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Photoperiodic and temperature responses in the growth and tetrasporogenesis of *Gigartina acicularis* (Rhodophyta) from Ireland*

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ABSTRACT: *Gigartina acicularis* is an intertidal, perennial red alga which reaches its northern distributional limit in the north-eastern Atlantic on the Irish coast. It has only rarely been found with reproductive structures in the British Isles. Plants isolated vegetatively from field-collected plants near the northern distributional limit in Ireland formed tetrasporangia, the tetraspores of which gave rise to plants which formed gametangia and carposporophytes at 16 °C, 8:$\overline{16}$ h. Sporelings grown from the carpospores of these plants formed tetrasporangia at all daylengths tested (16–8 h) at 13–20 °C; but there was a quantitative photoperiodic response in the numbers of plants forming tetrasporangia, and in the numbers of sori formed, at 13–16 °C. Only one in 20 plants became fertile at 16 °C, 16:$\overline{8}$ h and 8:$\overline{7.5}$:1:$\overline{7.5}$ h, but 16 in 20 plants reproduced at 16 °C, 8:$\overline{16}$ h. At 20 °C, 16:$\overline{8}$ h and 8:$\overline{16}$ h, all plants formed tetrasporangia, and formation was most rapid under the long-day regime. No tetrasporangia were formed at 9–10 °C, regardless of daylength. Apical elongation of these plants also appeared to show a quantitative photoperiodic response at 16 °C, 1 h light breaks in a 16 h night giving more or less a long-day response. This effect was apparent about 4 weeks before the formation of the first tetrasporangia. There would therefore appear to be quantitative photoperiodic control of tetrasporogenesis in the Irish strain of *G. acicularis*. Temperature and photoperiodic control of reproduction in this species only partially accounts for the observed rarity of reproductive structures in populations of this species near the northern limit of its distribution.

INTRODUCTION

Gigartina acicularis (Gigartinales, Gigartinaceae) is a relatively uncommon, perennial, intertidal red alga in the British Isles. It grows in the lower intertidal and the shallow subtidal in sheltered or semi-exposed localities and is often associated with silt or fine sand. The species is found from the British Isles (known northern limit is Roundstone, Co. Galway, Ireland; 53° 24′ N, 09° 55′ W) south to Cameroun, from North Carolina to Uruguay, and in the eastern Mediterranean (see Guiry & Cunningham, 1984). In the north-eastern Atlantic, records of reproductive plants are very rare; cystocarpic plants have only been found on one occasion in the British Isles (Devon in January, 1829), and tetrasporangial plants seem also to be extremely uncommon (only

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known record is from Galway Bay in November, 1966). Elsewhere in the north Atlantic (mainly France, Spain and Portugal), tetrasporangial plants have been reported from July to January and cystocarpic plants from November to March. Guiry & Cunningham (1984) found that male and female plants of this species from northern France only formed gametangia in culture at temperatures of 14–18 °C inclusive and at daylengths of 12 h and less. Gametogenesis is thus confined to the autumn in northern France and, at the northern distributional limit in the eastern Atlantic, would be restricted to exceptionally warm autumns. In a preliminary study of the effects of daylength and temperature on the formation of tetrasporangia in mature plants of *Gigartina acicularis*, Guiry & Cunningham (1984) found that they developed at all daylengths tested at 16 °C and none were formed at 10 °C; there did, however, seem to be a response to daylength as sporangia were formed more rapidly at the shorter daylengths.

The present paper describes a series of experiments designed to elucidate photoperiodic and/or temperature responses in tetrasporangial plants of a *G. acicularis* isolate from the Irish coast near the northern distributional limit of the species in the Atlantic.

MATERIALS AND METHODS

Sterile plants of *Gigartina acicularis* were collected at New Quay, Co. Clare, Ireland (53° 09.3′ N; 09° 13′ W) on 14 September 1982, and were isolated vegetatively into culture at 16 °C 8:$\overline{16}$ h (light:dark) at 5 μmol m^{-2} s^{-1}. Cultures were rendered unialgal as follows: Penicillin G (Na salt) was used at about 5 mg l^{-1} of culture medium to eliminate sensitive prokaryotic organisms; Germanium dioxide was used at concentrations of 5 μg l^{-1} of culture medium to control diatoms; tips were then excised continuously until they were free of any other contaminating algae. This technique works well for *G. acicularis* as the tips adapt quickly to culture conditions, and subsequently grow rapidly.

All plants were grown in enriched seawater, a modification of the Grund medium (McLachlan, 1973); Guiry & Cunningham (1984) give full details of its composition. Stock cultures were maintained in glass dishes of 200 ml capacity; dishes and media were changed every 14 days. Spores were inoculated on to glass microscope slides using fine-drawn Pasteur pipettes. For the studies on growth and reproduction of tetrasporangial plants, sporelings were excised from the glass slides at 2–4 mm long (about 8 weeks after spore inoculation) using a scalpel. For studies of the effects of daylength and temperature, disposable plastic petri dishes with a volume of about 50 ml were used. Two replicate cultures of 10 plants each were grown under each regime. The plastic dishes and the media were changed every 7 days, at which time the plants were gently wiped with paper tissues, measured, and examined under a binocular microscope for reproduction. When measuring plants, the maximum length was taken to the nearest 0.5 mm, and no effort was made to straighten curved plants. This species is a particularly suitable subject for growth measurements as growth is more or less linear for the first 40–50 mm of thallus formation, and the leading shoot persists after lateral branching.

