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Rietema, H

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Effects of Photoperiod and Temperature on Macrothallus Initiation in *Dumontia contorta* (Rhodophyta)

H. Rietema

Department of Systematic Botany, Biological Centre, University of Groningen, P.O. Box 14, 9750 AA Haren (Gr.), The Netherlands

ABSTRACT: Gametophytic and sporophytic microthalli of *Dumontia contorta* from Isle of Man appear to persist indefinitely in the vegetative state at photoperiods of 14 h and longer, but form erect, branched, tubular macrothalli at photoperiods of 12 h or less. Responses of microthalli kept under different daylengths at 2,000 lux, and those of microthalli kept under daylength-adjusted light intensities, giving equal daily light doses, did not differ from one another. The critical daylength for this short-day response is approximately 12 h. The response to short-day conditions was inhibited by a short white night-break of 0.25 h given in the middle of a 16 h dark period, irrespective of light intensity (2,000 or 180 lux); this suggests a genuine photoperiodic response as known from flowering plants. However, a relatively large number of short-day cycles (at least 31) are required to produce some effect. Macrothalli formation involves 2 separate steps. The first step (induction of macrothallus initials) depends entirely on daylength, the second (development of initials into macrothalli) on both daylength and temperature. This was deduced from the fact that macrothallus initials were formed under short-day conditions irrespective of temperature (4 to 24°), whereas macrothalli were formed from initials under short-day conditions but only at temperatures of 16° (critical temperature) or lower. At 26° microthalli died gradually. Like microthalli, macrothalli grow optimally at 16 to 18°. It follows, therefore, that macrothalli cannot be expected to grow from macrothallus initials above 16° and under short-day conditions, since elongation of short cells in the filaments of macrothallus initials (start of macrothallus growth) would be blocked. Elongation of these cells was probably also blocked by long-day conditions because macrothallus initials did not grow out after transfer of microthalli from short-day to long-day conditions at 12°

INTRODUCTION

The life history of the marine red alga *Dumontia contorta* (Dumontiaceae, Cryptonemiales) comprises isomorphic gametophytic and sporophytic phases. Carpospores and tetraspores produced by the gametophytic phase and sporophytic phase respectively, grow into crustose discs (microthalli) from which later tubular, branched, erect thalli (macrothalli) arise. The results of previous investigations on gametophytic plants indicate that the development of macrothalli from microthalli is affected by daylength and temperature (Rietema and Klein, 1981). Macrothalli sprouted from microthalli under short-day conditions and lower temperatures only. Under long-day conditions and higher temperatures the microthalli continued to grow as crusts. The development of macrothalli from crus-

tose microthalli of the brown alga *Petalonia fascia* and *Scytosiphon lomentaria* is influenced by temperature and daylength in the same way (Wynne, 1969; Roeleveld et al., 1974; Dring and Lüning, 1975; Nakamura and Tatawaki, 1975). In *Scytosiphon lomentaria* the photoperiodic response is a genuine photoperiodic short-day response of the type characteristic of flowering plants (Dring and Lüning, 1975). The characteristics of such a response are: (1) The plants show a response if the daylength does not exceed a critical day-length; (2) the short-day response is inhibited if a short night-break is given in the middle of a relatively long dark period; (3) the plants can be induced by a relatively short exposure to short-day conditions; after transfer into non-inductive daylength conditions they still remain in the induced state (Terborgh and Thimann, 1964; Vince-Prue, 1975). The pre-

sent investigation analyses in greater detail the influence of photoperiod and temperature on the formation of macrothalli from microthalli in both *Dumontia* gametophytes and sporophytes.

MATERIAL AND METHODS

Unialgal cultures of *Dumontia contorta* were established from spores released by plants collected on the Isle of Man (1979). The present experiments were conducted with spores released by cultured plants using techniques described previously (Rietema and Klein, 1981). Briefly these consisted of collecting released spores allowed to settle on glass squares cut from microscope slides. Glass squares with growing spores were kept separately for 5 wk at 12°, long-day conditions (16:8) and 2,000 lux in Petridishes (diameter 5 cm; 4 cm high) filled with enriched seawater (Provasoli, 1968) and transferred thereafter to experimental conditions (Figs. 1, 4, 5, 6) as mentioned otherwise. The culture fluid was renewed every fortnight. The number of microthalli per glass square in these experiments varied from ca. 10 to 35, and the number of microthalli exposed to each set of conditions amounted to 100 or more. Glass squares seeded too densely with spores were thinned out to avoid crowding when the microthallus discs were formed.

All experiments were done in culture cabinets (Fridina) with different temperature and daylength regimes. Light was emitted by white fluorescent tubes (Philips TL W/34; White de Luxe) and microthalli were kept at 2,000 lux and constant light doses so that the amount of light (= photometer reading [lux] × photoperiod [h]) in any 24 h period was constant. This value amounted to 16,000 lux h. Only at photoperiods of 2 and 2.5 h was this daily light dose somewhat lower. Temperature fluctuations in all experiments remained within 1.0°C, and all light values were ± 5%.

To test the effect of a night-break treatment the dark period of 8:16 photoperiod was interrupted in the middle by a white light night-break of 0.25 h. This light night-break had the same light intensity of 2,000 lux as the main photoperiod, or a lower intensity.

