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Life history regulation and phenology of the red alga *Bonnemaisonia hamifera**

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ABSTRACT: *Bonnemaisonia hamifera* Hariot (Rhodophyceae, Bonnemaisoniales) from Galway Bay, Ireland has been studied in the field and in laboratory culture. The reproductive behaviour of tetrasporophytes and gametophytes in the field appeared to be strictly regulated by their temperature/daylength responses as observed in culture. Tetrasporangia were abundant in early autumn when short days (< 12 h of light per day) coincided with seawater temperatures over about 11 °C, the lower limit for sporangium formation. Spermatangia were observed in very young gametophytes between mid-December and February, and in adult plants from late March until the end of May. They were absent in mid-winter when low temperatures of about 2 °C inhibited their formation. Carpogonia were first observed at the end of April as seawater temperatures had by then risen to the required value of around 10 °C. Carpogonia were fertilised and plants with mature cystocarps were present until early July. The onset of reproduction was accompanied by a cessation of growth and led to senescence within 2–3 months. Thus, gametophytes were absent in summer in spite of persistently favourable seawater temperatures. In various parts of the North Atlantic Ocean, annual temperature regimes are such as to cause a certain lack of synchronisation in the occurrence of reproductive male and female plants. This may account for the many anomalous reports of reproductive plants in the wild.

INTRODUCTION

The red alga *Bonnemaisonia hamifera* Hariot (Bonnemaisoniales) has a heteromorphic life history in which a multiseriate, radially branched, dioecious gametophyte alternates with a uniseriate, alternately branched tetrasporophyte, previously known as *Trailliella intricata* Batters (Feldmann & Feldmann, 1942; Harder & Koch, 1949; Koch, 1949; West & Hommersand, 1981). This species was first reported in the North Atlantic Ocean towards the end of last century, when both phases appeared more or less simultaneously on the southwest coast of Britain (Dixon & Irvine, 1977). Currently, the *Trailliella*-phase is found from Iceland (Munda, 1979) and northern Norway (Jaasund, 1965) south to the Canaries (Börgesen, 1930) and Sicily (Furnari, 1984), and from Labrador (South & Tittley, 1986) to Virginia (Humm, 1979). The *Bonnemaisonia*-phase has a more restricted distribution, extending from western Norway (Haugen, 1970) south

* Dedicated to Dr. Dr. h. c. P. Kornmann on the occasion of his eightieth birthday.

to Marocco (Feldmann & Feldmann, 1942) and southeastern Spain (Conde & Seoane, 1982), and from Nova Scotia (McLachlan et al., 1969) to Connecticut (Schneider et al., 1979).

Sexual plants of *Bonnemaisonia hamifera* are well known from eastern central Japan (Chihara, 1961), and this has been suggested as the most likely region of origin of the species (Feldmann & Feldmann, 1942; Koch, 1949; Dixon & Irvine, 1977; West & Hommersand, 1981). In contrast, collectors have often found only sterile plants, isolated male gametophytes or female gametophytes with "sterile pericarps"* in the North Atlantic Ocean (McLachlan et al., 1969; Dixon & Irvine, 1977; West & Hommersand, 1981). Moreover, in regions close to the geographical distribution limit of the *Bonnemaisonia*-phase, gametophytes have been found in some years and not in others (Kornmann & Sahling, 1962, 1983; Lye, 1965; Haugen, 1970; Lüning, 1980; Bird, 1980), whereas tetrasporangia are rarely found even in regions where gametophytes have been reported (McLachlan et al., 1969; Dixon & Irvine, 1977). These observations have led to the assumption that the sexual cycle is rarely completed in the North Atlantic Ocean and that both life history phases persist independently by means of vegetative propagation (McLachlan et al., 1969; Dixon, 1970; Dixon & Irvine, 1977). However, mature cystocarpic plants have been reported from Helgoland (Kornmann & Sahling, 1962), from various locations along the English Channel (Bichard-Bréaud & Floc'h, 1966; Simon-Bichard-Bréaud, 1970) and from southern Massachusetts (Simon-Bichard-Bréaud, 1970). Some of these anomalies may be due to a lack of systematic observations as no year-round phenological studies of both life history phases have been carried out to date.

Experimental work with *B. hamifera* has largely concentrated on the *Trailliella*-phase, but the temperature requirements for growth and the upper and lower limits of thermal tolerance have been examined for both life history phases (Koch, 1949; Lüning, 1981, 1984). Daylength and temperature were shown to be critical factors for the induction of the tetrasporangia (Lüning, 1980, 1981; Knappe, 1985), but no detailed experimental work has been carried out to date on the temperature and light requirements for reproduction of gametophytes.

In the present study we document the phenology of *B. hamifera* in Galway Bay on the west coast of Ireland. Additionally, the temperature and daylength requirements for reproduction and the upper limit of thermal tolerance have been tested for both life history phases in an isolate from Galway Bay. Our aim was to identify the critical factors that regulate the life history of this species in the wild, and to find an explanation for its enigmatic reproductive behaviour in the North Atlantic Ocean.