Photon fluence densities were measured using a LI-COR Model 185-B meter and a LI-190SB quantum sensor. Fluorescent light was provided by cool-white 65/80 W tubes placed vertically above the dishes. Temperature was measured using Nickel Chromium/Nickel Aluminium thermocouples immersed in 250 ml of distilled water. All temperature readings cited in the text are accurate to ± 1 °C.

RESULTS

Initial isolation of plants

Vegetative plants isolated from field-collected material regenerated well in culture after about 4 weeks at 16 °C, 8:$\overline{16}$ h. Tetraspores were released after about 8 weeks under this regime from tips only 2 mm long. Numerous tetraspores were released over a period of about a month. These were inoculated onto glass slides and were grown at 16 °C, 16:$\overline{8}$ h, 20 μmol m^{-2} s^{-1}. Upright fronds were formed which reached 16–21 mm long after 10 weeks; these were then transferred to 16 °C, 8:$\overline{16}$ h, 20 μmol m^{-2} s^{-1}. Male and female reproductive organs were formed on separate plants 14 days later. Cystocarps formed on the female plants and carpospores were released at 16 °C, 8:$\overline{16}$ h, 20 μmol m^{-2} s^{-1}, after a further 11 weeks. These carpospores were inoculated onto glass slides and were grown at 16 °C, 16:$\overline{8}$ h, 20 μmol m^{-2} s^{-1}. After 6 weeks the carposporelings were 3–4.5 mm long and were detached manually and grown in plastic petri dishes.

Effects of daylength and temperature on elongation and reproduction of tetrasporangial plants

Sporelings 3–4.5 mm long derived from carpospores from a single cystocarp were grown at the temperatures and daylengths shown in Table 1. The plants grew more rapidly at 20 °C, 16:$\overline{8}$ h than at 20 °C, 8:$\overline{16}$ h (Fig. 1), and started to release tetraspores after 4 weeks. All plants had released tetraspores by the fifth week (Table 1). There was, however, a high degree of necrosis apparent in both (replicate) cultures, particularly

Table 1. Effects of daylength (h) and temperature on numbers of plants (of twenty) of the Irish strain of *Gigartina acicularis* forming tetrasporangia at weekly intervals. * = light break of 1 h in a 16 h night. No tetrasporangia were formed before the fourth week

Temperature (°C)	Daylength (h light : dark)	Weeks from start									
		4	5	6	7	8	9	10	11	12	13
20	16 : 8	3	20								
20	8 : 16	–	4	9	13	13	16	20	20	20	20
18	8 : 16	2	3	4	8	14	14	19	19	19	19
16	16 : 8	–	–	–	–	–	1	1	1	1	1
16	14 : 10	–	–	–	–	–	–	1	2	3	3
16	10 : 14	–	–	–	–	–	6	11	15	15	16
16	8 : 16	–	–	–	–	–	7	15	16	16	16
16	LB*	–	–	–	–	–	–	–	1	1	1
15	16 : 8	–	–	–	1	1	2	2	2	2	2
13	16 : 8	–	–	–	–	1	2	2	2	2	2
10	16 : 8	–	–	–	–	–	–	–	–	–	–
10	14 : 10	–	–	–	–	–	–	–	–	–	–
10	10 : 14	–	–	–	–	–	–	–	–	–	–
10	8 : 16	–	–	–	–	–	–	–	–	–	–
10	LB*	–	–	–	–	–	–	–	–	–	–
9	16 : 8	–	–	–	–	–	–	–	–	–	–