RESULTS

Effects of Photoperiod and Temperature on Development of Discoid Gametophytic Microthalli

Results of experiments with discoid microthalli obtained from tetraspores and kept at 9 different photoperiods are given in Fig. 1. Macrothallus development occurred only under short-day conditions

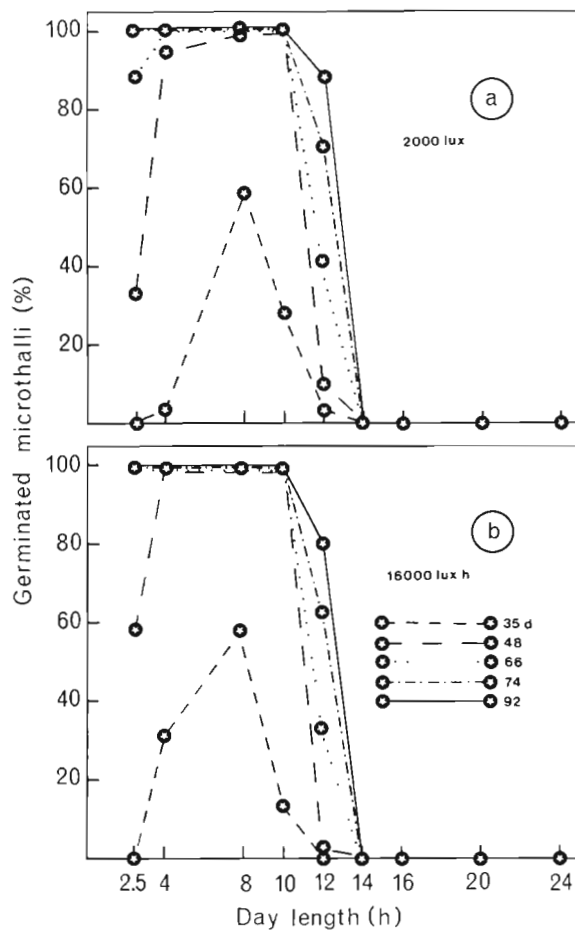


Fig. 1. *Dumontia contorta*. Development of 5 wk old discoid, gametophytic microthalli at different daylengths and 12°. Percentages of microthalli ($n \geq 100$) with macrothalli after 35, 48, 66, 74 and 92 d, exposed to 2,000 lux (a) and to equal daily light doses (b)

(4:20; 8:16; 10:14) in smaller numbers after a longer period of observation also at the intermediate daylength condition (12:12) and at a photoperiod of 2.5:21.5. In these respects microthalli kept at a light intensity of 2,000 lux (Fig. 1a) did not differ from those kept at daylength-adjusted light intensities (Fig. 1b).

Qualitative differences between discoid microthalli kept for 10 wk under long- and short-day conditions are shown in Fig. 2.

Macrothalli on 8-wk old microthalli kept at a photoperiod of 4 h, 2,000 lux and 12° were cut off from their microthalli which were subsequently exposed to 16°, long-day conditions and 2,000 lux (i.e. summer-like conditions). No new macrothallus development occurred in these conditions within 12 wk. Microthalli transferred thereafter into 12°, short-day conditions developed macrothalli within 6 wk, however, microthalli transferred into 12°, long-day conditions remained crustose (Fig. 3).

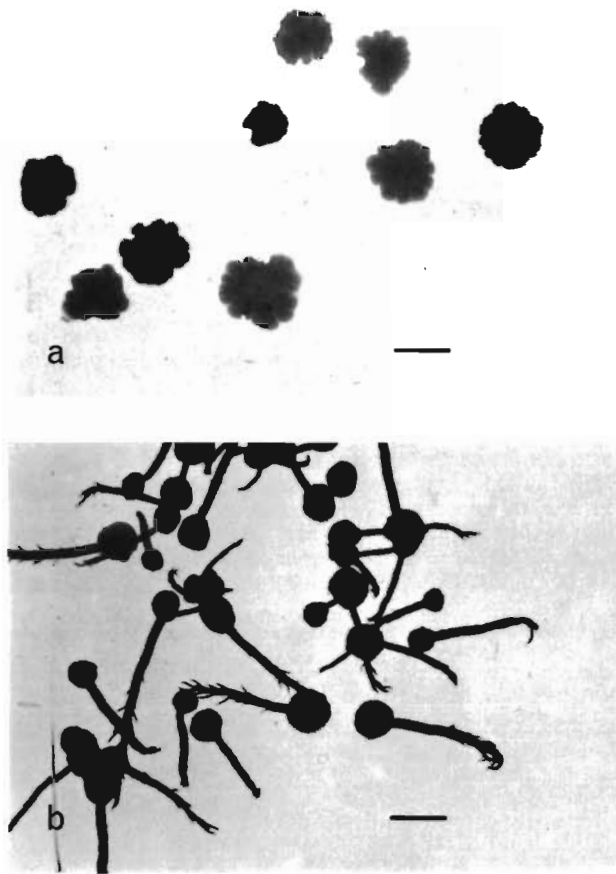


Fig. 2. *Dumontia contorta*. Photographs of cultures kept for 8 wk under long-day (16:8), 2,000 lux and 12° conditions (a) and short-day (8:16), 2,000 lux and 12° conditions (b). Scale bars = 2 mm