MATERIAL AND METHODS

The field study sites were Finavarra (53°09.5' N, 9°07' W) and New Quay (53°09.5' N, 9°04' W), both in County Clare, Ireland, on the southern shore of Galway Bay. The study period was September 1985 to August 1986. Tetrasporangial periodicity was recorded

* In this species protuberances resembling cystocarps but lacking carposporangia have been referred to as "sterile cystocarps" (Dixon & Irvine, 1977; West & Hommersand, 1981), "infertile or sterile pericarps", or "pseudopericarps" (Mc Lachlan et al., 1969; Bird, 1980). None of these terms is strictly correct but it is difficult to express the condition more precisely

between September 1985 and March 1986, when at least 30 *Trailliella* tufts were collected at each site at approximately 1–2 weekly intervals (see Fig. 1 for dates). Adult gametophytes were collected between February and July 1986, when both sites were visited at approximately monthly intervals (see Fig. 1 for dates). Whenever present, at least 15 gametophytes were sampled. Surface seawater temperatures were continuously recorded at the Shellfish Research Laboratory, Carna, Co. Galway, about 45 km due west of our study sites. In addition, greenhouse maximum-minimum thermometers, which were reset every 2–8 days, recorded extremes of temperature, in situ at both study sites between September and December 1985.

Stock cultures were initiated from *Trailliella* fragments collected at Finavarra in September 1984 (isolate MDG 494) and maintained at 12 °C and at a photon fluence rate of ca 10 µmol m^{-2} s^{-1} in a light : dark regime of 16 : 8 h. Experiments were performed in constant-temperature incubators (± 1.5 °C) or in waterbaths (± 0.2 °C) when the lower temperature limit for reproduction of tetrasporophytes was being established. Cultures were kept in Provasoli's enriched seawater medium with 10 % of the normal P and N concentration (see Lüning, 1980, 1981). General methods and equipment for culturing have been described by Breeman and ten Hoopen (1981) and Yarish et al. (1984). Procedures to quantify reproduction of the tetrasporophyte were similar to those described previously for *Rhodochorton purpureum* (Breeman et al., 1984). Individual plants ($n \approx 50$) were planted at regular distances in Whatmann GF/A 11 cm diameter glass microfibre filter paper covering the bottom of a culture dish. For each experiment 3–4 replicates were employed. The number of plants bearing tetrasporangia was determined at weekly intervals until no further plants had reproduced. Methods for determining the limits of thermal tolerance were as previously described (Cambridge et al., 1987). Growth responses were assessed as growth yields after 3 months, using total plant material for tetrasporophyte cultures and the 7 largest plants for gametophyte cultures.

RESULTS

Field observations

The *Trailliella*-phase was present at Finnavarra and New Quay all year round (Fig. 1). Tetrasporangia were observed in autumn and winter (Fig. 1; Table 1). They were most abundant from mid-October to mid-November, but occurred in smaller quantities until February (Table 1). At New Quay, some tetrasporangia were also present during the latter half of September (Table 1). Released spores and empty sporangia were observed from mid-September to mid-January (Fig. 1). During this period no adult gametophytic plants were observed. A small fragment, ca 10 mm in length, of what was evidently a perennating gametophyte was found on a single occasion (11 October, New Quay).

Gametophytic germlings started to appear in early October (Fig. 1). Sporelings were found growing attached to the *Trailliella*-phase filaments by basal, rhizoidal attachment structures. By the end of January, the largest germlings, about 2–5 cm long (Fig. 1), started to "escape" from the *Trailliella* tufts and attached by their hooks to other algae such as *Cystoseira* spp., *Polyides rotundus* and *Ceramium rubrum*. By the end of March plants had attained their final size of about 40 cm (Fig. 1), up to which time growth had been exponential (Fig. 2).

Table 1. *Bonnemaisonia hamifera*. Reproductive phenology of tetrasporophytes in Galway Bay during the autumn and winter of 1985/1986

Location/Date	Tetrasporangia	
	Initials	Mature sporangia
Finnavarra		
4–27 Sept.	absent	absent
3–18 Oct.	becoming abundant	becoming abundant
26 Oct.–10 Nov.	abundant	abundant
16 Nov.–10 Dec.	abundance decreasing	abundance decreasing
16–27 Dec.	reappearing in low numbers	present
10–28 Jan.	absent	few
from 12 Feb.	absent	absent
New Quay		
14–20 Sept.	few	few
27 Sept.–11 Oct.	becoming abundat	becoming abundant
18 Oct.–10 Nov.	abundant	abundant
16–30 Nov.	abundance decreasing	abundance decreasing
10–27 Dec.	reappearing in low numbers	present
28 Jan.–12 Feb.	absent	few
from 26 Feb.	absent	absent