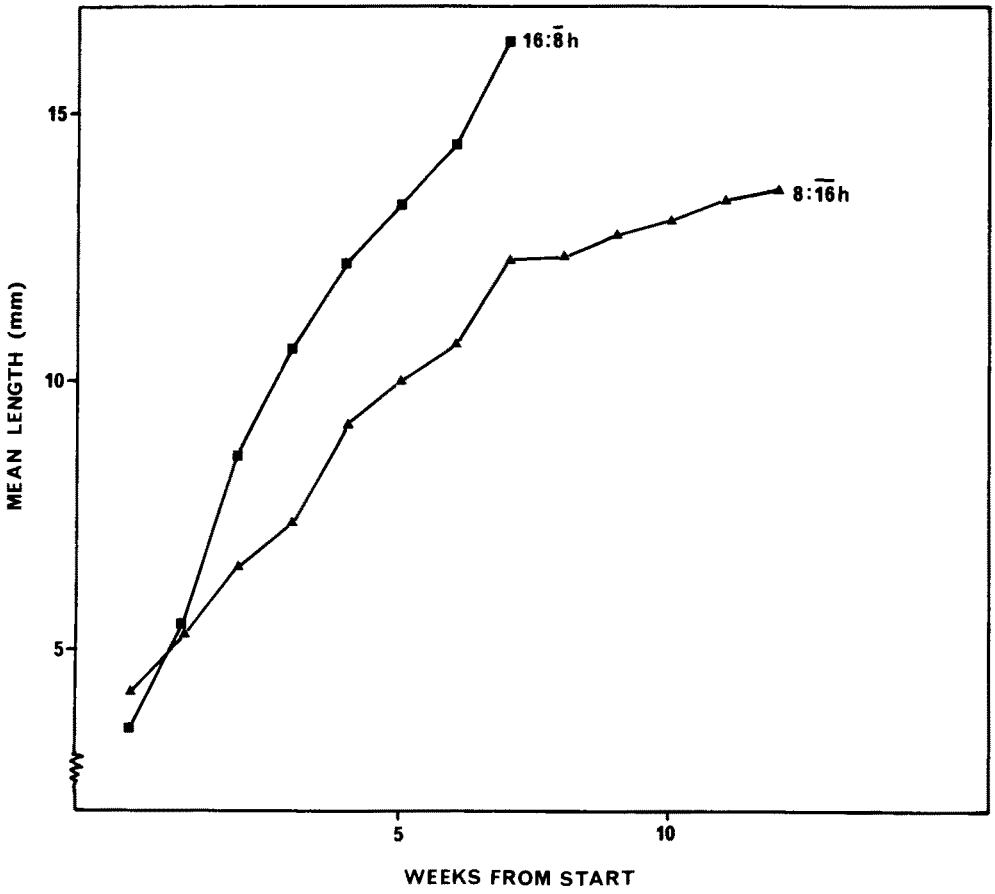

Fig. 1. Apical elongation of *Gigartina acicularis* tetrasporangial plants at 20 °C, 16:$\overline{8}$ h and 20 °C, 8:$\overline{16}$ h. Values represent the mean lengths of 20 plants at weekly intervals; standard deviations did not exceed ± 3.7 mm at 8:$\overline{16}$ h

after tetraspore release, and the plants died after the sixth week. This necrosis (West & Guiry, 1982; Guiry & Cunningham, 1984) initially manifests itself as a distal greening of the fronds which rapidly spreads to cover the whole thallus surface. Ultimately, the whole surface of the plant becomes white in colour. This phenomenon did not seriously affect the formation of tetrasporangia but growth rates were erratic (Fig. 1). At 20 °C, 8:$\overline{16}$ h, tetraspores were not released until the fifth week (Table 1), all plants had formed tetrasporangia by the tenth week, and tetraspore release was continuous from the fifth to the tenth week (Table 2). In contrast to plants grown at 20 °C, 16:$\overline{8}$ h, necrosis was only observed on one plant at 20 °C, 8:$\overline{16}$ h and this only at the base.

At 18 °C, 8:$\overline{16}$ h, two plants formed tetrasporangia after 4 weeks and thereafter there was a gradual increase in the number of plants forming tetrasporangia until the tenth week (Table 1) when 19 of the 20 plants had released tetraspores. The remaining plant did not form tetrasporangia. Elongation rates were roughly similar to those observed at

Table 1. Effects of daylength (h) and temperature on numbers of plants (of twenty) of the Irish strain of *Gigartina acicularis* forming tetrasporangia at weekly intervals. * = light break of 1 h in a 16 h night. No tetrasporangia were formed before the fourth week

Temperature (°C)	Daylength (light : dark)	Weeks from start 4	5	6	7	8	9	10	11	12	13
20	16 : 8	+	+								
20	8 : 16	−	+	+	+	+	+	+	+	+	+
18	8 : 16	+	+	+	+	+	+	+	+	+	+
16	16 : 8	−	−	−	−	−	+	−	−	−	−
16	14 : 10	−	−	−	−	−	−	+	−	+	−
16	10 : 14	−	−	−	−	−	+	+	+	+	+
16	8 : 16	−	−	−	−	−	+	+	+	+	+
16	LB*	−	−	−	−	−	−	−	+	−	−
15	16 : 8	−	−	−	+	−	+	+	−	−	−
13	16 : 8	−	−	−	−	+	+	−	−	−	−

20 °C, 8:$\overline{16}$ h. Tetraspores were released continuously from the fourth to the thirteenth week (Table 2).

At 16 °C, elongation rates were significantly affected by daylength (Fig. 2). At daylengths of 16:$\overline{8}$ h, 8:$\overline{7.5}$:1:$\overline{7.5}$ h, and 14:$\overline{10}$ h, elongation rates were very similar, whereas at 10:$\overline{14}$ h, and 8:$\overline{16}$ h, elongation rates were clearly suppressed from about the fourth week onwards. The formation of tetrasporangia at 16 °C showed quite a different pattern to that observed at 20 °C, none being produced before the seventh week (Table 1) and most started to release tetraspores at the ninth week (Table 2). At 16 °C, 16:$\overline{8}$ h, only one plant of twenty had formed tetraspores after 13 weeks whereas at 16 °C, 8:$\overline{16}$ h sixteen plants had reproduced after the same period (Table 1). At 16 °C, 8:$\overline{7.5}$:1:$\overline{7.5}$ h, only one plant had formed tetrasporangia after 13 weeks. After the same period at 16 °C, 14:$\overline{10}$ h, three plants of twenty had reproduced and at 10:$\overline{14}$ h, sixteen plants had reproduced (Table 1). Spore releases at 16 °C, 8:$\overline{16}$ h and 10:$\overline{14}$ h were continuous after the ninth week but were sporadic at 16 °C, 16:$\overline{8}$ h, 14:$\overline{10}$ h, and 8:$\overline{7.5}$:1:$\overline{7.5}$ h (Table 2). At 13 °C, 16:$\overline{8}$ h, and 15 °C, 16:$\overline{8}$ h, very few plants formed tetrasporangia during the course of the study (Table 1) and tetraspore releases were again sporadic (Table 2).