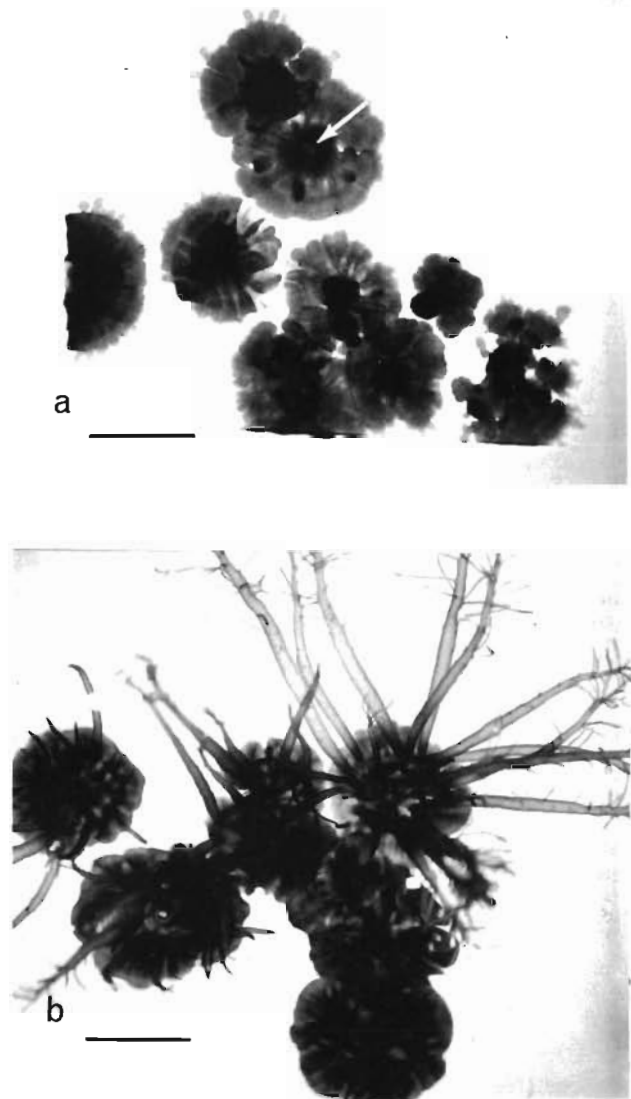


Fig. 3. *Dumontia contorta*. Photographs of cultures kept 10 wk under long-day (16:8), 2,000 lux and 12° (a) and short-day (8:16) 2,000 lux and 12° (b). Pre-cultured 8 wk under short-day, 12° conditions (after which macrothalli were cut from microthalli), subsequently 12 wk under long-day, 16° conditions (= summer-like conditions). Arrow: scars of cut off macrothalli. Scale bars = 5 mm

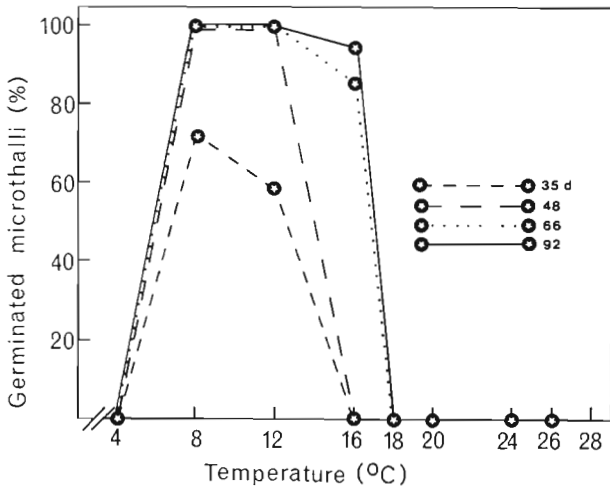


Fig. 4. *Dumontia contorta*. Development of 5 wk old discoid, gametophytic microthalli; various temperatures, short-day (8:16), 2,000 lux. Percentages of microthalli (n ≥ 100) with macrothalli after 35, 48, 66 and 92 d

The results of experiments with microthalli kept at 8 different temperature regimes (Fig. 4) show that macrothallus development occurred at 8 and 12°, after a longer period also at 16°. No macrothallus development occurred at the lowest temperature (4°) and the higher temperatures (18, 20 and 24°) investigated. At 26° the microthalli died gradually. Macrothallus initials visible as light coloured spots were formed under the same range of conditions as those on sporophytic microthalli (see below).

Effects of Photoperiod and Temperature on the Development of Discoid Sporophytic Microthalli

The results of experiments with discoid microthalli grown from carpospores kept at 8 different photoperiods are given in Fig. 5. Macrothallus development occurred either under short-day conditions (2:22; 4:20; 8:16) or, in small numbers, after a longer period under the intermediate daylength condition (12:12). In these respects microthalli kept at a light intensity of 2,000 lux (Fig. 5a) did not differ from those kept at the daylength-adjusted light intensities (Fig. 5b). No macrothalli sprouted from microthalli kept at a photoperiod of 2 h and 2,000 lux, the daily light dose apparently being too low for sufficient photosynthesis.

The results of experiments with microthalli kept at 8 different temperature regimes are illustrated in Fig. 6. This figure shows that macrothallus development occurred at 4, 8, 12 and 16°. The optimum temperature