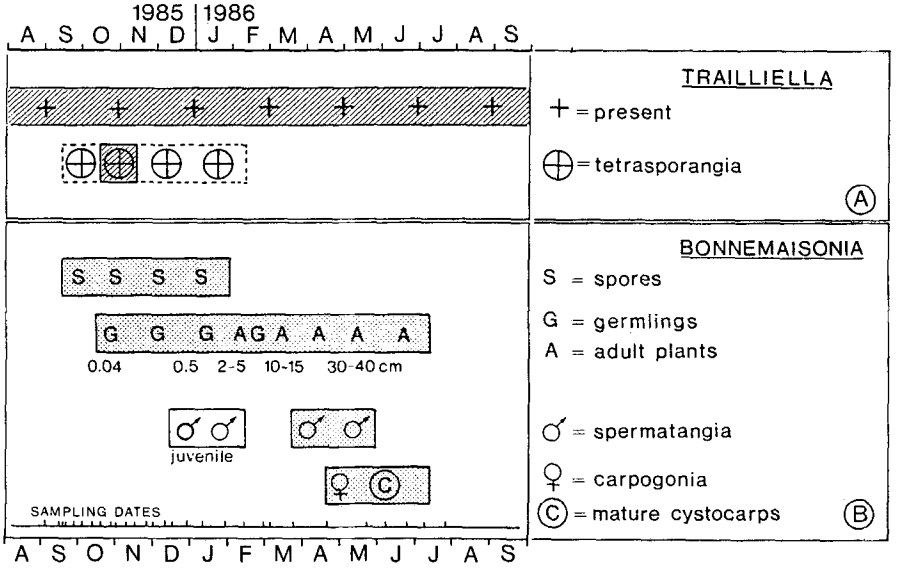

Fig. 1. *Bonnemaisonia hamifera*. Phenology in Galway Bay in 1985/1986; sampling dates indicated. A: *Trailliella*-phase: present (+); with tetrasporangia (⊕), tetrasporangia abundant (shaded). B: *Bonnemaisonia*-phase: tetraspores (S); germlings (G) and adult (A) gametophytes (size given); spermatangia (♂) in juvenile (blank bar) and adult plants (shaded bar); carpogonia and young cystocarps (♀), mature cystocarps (C)

Table 2. *Bonnemaisonia hamifera*. Reproductive phenology of gametophytes in Galway Bay during the winter and spring of 1985/1986. Number of plants (n)

Stage/Date/Location	Observations				
I. Germlings					
11 Oct.–10 Dec.	all plants sterile				
16 Dec.–12 Feb.	spermatangia present				
from 28 Feb.	all plants sterile				
II. Adult plants					
	Sterile (n)	Male Plants (n)	developmental stage	Female Plants (n)	developmental stage
Finnavarra					
3 March	11	0		0	
28 March	13	1	young spermatangial branches	0	
23 April	11	6	young & mature spermatangial branches	1	carpogonia
22 May	0	3	mature spermatangial branches	11	carpogonia & young cystocarps
6 June	1	0		35	young & mature cystocarps; spore release
23 June	0	0		15	(young) & mature cystocarps; spore release
				6	empty cystocarps
7 July	0	0		2	mature cystocarps; spore release
New Quay					
3 March	0	0		0	
28 March	19	3	young spermatangial branches	0	
23 April	6	7	young & mature spermatangial branches	1	carpogonia
22 May	0	6	mature spermatangial branches	23	carpogonia & young cystocarps
6 June	0	0		20	young & mature cystocarps
23 June	0	0		12	(young) & mature cystocarps; spore release
				2	empty cystocarps
7 July	0	0		0	

Fertile male plants were first observed in mid-December, when germlings of no more than a few mm long, which were still attached to the *Trailliella*-phase filaments, bore young spermatangial branches (Fig. 1; Table 2). Such precociously mature males were observed until mid-February. Fertile male plants were absent from mid-February until

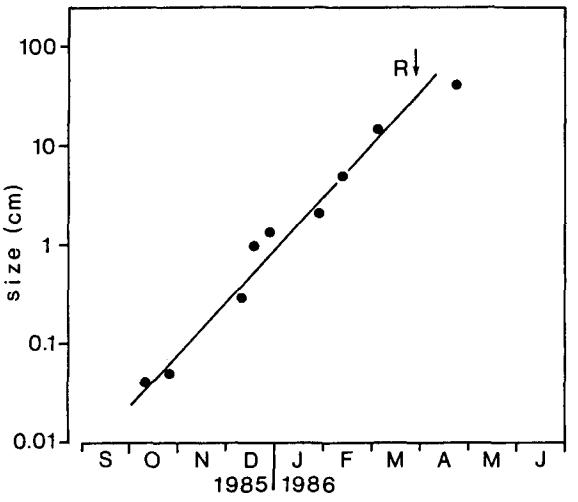

Fig. 2. *Bonnemaisonia hamifera*. Size of largest gametophyte in field samples between October 1985 and May 1986. Note logarithmic scale. Onset of reproduction in adult plants indicated (R)

the end of March, when young spermatangial branches were found on adult plants. Male plants were present for only two more months; they were last observed at the end of May when a few of the surviving plants had fully mature spermatangial branches (Table 2).

Reproductive female plants were first collected at the end of April, when some plants bore carpogonia over the entire thallus length (Fig. 1; Table 2). Mature cystocarps containing carpospores were observed from the end of May, and by early June spore release had started (Table 2). Plants released spores from the entire thallus length, suggesting that all cystocarps were of approximately the same age. By the end of June several plants bore only empty cystocarps, and the last female plants were collected in the first week of July (Fig. 1; Table 2). During the rest of the summer *Bonnemaisonia*-phase plants were not seen at either of the two stations.

Culture experiments

Gametophytes and tetrasporophytes survived temperatures between 0 and 25 °C, but 30 °C was lethal after 2–6 weeks. Growth responses were similar at low temperatures (Fig. 3), but at 20–25 °C tetrasporophytes grew much better than gametophytes (Fig. 3). Maximum growth yields of tetrasporophytes were obtained at 15–25 °C and of gametophytes at 15 °C (Fig. 3). At 25 °C gametophytes showed abnormal growth forms consisting of branched rhizoidal filaments from which small plants of normal morphology occasionally arose but these died after a few weeks. At 20 °C the development of very young sporelings was also abnormal, particularly at high photon fluence rates.