Growth rates at 16:8 h under a range of temperatures are shown in Fig. 3. Initially, elongation rates were greatest at 20 °C but after the fifth week the formation of tetrasporangia gradually affected the rate of elongation. Growth was slightly more rapid at 15 °C than at 16 °C, suggesting that this is the optimum temperature for the Irish strain of *G. acicularis*. A considerable gap is evident between 13 and 10 °C (Fig. 3) but this may not be particularly significant in the light of the 2 °C difference.

At 9–10 °C, no tetrasporangia were formed regardless of daylength (Table 1) and elongation rates were significantly depressed compared to those at 13–20 °C (Figs 3 and 4). At 10 °C, elongation rates were clearly dependent on hours of light and no photoperiodic effect was apparent (Fig. 4). In general, plants grown at 10 °C were whitish or yellowish at their tips and the immediate apical area was rather distorted. No necrosis was observed at 10 °C.

No differences in branching of any significance were observed between the plants

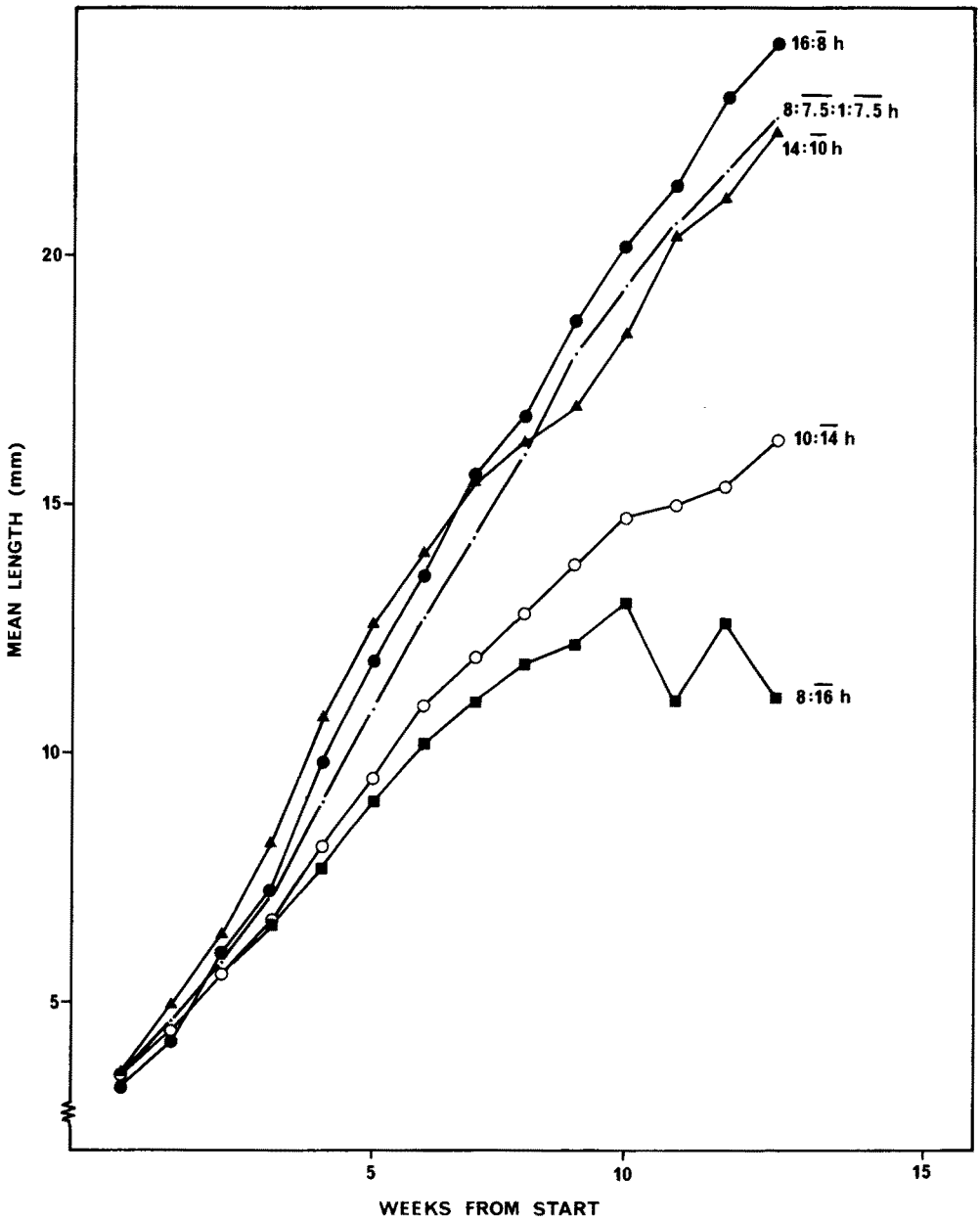

Fig. 2. Apical elongation of *Gigartina acicularis* tetrasporangial plants under various photoregimes at 16 °C. Values represent the mean lengths of 20 plants at weekly intervals; standard deviations did not exceed ± 3.5 mm. The erratic apical elongation figures at 8:16 h, from the tenth week were due to the plants forming large numbers of tetrasporangial sori which caused the plants to curl