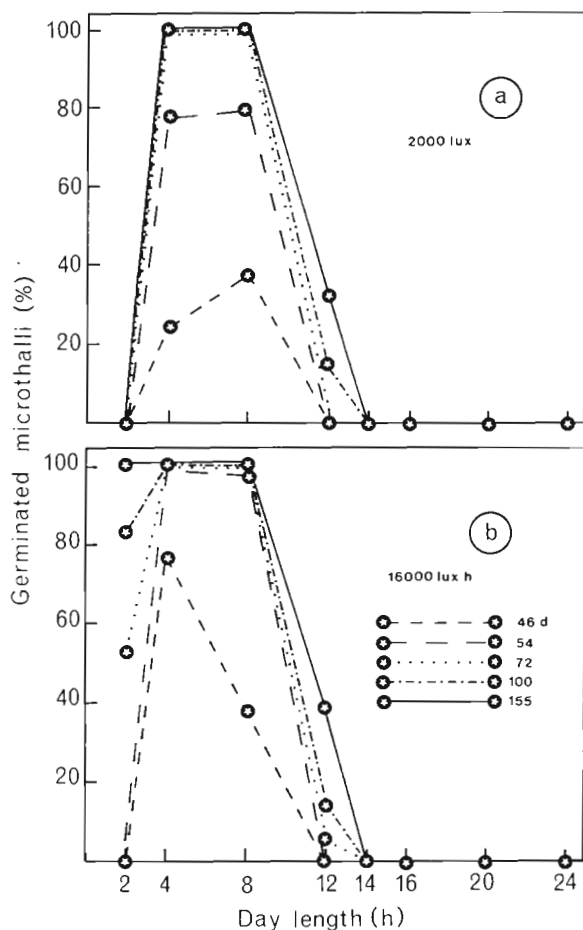


Fig. 5. *Dumontia contorta*. Development of 5 wk old discoid, sporophytic microthalli at different daylengths. Percentages of microthalli ($n \geq 100$) with macrothalli after 46, 54, 72, 100 and 155 d and exposed to 2,000 lux (a) and to equal daily light doses (b)

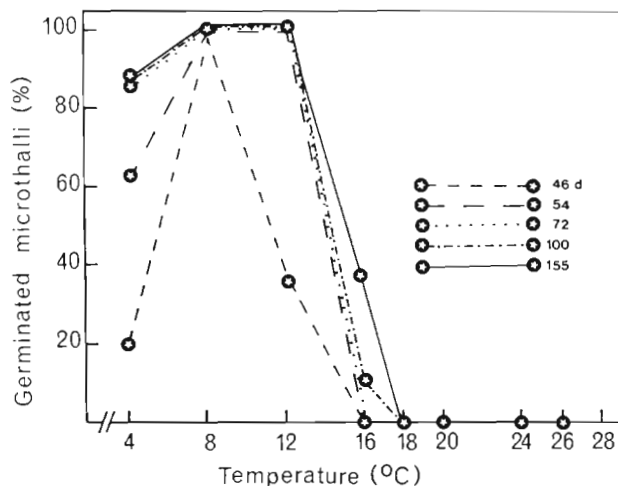


Fig. 6. *Dumontia contorta*. Development of 5 wk old discoid, sporophytic microthalli; various temperatures, short-day (8:16), 2,000 lux. Percentages of microthalli ($n \geq 100$) with macrothalli after 46, 54, 72, 100 and 155 d

range for the initiation of macrothalli from microthalli was 8 to 12°.

Appearance of macrothalli was always preceded by the appearance of light-coloured spots which represented initial stages of macrothalli (cf. Rietema and Klein, 1981; Fig. 7). Although under intermediate daylength conditions only a small number of microthalli germinated into macrothalli, all microthalli bore one to several light coloured spots 76 d after the start of the experiment. Sometimes light-coloured spots occurred at a photoperiod of 14 h but under this daylength regime never developed into macrothalli. These macrothallus initials did not occur on microthalli kept at a photoperiod of 16 h or longer.

All microthalli kept at 18° and 20° and short-day conditions (8:16) bore 76 d after the start of the experiment, one to several macrothallus initials; some were also observed at 24°. However, microthalli kept at these temperature regimes never developed macrothalli. Transverse sections through discs with light-coloured spots (macrothallus initials) showed that these were composed of bundles of erect filaments consisting of short cells (Fig. 8).

Transfer of Sporophytic Microthalli from Short-Day Conditions into Long-Day Conditions

In order to determine the number of short-day cycles sufficient for the initiation of macrothalli a large number of 5-wk old microthalli were kept for a varying number of days under short-day conditions (8:16), 2,000 lux and after that they were transferred to long-day conditions (16:8), 2,000 lux in portions of about 90

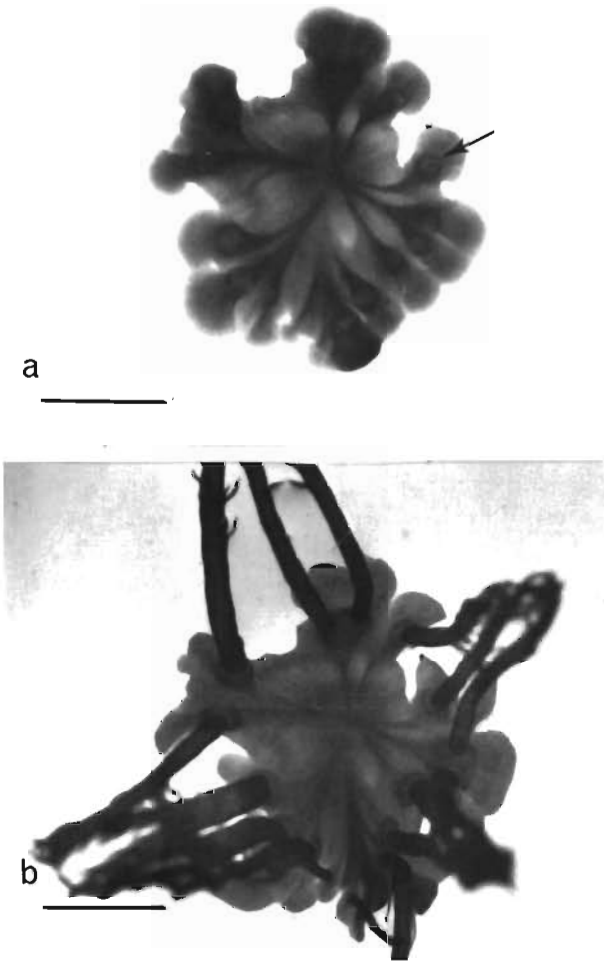


Fig. 7. *Dumontia contorta*. Microthallus grown in culture; 12°, short-day. (a) Microthallus with macrothallus initials visible as light-coloured spots. Arrow: incipient macrothallus. (b) Same microthallus 6 wk later. Scale bars = 2.5 mm