Tetrasporophytes reproduced under short day conditions of less than 12 h of light per day, and at temperatures between 11 and 18 °C (Fig. 4). There was a very sharp transition in the response at 12 and 18 °C; at these temperature extremes results were rather variable (Fig. 4a). Tetrasporangia were first observed after 10–14 days of incubation, but in many experiments tetrasporangium formation took at least 3 weeks. Once tetrasporan-

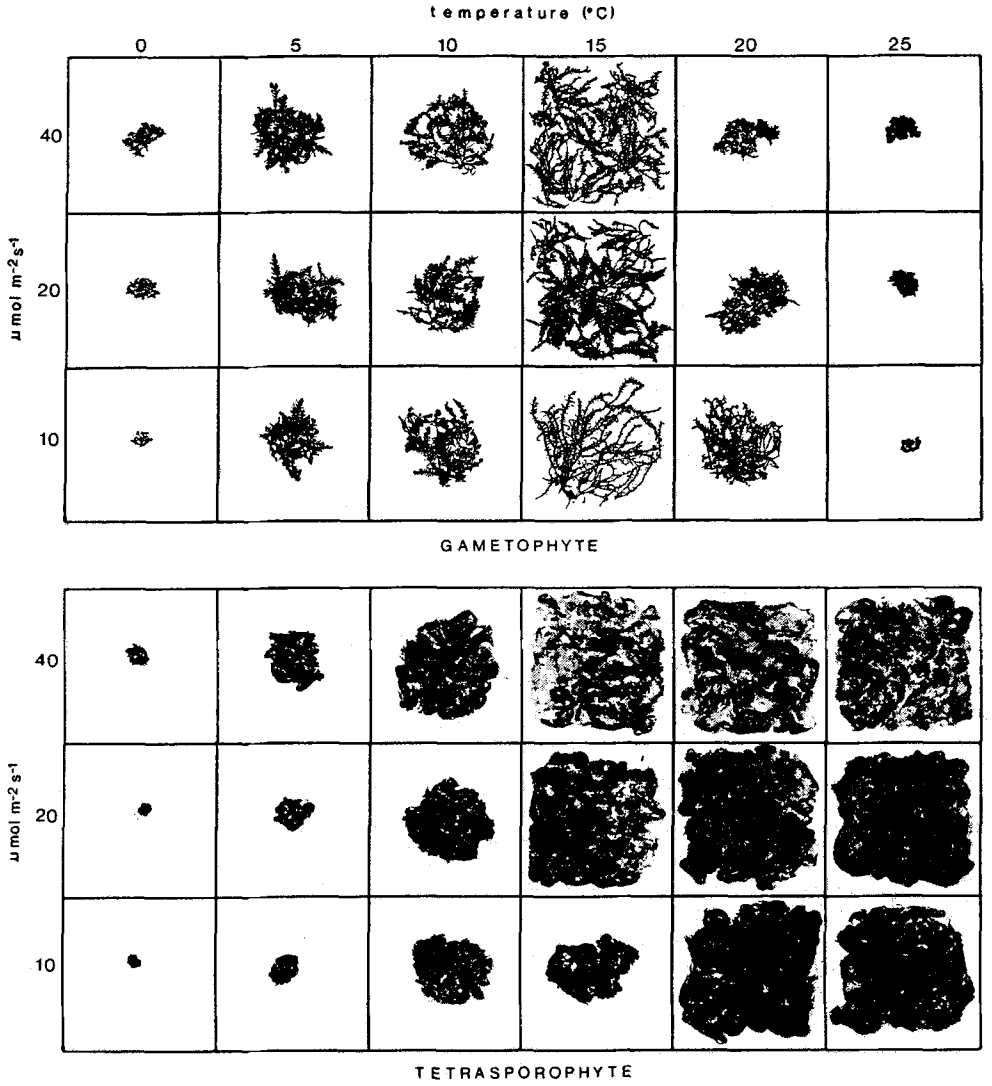

Fig. 3. *Bonnemaisonia hamifera*. Growth yield of gametophytes and tetrasporophytes after 3 months' incubation at 6 different temperatures at 3 photon fluence rates; at 0 °C in short days (8:$\overline{16}$), at 5–25 °C in long days (16:$\overline{8}$)

gia had developed, spore release started within a few days, and spore germination occurred at all conditions where tetrasporangia had been formed.

