (1974) growth analysis program. Bars represent 95% confidence intervals.

## DISCUSSION

The results in Fig. 2 illustrate the capacity of *Brachythecium rutabulum* for sustained and rapid dry matter production and provide a marked contrast with those obtained for slow-growing species (e.g. Keever 1957; Tallis 1957, 1959a). It is also interesting to note that the mean relative growth rate recorded here for *B. rutabulum* ( $0.071 \text{ day}^{-1}$ ) exceeded those estimated for seedling trees (*Acer pseudoplatanus* (0.049), *Fraxinus excelsior* (0.069), *Picea abies* (0.060), *Pinus nigra* (0.047), *P. sitchensis* (0.031), *P. sylvestris* (0.051)) and slower-growing herbs and shrubs (*Calluna vulgaris* (0.050), *Lathyrus montanus* (0.066), *Sanicula europaea* (0.067), *Vaccinium vitis-idaea* (0.033)) by Grime & Hunt (1975) in a comparative study of growth of vascular plant species.

The potentially rapid relative growth rate of *Brachythecium rutabulum* is consistent with the marked seasonal changes in biomass recorded for the species (Al-Mufti *et al.* 1977) in the field. It seems possible also that the capacity for rapid growth may allow the species to exploit favourable conditions of temperature, irradiance and moisture supply when these occur for short periods during the autumn, winter and early spring. This in turn may explain the capacity of *B. rutabulum* to co-exist with potentially productive vascular

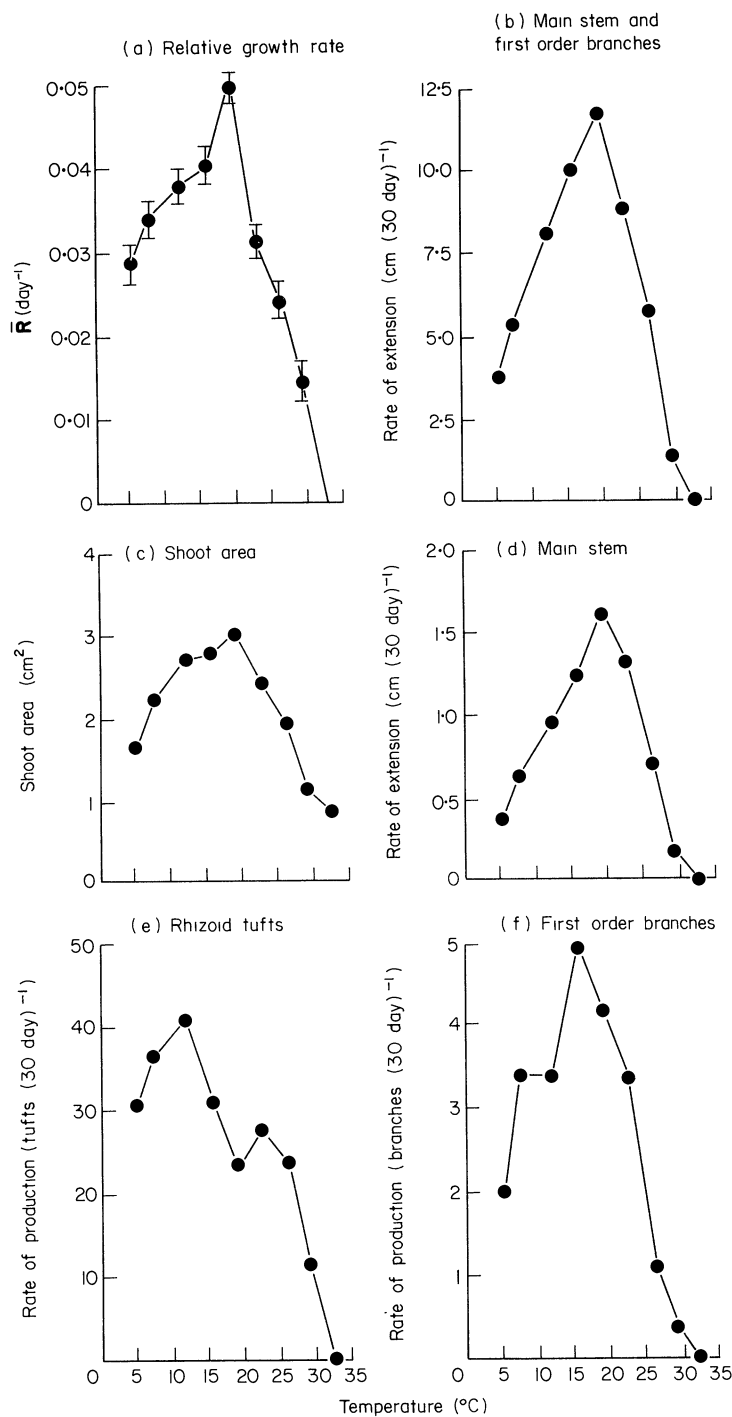


FIG. 3. Effects of temperature on *Brachythecium rutabulum* shoots cultured for 30 days on the temperature-gradient bar: (a) mean relative growth rate,  $\bar{R}$ ; (b) mean rate of extension of main stem and first order lateral branches; (c) mean shoot area; (d) mean rate of extension of main stem; (e) rate of production of rhizoid tufts; (f) mean rate of production of first order branches.



plants in habitats such as lawns, woodland clearings and wasteland dominated by various types of tall herbs.