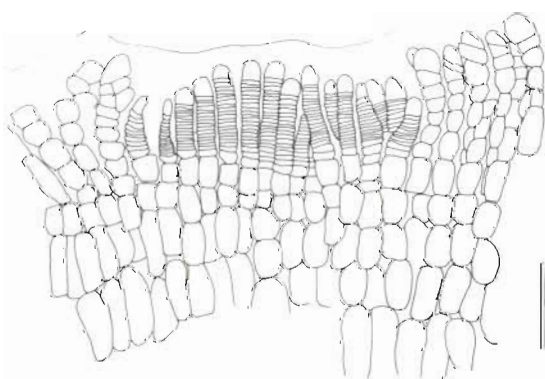


Fig. 8. *Dumontia contorta*. Section through disc (12°, short-day) with macrothallus initial (visible as light-coloured spot), composed of several primordia of axial filaments consisting of short cells. Scale bar = 50 µm

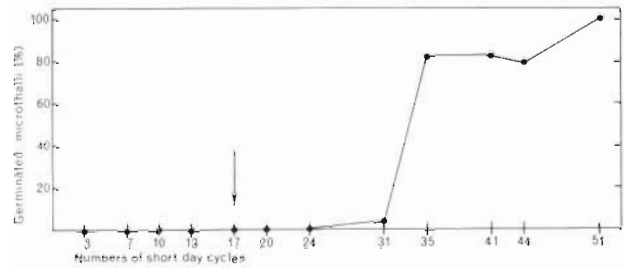


Fig. 9. *Dumontia contorta*. Sporophytic microthalli kept for a varying number of days under short-day (8:16), 2,000 lux, 12° conditions and subsequently transferred into long-day, 2,000 lux and 12° conditions. Percentages: microthalli germinated into macrothalli 51 d after start of experiment. Arrow: time when first macrothallus initials were observed

microthalli in a large Petridish (diameter 10 cm). The number of germinated microthalli in each culture was determined 51 d after start of the experiment. The results (Fig. 9) show that at least 31 short-day cycles were required to bring about some effect.

Transfer of Sporophytic Microthalli from Intermediate into Short- and Long-Day Conditions

Microthalli kept for 100 d under intermediate day-lengths (12:12), 12° were transferred to short (8:16) and long daylength (16:8) conditions, 12° or were kept as a control under the intermediate daylength conditions, 2,000 lux. Eight to 10 microthalli were kept under each experimental condition. At the moment of transfer the average number of macrothallus initials per microthallus (light spots) amounted to 7. The results (Fig. 10) indicate no macrothallus development at all from microthalli under long daylength (Fig. 10A), a large increase of the average number of macrothalli per microthallus under short daylength (Fig. 10B), and a very slight increase under intermediate daylength (Fig. 10C) conditions. In the course of the experiment the average number of macrothallus initials decreased distinctly under short daylength and this occurred also under long daylength where the macrothallus initials vanished. Under intermediate daylength the number of initials amounted constantly to about 7 per microthallus.

Of the microthalli transferred into short-day conditions, the initials – laying in a concentric ring near the centre and formed under intermediate-day conditions – developed into macrothalli.

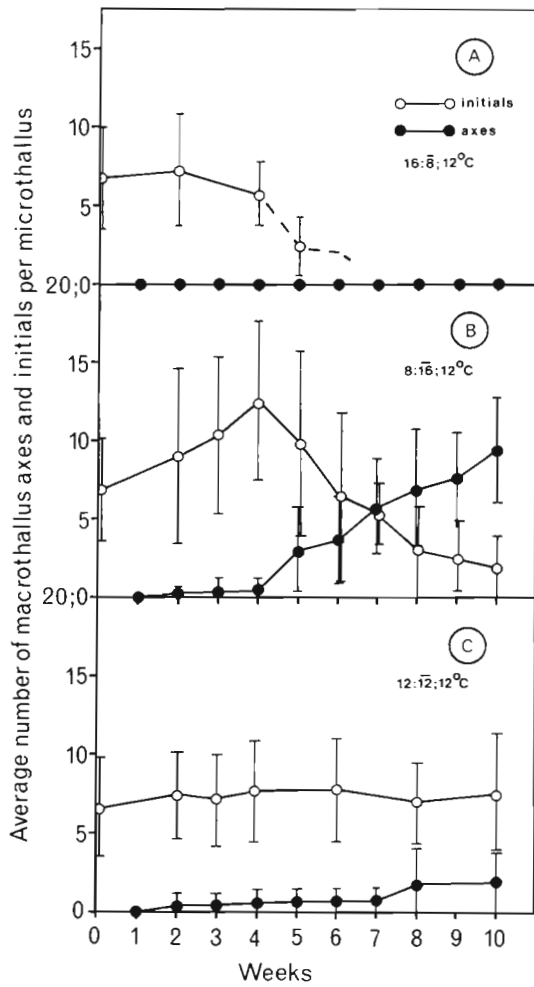


Fig. 10. *Dumontia contorta*. Production of macrothalli from macrothallus initials formed on microthalli pre-cultured for 100 d (intermediate daylength, 2,000 lux, 12°) subsequently transferred to long-day conditions (A), short-day conditions (B) or kept as control under intermediate daylength conditions (C), all at 2,000 lux and 12°. Open circles: average number of macrothallus initials per microthallus. Closed circles: ditto for macrothallus axes. Vertical bars: standard deviation. Number of microthalli per condition: ca. 8. Broken line: period of infrequent observations when the initials vanished