Gametophytes became fertile between 5 and 20 °C , but not at 0 and 25 °C (Fig. 5). Spermatangia developed more rapidly than carpogonia under similar conditions (Fig. 5). Male plants became fertile both in long and in short days at 5–20 °C, and the formation of spermatangia took between 6 and 18 weeks from the germination of tetraspores, depending on temperature and light conditions (Fig. 5). Carpogonia developed between

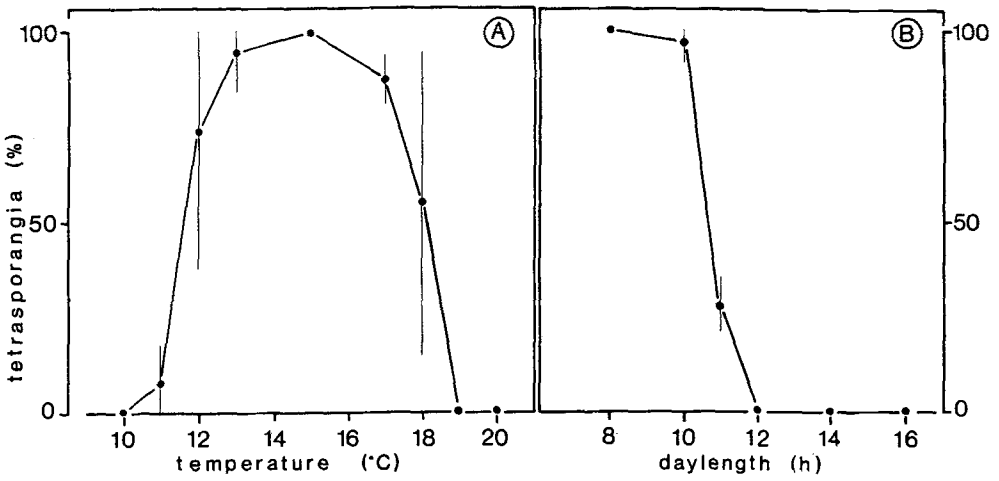

Fig. 4. *Bonnemaisonia hamifera*. Temperature and daylength requirements for formation of tetrasporangia. A: in short days (8:$\overline{16}$) at 20 µmol photons m^{-2} s^{-1}. B: at 15 °C and 20 µmol photons m^{-2} s^{-1}. Values represent means of 3–4 replicate experiments each with 32–50 plants per treatment. Vertical bars (s. dev.)

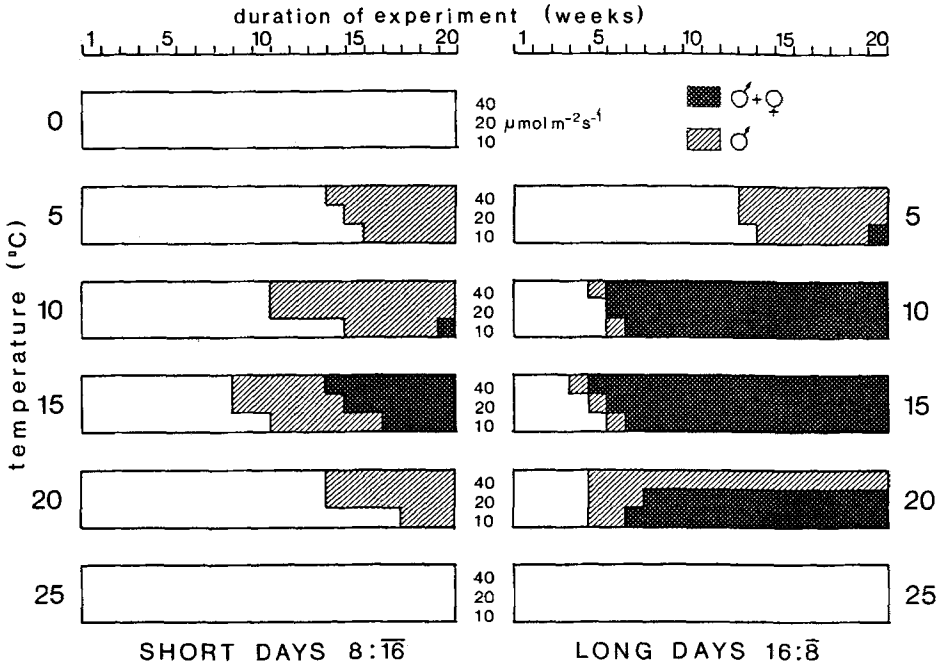

Fig. 5. *Bonnemaisonia hamifera*. Time course for the development of spermatangia and carpogonia in male and female gametophytes kept at 6 different temperatures in long (16:$\overline{8}$) and in short (8:$\overline{16}$) days at 3 photon fluence rates. Experiment was carried out using newly released tetraspores. Mean number of plants per treatment: n = 15

(5–)10 and 20 °C, but mainly in long days, where their formation took about 5–7 weeks (Fig. 5). In short days, carpogonia were only formed in abundance at 15 °C (Fig. 5).

Under some conditions (i.e. 10 and 15 °C long days at 10, 20 and 40 μmol photons m^{-2} s^{-1}) all gametophytes eventually developed reproductive structures. Of a total of 91 plants there were 53 male and 37 female plants, which is not significantly different from the expected 1:1 sex ratio ($P > 0.05$, Chi-square). Plants stopped growing once they had reached reproductive maturity and at the end of the experimental period of 3 months fertile plants showed indications of senescence.

DISCUSSION

Life history regulation in Galway Bay

In Galway Bay, on the west coast of Ireland, the reproductive phenology of *Bonnemaisonia hamifera* was strictly regulated by temperature and daylength. Tetrasporangia were abundant only during the brief period from mid-October to early November when short day conditions (< 12 h of light per day) coincided with mean seawater temperatures in excess of 11 °C (Fig. 6). Tetrasporangia were also observed before and after this period, although in lower numbers. These suboptimal responses have been attributed to short-term inductive effects of microclimatic factors which will be discussed in detail elsewhere (Breeman & Guiry, unpublished).