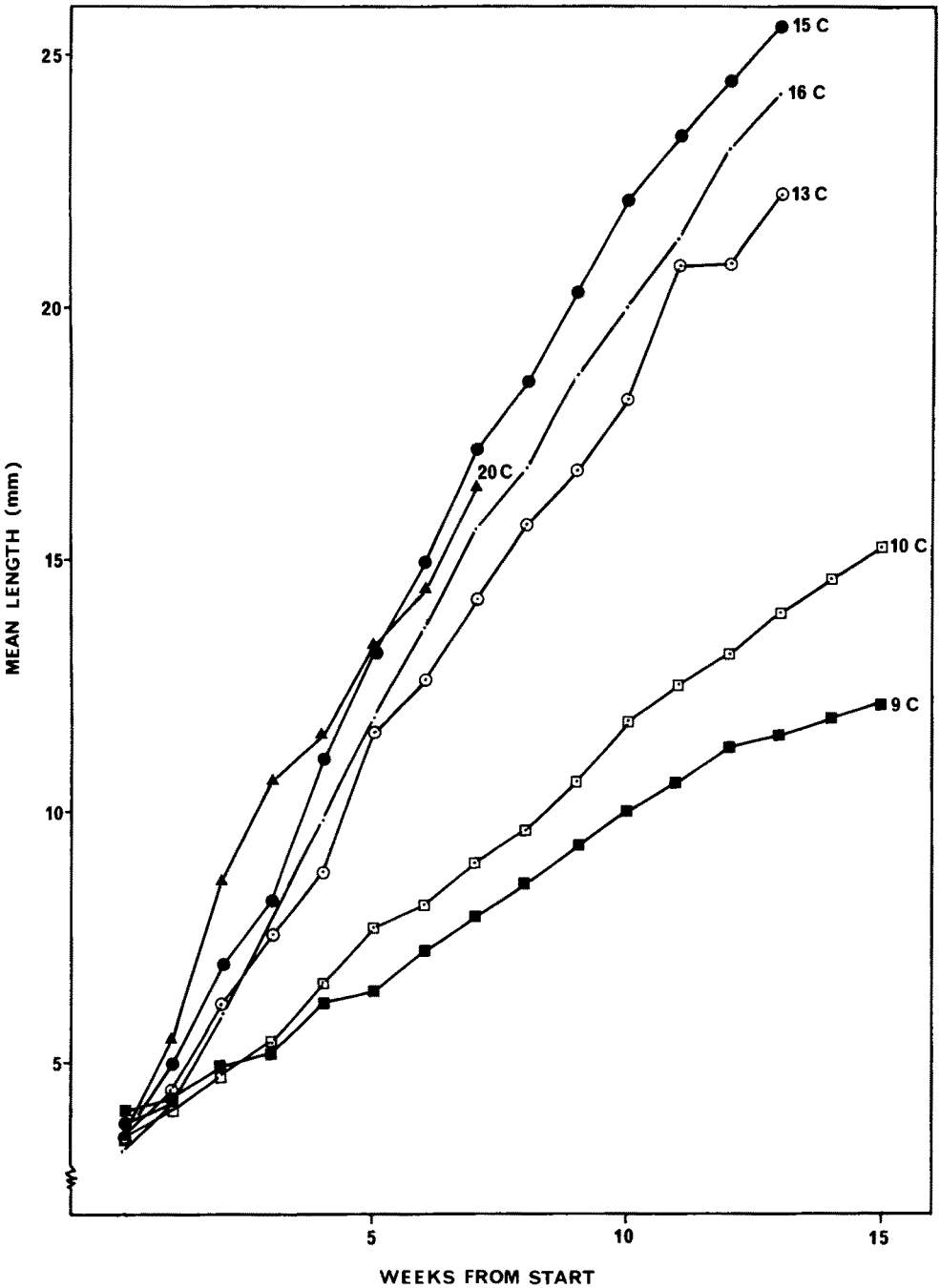

Fig. 3. Apical elongation of *Gigartina acicularis* tetrasporangial plants at various temperatures under a photoregime of 16:$\bar{8}$ h. Values represent the mean lengths of 20 plants at weekly intervals; standard deviations did not exceed ± 3.7 mm