Transfer of Sporophytic Microthalli from Higher to Lower Temperatures

Microthalli kept for 86 d under 16°, short-day conditions (8:16) were transferred to 12°, short-day (8:16) or long-day (16:8) conditions, 2,000 lux or were kept as a control under 16° short-day conditions, 2,000 lux. Eight to 10 microthalli were kept under each condition. At the moment of transfer the average number of macrothallus initials per microthallus was about 10. The results are given in Fig. 11. Macrothallus initials on the microthalli transferred to 12° long-day conditions (Fig. 11A) gradually vanished. The difference between pre-

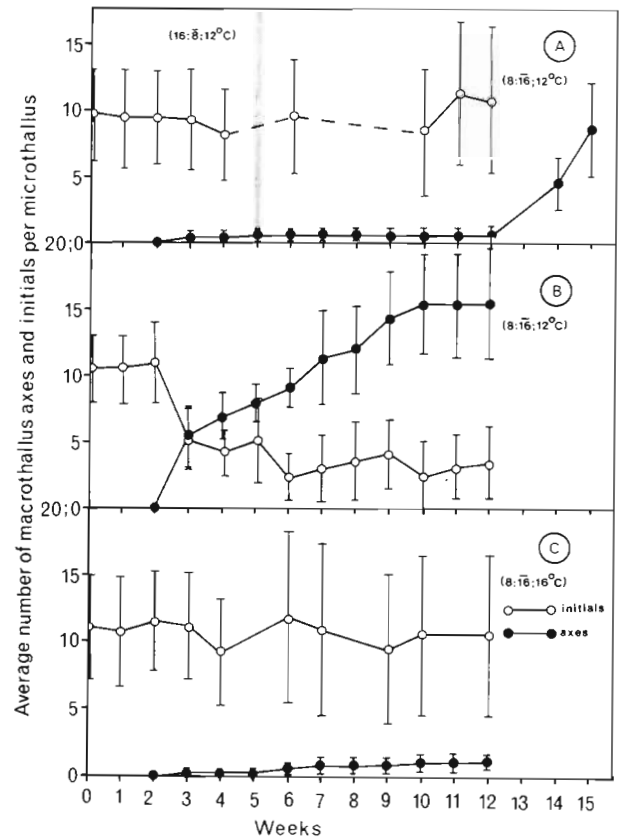


Fig. 11. *Dumontia contorta*. Production of macrothalli from macrothallus initials formed on microthalli pre-cultured for 86 d; first 16° short-day, 2,000 lux, then transferred to 12°, long-day conditions for 5 wk, and finally into 12°, short-day conditions (A), 12°, short-day conditions (B), or kept as control under 16°, short-day conditions (C), all at 2,000 lux. Open circles: average number of macrothallus initials per microthallus. Closed circles: ditto for macrothallus axes. Vertical bars: standard deviation. Number of microthalli per condition: ca. 10

sence (as a diminutive spot) and absence of an initial is often difficult to determine. Therefore between the 4th and 10th wk after start of the experiment the initials were not counted regularly. However, the initials reappeared on exactly their original locations after transfer of these microthalli into 12° short-day conditions (which occurred after the 5th wk) and subsequently developed into macrothalli. The results also indicate a distinct increase of the average number of macrothalli on microthalli transferred directly after start of the experiment into 12°, short-day conditions, whereas the average number of macrothallus initials per microthallus decreased (Fig. 11B). Under 16°, short-day conditions the average number of macrothalli and macrothallus initials per microthallus changed only slightly (Fig. 11C).

Macrothallus initials on microthalli kept under 18° and 20° short-day conditions also grew into macrothalli after transfer of microthalli to 12°, short-day conditions.

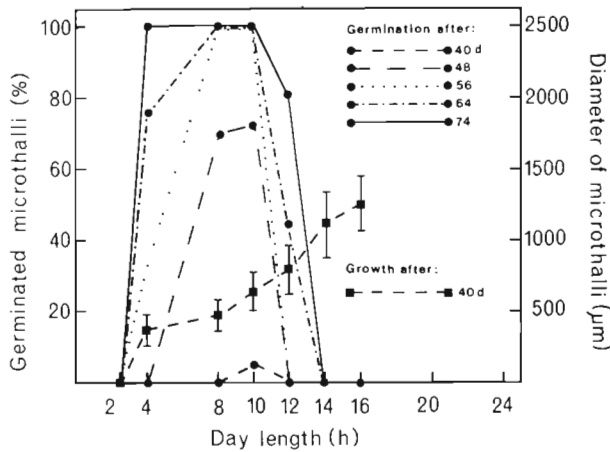


Fig. 12. *Dumontia contorta*. Germination rate (percentages of microthalli with macrothalli) and growth rate of microthalli (as diameter) grown from tetraspores transferred directly after release into different daylength regimes; 2,000 lux, 12°. Percentages of microthalli (n > 50) with macrothalli after 40, 48, 56, 64 and 74 d (circles) and average diameter of microthalli (squares) after 40 d. Vertical bars: standard deviation

Effect of Photoperiod and Temperature on Growth Rates of Microthalli

The influence of photoperiod on growth rates of microthalli was investigated by transferring tetraspores directly after release into the varying daylength regimes (Fig. 12). Growth rates of microthalli were determined by measuring their diameter. The results ((Fig. 12) suggest that growth rates of microthalli