The temperature optimum for relative growth rate is significantly lower in *B. rutabulum* than in the tall herb *Urtica dioica* with which it is strongly associated in the field (Fig. 4). This difference is consistent with the observed patterns of seasonal shoot expansion within these communities (Al-Mufti *et al.* 1977), the growth of *Brachythecium rutabulum* occurring during spring and autumn and that of *Urtica dioica* during early summer. It is also interesting to note that in contrast with the vascular species, considerable growth of *Brachythecium rutabulum* occurred at 5 °C. In the experiment described in this paper the maximum growth rate achieved by the moss is almost a third of that achieved by *Urtica dioica*, which is one of the most rapid growing of native vascular species.

Although the maximum rate of increase of dry weight, shoot length (main stem and total) and shoot 'area' occurred at the same temperature (19 °C), these variables showed different patterns of response to temperature. At low temperature the shoots were compact

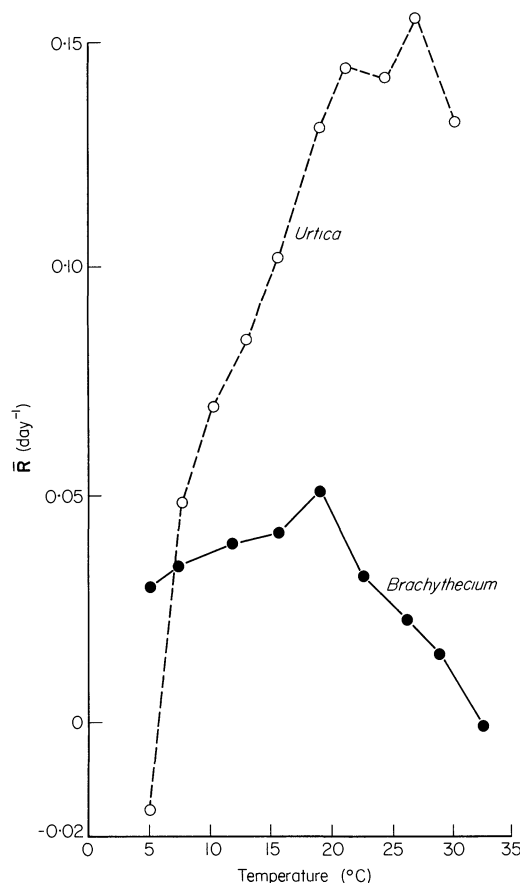


FIG. 4. Comparison of the response of mean relative growth rate,  $\bar{R}$ , to temperature in the tall herb *Urtica dioica* (Al-Mufti 1978) and the moss *Brachythecium rutabulum* (this paper). Measurements on both species were made under an irradiance of 25 W m<sup>-2</sup> (16 h for *Urtica dioica*, 12 h for *Brachythecium rutabulum*).

with overlapping leaves, whilst at high temperature the shoots appeared etiolated, and resembled those grown at low light flux. This plasticity within *Brachythecium rutabulum* populations has been noted before (Wigh 1975) and raises questions about the validity of the use of measurements of shoot length as a measure of performance in bryophytes. In previous studies, stem elongation has been the most widely used variable with which to assess the growth of bryophytes both in the laboratory and the field. If dry matter accumulation is considered the best criterion with which to judge a plant's performance then (at least in *B. rutabulum* and in *Sphagnum* species (Clymo 1970)) measurements of shoot extension do not appear to reflect this accurately, particularly if comparisons between populations in different environments are involved.

Observations of *Brachythecium rutabulum* in a range of habitats in the Sheffield region have revealed that it is most frequently associated with mesic conditions and is especially vigorous and abundant in productive tall herbaceous vegetation. In five tall herb communities in the Sheffield area *B. rutabulum* accounted for between 10% and 30% of the above-ground biomass (Al-Mufti *et al.* 1977; Al-Mashhadani 1980). At one site the maximum summer standing crop of *Urtica dioica* was about 500 g m<sup>-2</sup> compared with a biomass of 150 g m<sup>-2</sup> for *Brachythecium rutabulum*. It is commonly the case that *B. rutabulum* is the only species in the understorey and is characteristically in close association with herbaceous stem litter. Observation of nettle patches reveals that each autumn freshly fallen herbaceous stem litter of *Urtica dioica* is rapidly overgrown by the shoots of *Brachythecium rutabulum*. Rhizoids penetrate the litter, and shoots attached to the litter appear to be considerably more robust than material growing on adjacent soil. A higher rate of growth in response to the presence of litter has also been observed in the laboratory (van de Dijk 1977). Although the precise nature of this effect is not fully understood it seems likely that the moss is intercepting nutrients during the microbial decay of the litter; this hypothesis is of particular interest in view of the capacity of *B. rutabulum* for rapid growth in the field. An additional benefit from this association may be derived from the water-holding capacity of the stem litter.

In tall-herb communities exploited by *B. rutabulum*, the dominant herbs attain peak biomass in mid-summer, corresponding with maxima in day length, irradiance and temperature, followed by a rapid decline accelerated by autumn frosts. In contrast, *B. rutabulum* exhibits a complementary phenology with spring and autumn peaks of biomass coinciding with the cool moist conditions at the time of year when maximum light reaches the moss layer due to the absence of a herbaceous canopy (Al-Mufti *et al.* 1977). The timing and amplitude of the fluctuations of living bryophyte material in these communities are consistent with the relatively rapid growth of *B. rutabulum* at low (<10 °C) temperatures and the optimum temperature for growth which is 8 °C lower than that of *Urtica dioica*. The data obtained from the field and from growth studies at various temperatures in the laboratory suggest that the co-existence of *U. dioica* and *Brachythecium rutabulum* may be related at least in part to the complementary phenologies and temperature responses of the two species.

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