Male gametophytes first started reproducing by mid-December when they were still in a juvenile stage and attached to the *Trailliella* filaments. The appearance of spermatangial branches within 11 weeks of the onset of tetraspore release (Figs 1, 6) accords well with experimental results. In culture, their development also took 11 weeks under similar temperature conditions (ca 10 °C, short days; Figs 5, 6). No fertile male plants were found in midwinter which must be attributed to the unusually low seawater temperatures of ca 2 °C in February 1986 (Figs 5, 6). Spermatangia reappeared at the end of March, shortly after seawater temperatures had risen to around 5 °C again.

Female plants reached reproductive maturity by the end of April, shortly after seawater temperatures had risen to the required value of about 10 °C (Fig. 6). Moreover, daylength had increased during March, also promoting their rapid formation (Fig. 5). The fact that carpogonia developed more or less simultaneously over the whole length of the thalli also shows that critical requirements for their induction had suddenly been met.

The initiation of reproduction in gametophytes is thus strictly regulated by temperature. However, the duration of fertility and the longevity of gametophytes is clearly not a function of temperature as they were absent after mid-July, when seawater temperatures of 15–16 °C were still optimal for growth and reproduction (Figs 3, 5, 6). Both in culture and in the field, gametophytes ceased growth once they had reached reproductive maturity, and they subsequently disintegrated after 2–3 months. Gametophytes thus seem to be unable to perennate independently of the tetrasporophyte as has been suggested by various authors (e.g. McLachlan et al., 1969; Dixon, 1970; Dixon & Irvine, 1977). Gametophytes may be able to persist as unorganised rhizoidal filaments capable of regenerating into normal plants (Chen et al., 1970). In our cultures such unorganised filaments also developed, but only under unfavourable temperature conditions (> 20 °C; Fig. 3) and normal development was quickly resumed under more favourable conditions.

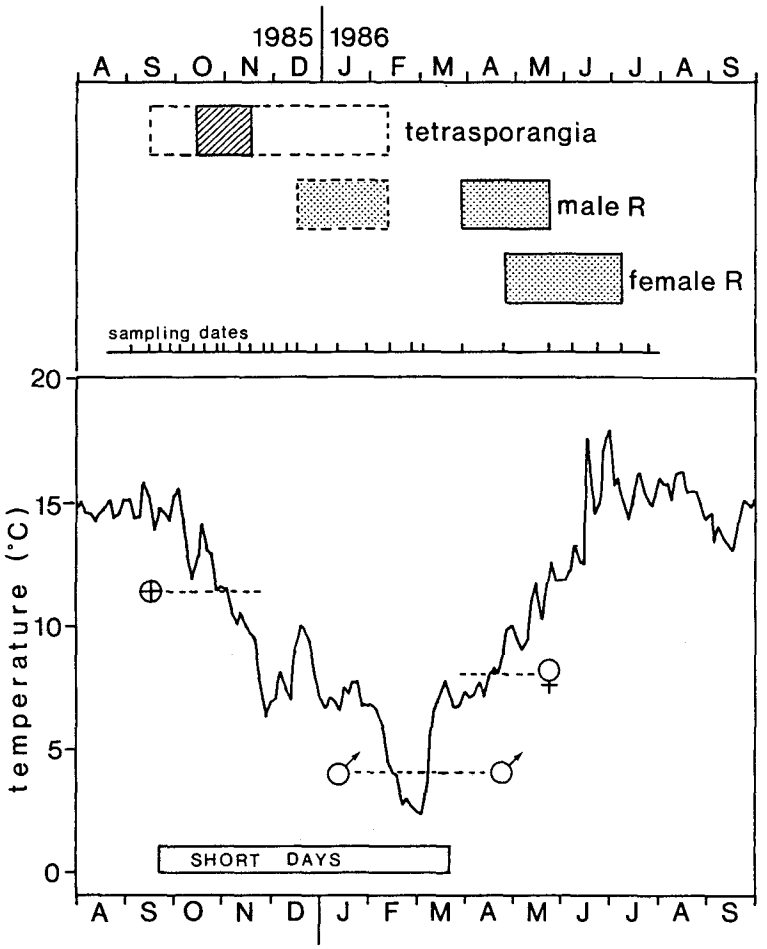

Fig. 6. *Bonnemaisonia hamifera*. Reproductive phenology of tetrasporophytes, male and female gametophytes in relation to seawater temperature and daylength in Galway Bay during 1985/1986. Sampling dates indicated. Tetrasporangia present (blank bar), abundant (shaded bar); reproductive adult male and female plants (shaded bar, solid line); spermatangia in juvenile plants (shaded bar, dashed line). Experimentally determined lower temperature limits for reproduction of tetrasporophytes (⊕), male (♂) and female (♀) gametophytes are indicated. Temperatures are 3-day mean values for Carna (Co. Galway, Ireland)

On the west coast of Ireland temperatures were favourable for normal development of gametophytes throughout the summer, but no evidence has been found for regeneration of gametophytic plants from unorganised filaments or for large-scale survival of fragments. In fact, during our very extensive sampling program in the autumn of 1985, a small fragment of what was evidently a perennating gametophyte was found only once. One argument for the independent vegetative propagation of the gametophyte was the absence of basal attachment structures, which would indicate origin from a spore, in the adult plants (Dixon, 1970). However, tetrasporelings do attach to the *Trailliella*-phase

filaments upon germination (see also Chen et al., 1969; Kornmann & Sahling, 1983). The *Trailliella* tufts thus act as a kind of „nursery" for the young gametophytes until these are old enough to have developed their attachment hooks. These hooks probably promote vegetative reproduction through fragmentation of the adult plant, but this does not prevent senescence of the plants after they have reached sexual maturity. Thus the occurrence of gametophytes in the field is probably completely dependent of the induction of tetrasporangia during the previous year.