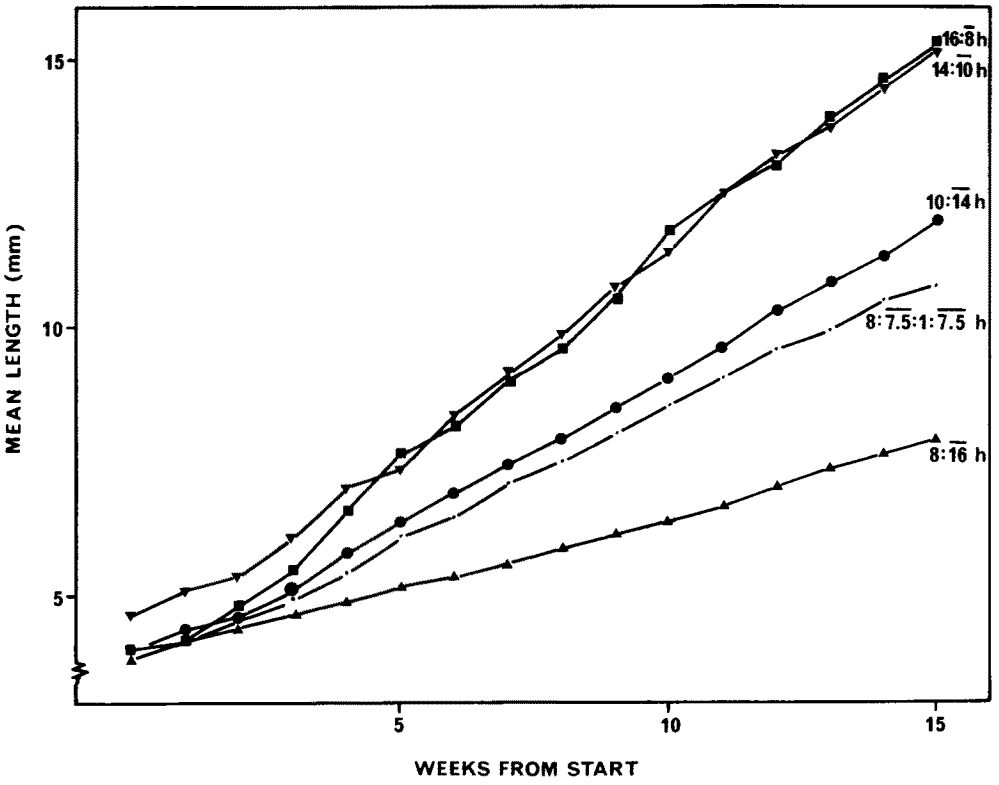

Fig. 4. Apical elongation of *Gigartina acicularis* tetrasporangial plants at various photoregimes at 10 °C. Values represent the mean lengths of 20 plants at weekly intervals; standard deviations did not exceed ± 1.95 mm

grown at different temperatures and daylengths (Fig. 5 A–J). Plants grown at 20 °C tended to be narrower than those grown at 15–16 °C; and plants grown at 10 °C tended to be broader.

DISCUSSION

Although a full set of daylengths at 20 °C has not been attempted, it seems from the available data that a daylength effect on tetrasporangial formation and tetraspore release similar to that found at 13–16 °C does not exist (Table 3). Tetrasporangia are formed very rapidly and in large numbers at 20 °C, 16:$\overline{8}$ h; formation and release is rather more gradual at 20 °C, 8:$\overline{16}$ h, but all plants become fertile. Elongation rates at 20 °C were clearly affected by daylength from the very beginning (Fig. 1). However, the formation of tetrasporangial sori in large numbers eventually curtails growth rates at 20 °C, 8:$\overline{16}$ h (Fig. 1). At 18 and 20 °C, 8:$\overline{16}$ h, tetraspore release is almost continuous once it has been initiated (Table 2); similarly tetraspore release is continuous at 16 °C, 10:$\overline{14}$ h and 8:$\overline{16}$ h but is initiated much later than at 18 °C. At 16 °C, 16:$\overline{8}$ h and 14:$\overline{10}$ h; 15 °C, 16:$\overline{8}$ h; and 13 °C, 16:$\overline{8}$ h releases are sporadic and very few plants become fertile.

At 16 °C, daylength clearly affects elongation rates (Fig. 2). At 14:$\overline{10}$ h, 8:$\overline{7.5}$:1:$\overline{7.5}$ h