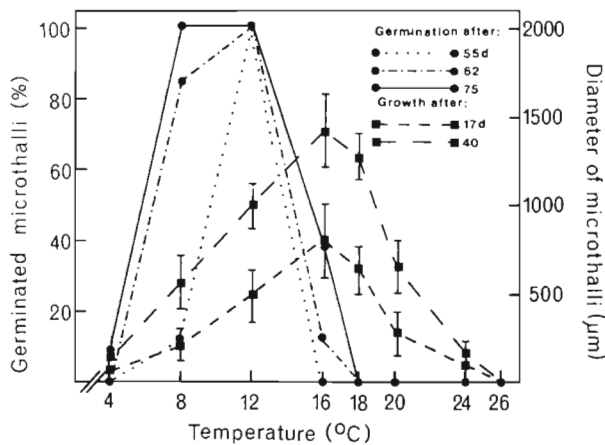


Fig. 13. *Dumontia contorta*. Germination rate (percentages of microthalli with macrothalli) and growth rate of microthalli (as diameter) grown from tetraspores transferred directly after release into different temperature regimes and short-day conditions (8:16). Percentage of microthalli (n > 50) with macrothalli after 55, 62 and 75 d (circles) and average diameter of microthalli (squares) after 17 and 40 d. Vertical bars: standard deviation

increased with increasing daylength. The largest microthalli were obtained under the longest daylength regimes investigated (14:10; 16:8). Under these regimes macrothalli did not develop at all.

Macrothalli only sprouted from the smaller microthalli grown under short-day conditions (4:20; 8:16; 10:14) and, after a longer period of observation, also under the intermediate daylength condition (12:12).

The influence of temperature on the growth rate of microthalli was investigated by transferring tetraspores almost directly after release into the different temperature regimes (Fig. 13). The results suggest an optimum temperature for microthallus growth of 16 to 18° and an optimum temperature of 8 to 12° for the development of microthalli to macrothalli. No macrothallus development occurred at either the lowest temperature (4°) or the higher temperatures (18, 20, 24°) investigated. At 26° the spores died. Also in this experiment macrothallus initials were formed on all microthalli kept at 18 and 20°.

Effect of Temperature on Growth Rates of Macrothalli

The influence of temperature on the growth rates of macrothalli was investigated by exposing 15 small macrothalli – of about equal size and cut from microthalli – to 8, 12, 16, 18 and 20° long-day conditions and 2,000 lux. Growth was measured as fresh and dry weight after 70 d. The results (Table 1) indicate

Table 1. *Dumontia contorta*. Fresh and dry weight of 15 macrothalli of about the same age and size, kept for 70 d under 20, 18, 16, 12 and 8°C, long-day, 2000 lux conditions

Temperature (°C)	Fresh weight (mg)	Dry weight (mg)
20	414.2	61.1*
18	754.0	79.0*
16	614.7	84.0*
12	291.6	59.3
8	361.1	52.8

* Fertile plants

optimum growth at 16 and 18°. Fertile plants were observed at 20, 18 and 16° but not at the lower temperatures.

Effect of Night-Break Treatment on the Development of Microthalli into Macrothalli

The results of a short night-break treatment given in the middle of a 16 h dark period with white light, on

Table 2. *Dumontia contorta*. Effect of night-break on the development of macrothalli from 5 wk old gametophytic microthalli

Main photoperiod (h)	Night-break treatment (h)	(specification)	% germinated microthalli after			
			40 d	56 d	74 d	92 d
16	--	--	0	0	0	0
8	--	--	93	100	100	100
8	0.25	2000 lux	0	0	0*	0*

* About 50 % of the microthalli bear macrothalli initials

Table 3. *Dumontia contorta*. Effect of night-break on development of macrothalli from 5 wk old sporophytic microthalli

Main photoperiod (h)	Night-break treatment (h)	(specification)	% germinated microthalli after			
			36 d	44 d	54 d	100 d
16	--	--	0	0	0	0
8	--	--	57.4	100	100	100
8	0.25	1500 lux	0	0	0	0
8	0.25	180 lux	0	0	0	0

the growth of macrothalli from microthalli is shown in Tables 2 and 3. Night-break treatments of 0.25 h with white light, suppressed the development of macrothalli and usually had the same effect as a long-day treatment. However, on some microthalli light coloured spots were observed and cross sections revealed initial stages of macrothalli. Such light coloured spots did not occur under long-day conditions so that a white night-break treatment did not precisely simulate long-day conditions.

DISCUSSION

Responses of *Dumontia concorta* to different light and temperature regimes confirm our preliminary investigations in which we found that macrothalli sprouted from microthalli under short-day conditions and low temperatures (Rietema and Klein, 1981). The present results indicate that gametophytes (Figs. 1 and 4) and sporophytes (Figs. 5 and 6) do not differ appreciably from one another in this respect. This daylength effect was not brought about by lower daily light doses, since the responses both of microthalli kept in different daylength conditions at a light intensity of 2,000 lux and of those kept at the daylength-adjusted light intensities did not differ from one another. However, at a photoperiod of 2 h macrothallus development occurred only at the daylength-adjusted light intensity level, not at 2,000 lux. Probably at a photoperiod of 2 h and 2,000 lux the daily amount of light energy is too small for producing a photosynthetic surplus and consequently for macrothallus formation. For this reason also the formation of macrothalli from microthalli

could be delayed at a photoperiod of 2 h at the daylength-adjusted light intensity and at a photoperiod of 2.5 h 2,000 lux and at the daylength-adjusted light intensity. At a photoperiod of 12 h macrothallus development is also reduced and sometimes microthalli do not give off macrothalli at all. No macrothallus development occurs at all at a photoperiod of 14 h or longer. The large differences in response between short-day cultures (4:20; 8:16; 10:14) and intermediate daylength cultures (12:12), the absence of any response at daylengths of 14 h or longer, and the increase of the average number of macrothalli per microthallus after transfer of microthalli from the intermediate daylength condition into short daylength condition (Fig. 10) indicates a critical daylength for macrothallus 'induction' of approximately 12 h.