Phenology and distribution in the North Atlantic Ocean

The greater geographical range of the *Trailliella*-phase in the North Atlantic Ocean (Fig. 7) indicates that this phase must be able to persist solely by means of vegetative propagation. Gametophytes have been reported only from regions where tetrasporangium induction is possible (Fig. 7; van den Hoek, 1982; Lüning, 1985) indicating that this phase generally originates from spores. Failure to form tetrasporangia is the most likely reason for the absence of gametophytes from parts of the distribution range (van den Hoek, 1982; Lüning, 1985). However, this explanation seems to be valid only in the northeastern Atlantic (Fig. 7), where temperatures fall below the lower limit for tetrasporangial formation (ca 11 °C) before the autumnal equinox. Elsewhere, the appropriate temperature/daylength combinations for tetrasporangial induction occur for some part of

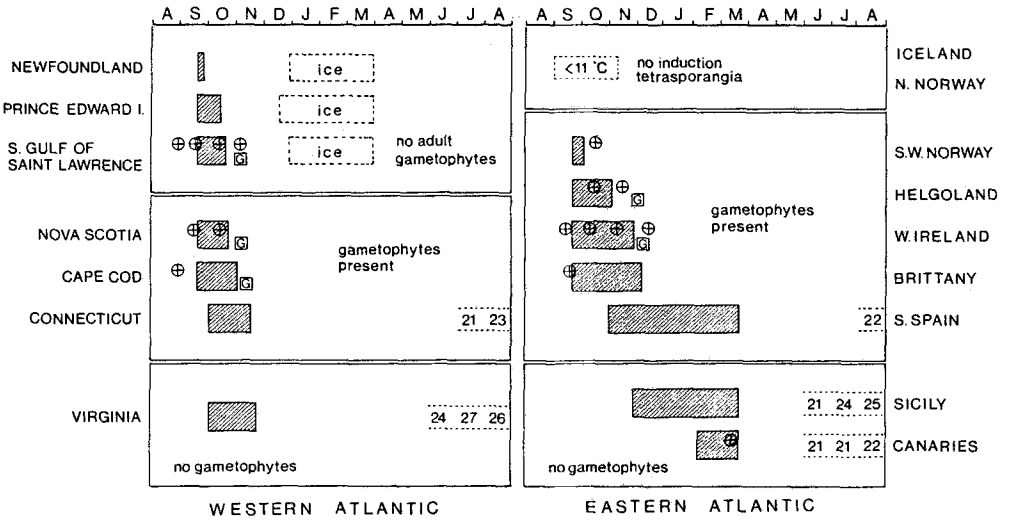

Fig. 7. *Bonnemaisonia hamifera*. "Reproductive window" for tetrasporophytes in relation to the geographic distribution of the gametophyte in the eastern and western Atlantic. Shaded bars indicate periods when temperature and daylength conditions are favourable for the induction of tetrasporangia in an average year; symbols show when tetrasporangia (⊕) and germlings of gametophytes (G) have been reported in the field (Börgesen, 1930; Printz, 1953; Feldmann, 1954; Chen et al., 1969; Sears & Wilce, 1975; Kornmann & Sahling, 1983). Periods when temperatures above 20 °C would prevent normal development of juvenile gametophytes are indicated. Temperature data based on Gorshkov (1978) and local records for Helgoland and all western Atlantic locations (cf. Breeman, 1988). See text for further explanation

the year (Fig. 7). In fact, tetrasporangia have been found in some regions where gametophytes are apparently absent. In the southern Gulf of Saint Lawrence, for instance, both tetrasporangia and germlings of gametophytes were found in autumn but no adult gametophytes could be detected during the following spring (Chen et al., 1969). Possibly the germlings perish under winter ice (Fig. 7). Tetrasporangia have also been reported (Börgesen, 1930) from the Canary Islands (Fig. 7), but here they were found no earlier than March, probably because temperatures above 19 °C had prevented their induction earlier in the year. Since temperatures over 20 °C would prevent normal development of the germlings from the end of May, gametophytes would have insufficient time to develop into adult plants, which explains their absence in the Canary Isles. The absence of gametophytes from the central Mediterranean and Virginia (Fig. 7) is less easily explained, because in these areas they would be able to occur as short-lived spring annuals.