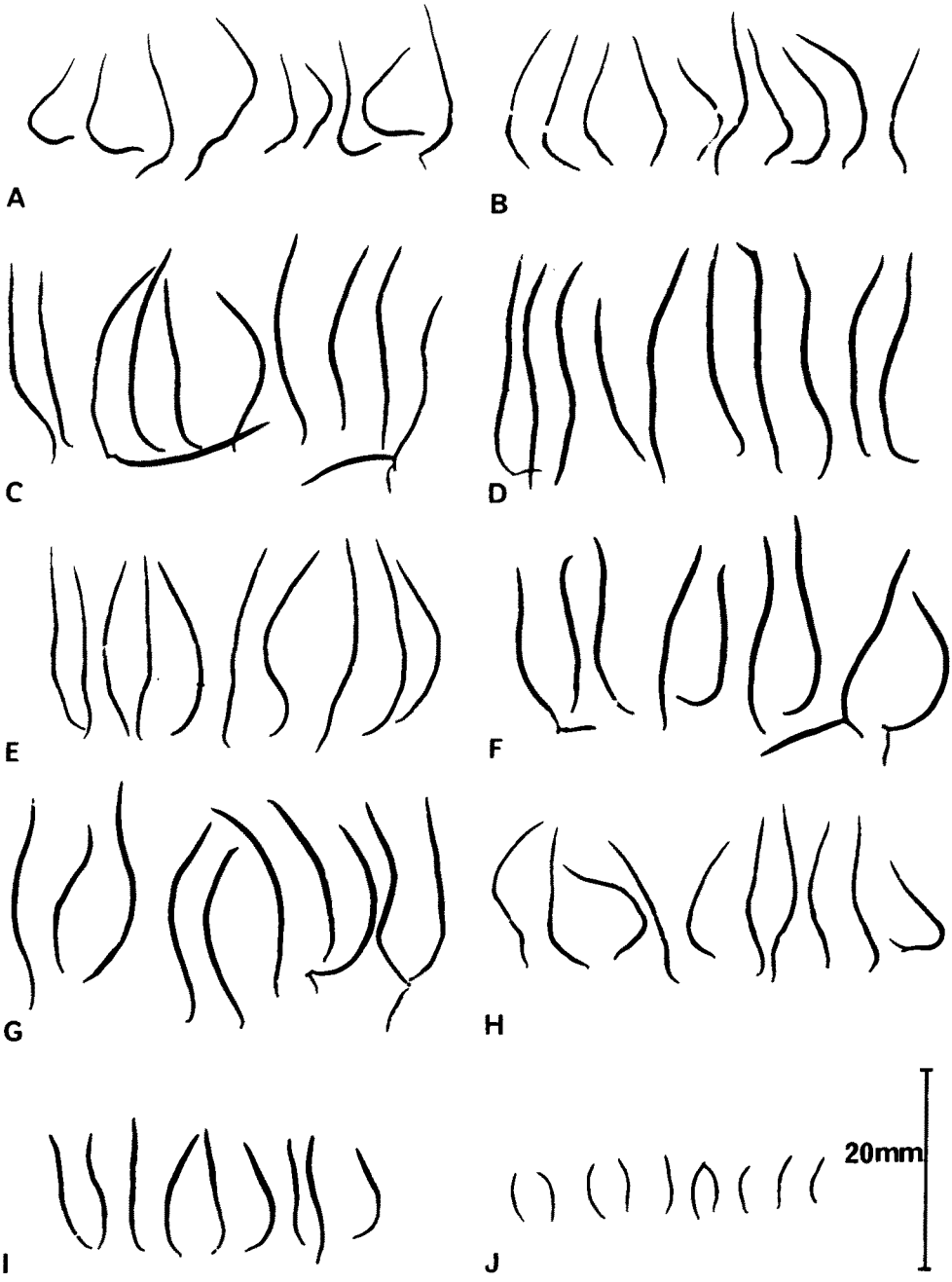

Fig. 5 A–J. Plants of *Gigartina acicularis* derived from carpospores grown under various regimes. All plants are 16 weeks old and were derived from carpospores from a single cystocarp. A: 18 °C, 8:$\overline{16}$ h; B: 16 °C, 8:$\overline{16}$ h; C: 16 °C, 16:$\overline{8}$ h; D: 15 °C, 16:$\overline{8}$ h; E: 16 °C, 8:$\overline{7.5}$:1:$\overline{7.5}$ h; F: 13 °C, 16:$\overline{8}$ h; G: 16 °C, 14:$\overline{10}$ h; H: 16 °C, 10:$\overline{14}$ h; I: 10 °C, 16:$\overline{8}$ h; J: 10 °C, 16 °C, 8:$\overline{16}$ h

Table 3. Summary of effects of daylength and temperature on tetrasporangial formation in plants of *Gigartina acicularis*. Numbers of plants (of twenty) forming tetrasporangia 11 weeks after initiation of experiment. – = conditions not attempted; * = light-break of 1 h in a 16 h night

Daylength (h light : dark)	Temperature (°C)						
	9	10	13	15	16	18	20
16 : 8	0	0	2	2	1	–	20 (after 5 weeks)
14 : 10	–	0	–	–	2	–	–
10 : 14	–	0	–	–	15	–	–
8 : 16	–	0	–	–	16	19	20
LB*	–	0	–	–	1	–	–

and 16:$\overline{8}$ h elongation rates are roughly the same. Although the differential rates become apparent before tetrasporangial formation, it is probable that energy is being diverted away from growth to the formation of energy reserves for tetrasporangial initiation and support. That the rate of elongation is not merely an effect of total incident light energy is clear from the observation that the night-break regime (9 h light in 24 h) gave more or less the same growth rate as the 14:$\overline{10}$ h regime (14 h light in 24 h). It should, however, be borne in mind that night-break plants formed only one tetrasporangial sorus (Tables 1 & 2). At 10 °C, on the other hand, growth rates seemed to be strictly related to the number of hours of light (Fig. 4). It is therefore difficult to postulate a long-day, true photoperiodic response in the apical elongation of fronds at 16 °C, as it is impossible to separate it from tetrasporangial formation with any degree of certainty.

Tetrasporangial formation at 16 °C does, however, seem to display a true photoperiodic response. Light breaks of 1 h in the middle of a 16 h night reduce the response to that of a 16:$\overline{8}$ h regime and decreasing daylengths cause an increasing response. It is interesting to note that long daylengths, in addition to reducing the number of plants forming tetrasporangia, probably also depress the number of sori produced on individual plants; this is evident from the incidence of spore releases at these daylengths (Table 2). At 16 °C, 14:$\overline{10}$ h and 8:$\overline{16}$ h, tetraspores are released continuously once formed, whereas at 13, 15 and 16 °C, 16:$\overline{8}$ h, and 16 °C, 14:$\overline{10}$ h, tetraspore releases are sporadic. The latter is also true of the night-break regime.