Macrothallus development occurs at all temperature regimes investigated from 4 to 16°. At 4°, the development of macrothalli is delayed; at 16° it is reduced. No macrothalli develop at 18° or higher. The large differences in response between microthalli kept at low temperatures (8° and 12°) and microthalli kept at 16°, the absence of macrothallus development at 18° or higher, and the increase of the average number of macrothalli per microthallus after transfer of the microthalli from 16 into 12° short-day condition (Fig. 11) suggest a critical temperature for erect macrothallus development of approximately 16°.

However, macrothallus initials were observed at all temperature regimes under which the microthalli survived (in combination with short daylengths), from 4 to 24°. These results suggest that the formation of macrothalli involves 2 separate steps: (1) Formation of macrothallus initials; (2) development of these initials

into macrothalli. The first step is initiated by short photoperiods alone, whilst the second step is brought about by short photoperiods in conjunction with low temperatures. Therefore macrothallus initials on microthalli do not develop further after transfer from 'inductive' short-day conditions to 'non-inductive' long-day conditions (Figs. 10 and 11). In *Dumontia contorta*, macrothallus development could be suppressed by white light night-break treatment in the middle of the dark period (Tables 2 and 3). White light night-breaks of 0.25 h and 2,000 lux were as effective as those of lower light intensities (1,500 or 180 lux). Therefore it is extremely unlikely that the effect of night-break treatment was caused by extra photosynthesis. Inhibition of erect macrothallus development from microthalli by a short night-break indicate that the photoperiodic response of *D. contorta* is a genuine photoperiodic response.

This is well known for flowering plants (Vince-Prue, 1975) and for the brown alga *Scytosiphon lomentaria* (Dring and Lüning, 1975). However, in *Dumontia contorta* a relatively large number of short-day cycles must be given before the development of macrothalli from microthalli will occur (Fig. 9).

The negligible differences in response between microthalli derived from spores transferred directly after release into different regimes of light and temperature (Figs. 12 and 13) and microthalli pre-cultured for 5 wk under long-day conditions (Figs. 1, 4, 5 and 6) suggest that perception of daylength takes place in both recently- and long-established microthalli. This is confirmed by an experiment with long-established microthalli which appeared to be capable of producing more than one generation of macrothalli under short-day conditions (Fig. 3).

The responses of *Dumontia contorta* microthalli to different daylength and temperature regimes show that macrothalli are only formed at low to moderate temperatures and under short-day conditions; this is reflected by the seasonal reappearance of *D. contorta* in autumn (Rosenvinge, 1909; Dunn, 1917; den Hartog, 1959; Kilar and Mathieson, 1978; Kristiansen and Pedersen, 1979). The present results indicate that daylength is the primary factor in the control of macrothallus development since macrothallus initials are formed under short-day conditions irrespective of temperature.

Temperature appeared to be an additional factor in the control of macrothallus development and to prevent the development of macrothallus initials into macrothalli above 16°. The formation of macrothalli from microthalli in *Dumontia contorta* is influenced by temperature-daylength conditions in a way similar to that in *Scytosiphon lomentaria* (Dring and Lüning, 1975). Based on field data, Kilar and Mathieson (1978)

believe that the growth of *D. contorta* is optimal at low temperatures (<10°). However, in the present study – and this roughly agrees with observations by Fortes and Lüning (1980) – the optimum temperature for growth of *D. contorta* macrothalli appeared to be 16 to 18° (Table 1), whilst macrothallus initials can develop into macrothalli only at temperatures ≤16°. Possibly the elongation of the short cells in young initials of *D. contorta* macrothalli (Fig. 8) is blocked in some way above 16°. Possibly, this can also be caused by long-day conditions after transfer of microthalli from short-day conditions into long-day conditions (Figs. 10 and 11). Details of the development of macrothallus initials into macrothalli will be published later.

According to Lüning (1980) the main ecological significance of *Scytosiphon lomentaria*'s photoperiodic response, which resembles the photoperiodic response of *Dumontia contorta* in many respects, lies in the fact that swimmers released by macrothalli in the summer are forced to develop into solid 'oversummering' crusts (solid crusts are formed in this species only at long-day conditions and relatively high temperatures). Spores released by *D. contorta*, however, develop into solid crusts irrespective of daylength conditions and temperature, although their fastest growth occurs at higher temperatures (16 and 18°; Fig. 13). Higher temperatures also promote the growth rate of *D. contorta* macrothalli, as well as the onset of reproductive maturation (Table 1). Higher temperatures promote growth of macrothalli also in the brown alga *Desmotrichum undulatum*, but here the largest macrothalli are formed at lower temperatures and relatively small macrothalli at higher temperatures; at higher temperatures vegetative growth is soon curtailed by intense formation of reproductive cells (Rietema and van den Hoek, 1981). Probably this also occurs in *D. contorta*. The daylength and temperature responses discussed above assure that macrothalli of *D. contorta* are produced during the cold season and thus develop into large plants.

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