Most of the photoperiodic responses that have been reported to date in marine red algae have been "absolute" (Lüning, 1980, 1981a) responses (Table 4), and most have been in the formation of tetrasporangia or in the initiation of upright fronds. Dring (1967) and Rentschler (1967) have reported a quantitative photoperiodic response in the formation of conchosporangia in *Porphyra tenera* Kjellman. These reproductive structures are generally the site of meiosis in the Bangiales and are homologous with tetrasporangia. Maggs & Guiry (1982) have reported a quantitative photoperiodic response in the formation of tetrasporangia in *Halymenia latifolia* Kützing (Rhodophyta) from Ireland; but tetrasporangial formation was completely blocked at daylengths of 20:$\overline{4}$ h. It may be that similar long-day blockages of sporogenesis may be present in *Porphyra tenera* and *G. acicularis* and that there is no real difference between qualitative and quantitative photoperiodic responses except that the critical daylength exceeds 16 h in the latter.

It has become increasingly apparent in recent years that the vast majority of the Florideophycidae (= Nemaliophycidae) have a *Polysiphonia*-type life history. There are, however, persistent reports that one phase of a *Polysiphonia*-type life history is of much more frequent occurrence in nature than another. Tetrasporangial plants often outnumber gametangial plants in many species of Ceramiales (e.g. Drew, 1955; Dixon, 1970; Fritsch, 1945; Edwards, 1973). *Iridaea cordata* (Gigartinaceae) exhibits a higher

Table 4. Species of Rhodophyta which show a short-day photoperiodic response and in which a night-break is effective in reducing the response to the level of long-day response. Q = quantitative response. A = absolute response. L = latitudinal ecotypes are known

Species	Response	Type	Source
Porphyra tenera	Conchosporangia	Q	Dring (1967), Rentschler (1967)
Bangia fuscopurpurea	Conchosporangia	A	Richardson & Dixon (1968)
Calosiphonia vermicularis	Tetrasporangia	A	Mayhoub (1975); Mayhoub et al. (1976)
Asparagopsis armata	Tetrasporangia	A	Lüning (1981b)
Bonnemaisonia hamifera	Tetrasporangia	A	Lüning (1980, 1981a, 1981b)
Acrochaetium asparagopsis	Tetrasporangia	A	Abdel-Rahman (1982)
Halymenia latifolia	Tetrasporangia	Q, L	Maggs & Guiry (1982, unpubl.)
Dumontia contorta	Upright fronds	A	Rietema & Breeman (1982)
Bonnemaisonia asparagoides	Upright fronds	A	Rueness & Åsen (1982)
Meredithia microphylla	Tetrasporangia	A	Guiry & Maggs (1982, unpubl.)
Rhodochorton purpureum	Tetrasporangia	A, L	Dring & West (1983)
Mastocarpus stellatus•	Tetrasporangia	A	Guiry & West (1984)
Gigartina acicularis	Gametangia	A	Guiry & Cunningham (1984)
	Tetrasporangia	Q	This study

• Previously known as *Gigartina stellata* (see Guiry et al., 1984)

frequency of tetrasporophytes than gametophytes in the wild (Hansen & Doyle, 1976) whereas *Iridaea flaccida* has a very low frequency of tetrasporophytes (20 %) (Abbott, 1980). These differences in frequency of phases may, of course, be due to factors other than photoregime and/or temperature limitations; such environmental parameters as differential grazing pressure, growth rates, survival abilities and spore production and germination all may be involved in preferentially selecting one phase or another (West & Hommersand, 1982). The gametophytes of *Gigartina acicularis* rarely become fertile at these latitudes (Guiry & Cunningham, 1984) due to limitation by both temperature and photoregime. The paucity of reports of tetrasporangial plants in the wild in the British Isles is rather more difficult to explain as the factors controlling the formation of tetrasporangia are not as limiting seasonally as those controlling gametangial formation. At least some plants should form tetrasporangia during the summer and autumn when water temperatures are in excess of 13 °C. The apparent lack of reports of tetrasporangial plants of *G. acicularis* in the Mediterranean and in tropical and subtropical regions may be a result of summer temperatures in excess of 18 °C stimulating the formation of tetrasporangia on very small plants, and these plants are not apparent in routine field collections. Further phenological studies of reproduction in these areas are clearly necessary.

The factors which control the geographical distribution of *Gigartina acicularis* are obviously complex. The present British Isles populations of this species seem to reproduce very rarely by spores. Populations seem to maintain themselves by vegetative reproduction. Successful reproduction by spores at more southerly latitudes may be crucial for survival as intertidal populations may be decimated by high summer temperatures and low humidity. A crucial question is: why has an alga with an "isomorphic" life history evolved a means of producing the maximum number of spores during the autumn period? One can understand that algae with "heteromorphic" life histories do so in order to produce spores from the crustose or filamentous overwintering phase for the subsequent spring/summer erect growths. I am afraid that we have a long way to go before we fully understand the growth and reproductive strategies of many of these red algae.

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