In general, induction of tetrasporangia will be confined to a brief period in autumn (Fig. 7) when short days coincide with seawater temperatures above 11 °C . During the rest of the short day season, in winter and early spring, temperatures are too low for induction. This applies to the entire distribution range on American coasts and to the more northerly locations on European coasts (Fig. 7). The "reproductive window" (Lüning, 1980, 1981) will be somewhat narrower on western than on eastern Atlantic coasts (Fig. 7), because of the steeper autumnal fall in seawater temperatures in the west (Breeman, 1988). This may account for the scarcity of records of tetrasporangia from the American coast (McLachlan et al., 1969; Dixon & Irvine, 1977). At the more northerly locations (e.g. Norway, Helgoland, Nova Scotia; Fig. 7) tetrasporangium induction may fail to occur during years with unusually cold autumns. This ist probably the reason for the sporadic occurrence of gametophytes in these areas (Bird, 1980; Lüning, 1980, 1981; Kornmann & Sahling, 1983). As was the case in Galway Bay, tetrasporangia were occasionally observed also before and/or after the main inductive season, although in lower numbers (e.g. Chen et al., 1969). This points to the effectiveness of intermittent, brief exposures to inductive conditions brought about by microclimatic factors. Tetrasporangial periodicity may thus vary considerably, both between years and between habitats at any one location.

The reproductive success of gametophytes depends on the simultaneous occurrence of fertile male and female plants. Reproductive plants of *Bonnemaisonia hamifera* will be present only for a brief period of time, because senescence rapidly follows the onset of reproduction. Moreover, there will be little variation among plants because they are all initiated from tetraspores over a relatively brief period of time (Fig. 7), are thus of approximately the same age, and will have been exposed to similar environmental conditions.

In most of the North Atlantic Ocean, temperatures below ca 10 °C and short days will prevent the onset of reproduction in female plants until early or late spring (Fig. 8: Galway Bay and Halifax). Reproduction may as a result start later at more northerly locations, particularly in the western Atlantic, because of persistent low temperatures in spring. Indeed, reproductive female plants were observed from April/May in the English Channel and on the Irish west coast (Simon-Bichard-Bréaud, 1970; this paper), from June on Helgoland (Kornmann & Sahling, 1962), from July/August in Massachusetts (Simon-Bichard-Bréaud, 1970; Sears & Wilce, 1975) and only from August/September in Halifax

(Bird, 1980) and Norway (Lye, 1965; Haugen, 1970). In each case this was shortly after mean seawater temperatures had risen to the required value of about 10 °C (Gorshkov, 1978).

The timing of reproduction of male gametophytes is less predictable than that of female gametophytes as gametogenesis also occurs at lower temperatures and in short days, the amount of time required for spermatangium formation varying considerably with the precise temperature and light conditions. Male gametophytes may as a result reach reproductive maturity at any time during winter and spring. In the western Atlantic, where tetraspore production will have ceased relatively early in autumn (Fig. 7), all male plants may have started reproducing in early winter when they are still juveniles. This would account for the reported scarcity of male plants on American coasts, because such plants could easily be missed in field surveys. In fact, the only report of a male plant from the American coast dates from February, when small plants (ca 10 cm long) bearing mature spermatangia were found near Halifax, Nova Scotia (Chen et al., 1969).

In the eastern Atlantic, where tetrasporangial formation appears to be of longer duration (Fig. 7), the timing of reproduction of male plants will be more variable. Male plants formed early in autumn may reproduce prematurely but those initiated relatively late in autumn may not start reproducing before the following spring. However, they will always do so earlier than the females because of their lower temperature requirements; thus, they will also undergo senescence earlier in the year. Several field observations confirm that male plants disappear earlier than females (e.g. Helgoland: Kornmann & Sahling, 1962; Galway Bay: this paper; Brittany: Bichard-Bréaud & Floc'h, 1966; various locations on the English Channel: Simon-Bichard-Bréaud, 1970). Frequently, there is only a brief temporal overlap in the occurrence of fertile male and female plants (e.g. in Helgoland: Kornmann & Sahling, 1962; Galway Bay; Fig. 8), whereas at some locations, particularly in the western Atlantic (e.g. Halifax; Fig. 8), reproduction in male and female plants appears to have become completely separated in time (Chen et al., 1969; Bird, 1980). As a result, carpogonia will fail to be fertilised, which explains why only carpogonia and rudimentary pericarps have been reported from this location (Bird, 1980).

It thus appears that both in the eastern and western Atlantic the formation of male and female reproductive structures has, to some extent, become separated in time. In contrast, in Japan, where mature cystocarps were observed regularly (Chihara, 1961), the sexual cycle of *B. hamifera* is very well synchronised. For instance at Shimoda (Chihara, 1961; Fig. 8), induction of tetrasporangia may be expected from late autumn to early spring. Gametophytes thus start their development in winter when temperatures of around 15 °C are optimal for growth and reproduction of both male and female plants (Figs 3, 5). As a result, they will reach reproductive maturity in spring, the males somewhat earlier than the females, because they develop more rapidly. Field observations support these conclusions, as in Shimoda reproductive male and female plants were observed from early and late April, respectively (Chihara, 1961). At this location, gametophytes have disappeared from the field by mid-June, probably because seawater temperatures reach lethal high values of around 25 °C. However, before this time, they will have had sufficient time to have completed their sexual cycle (Fig. 8). An interesting point is that Japanese plants also stopped growing once they had reached reproductive maturity, but their final size was only 12 cm (Chihara, 1961), compared with 40 cm in Galway Bay. The reason for this difference must be that, in Japan, reproduction, and with

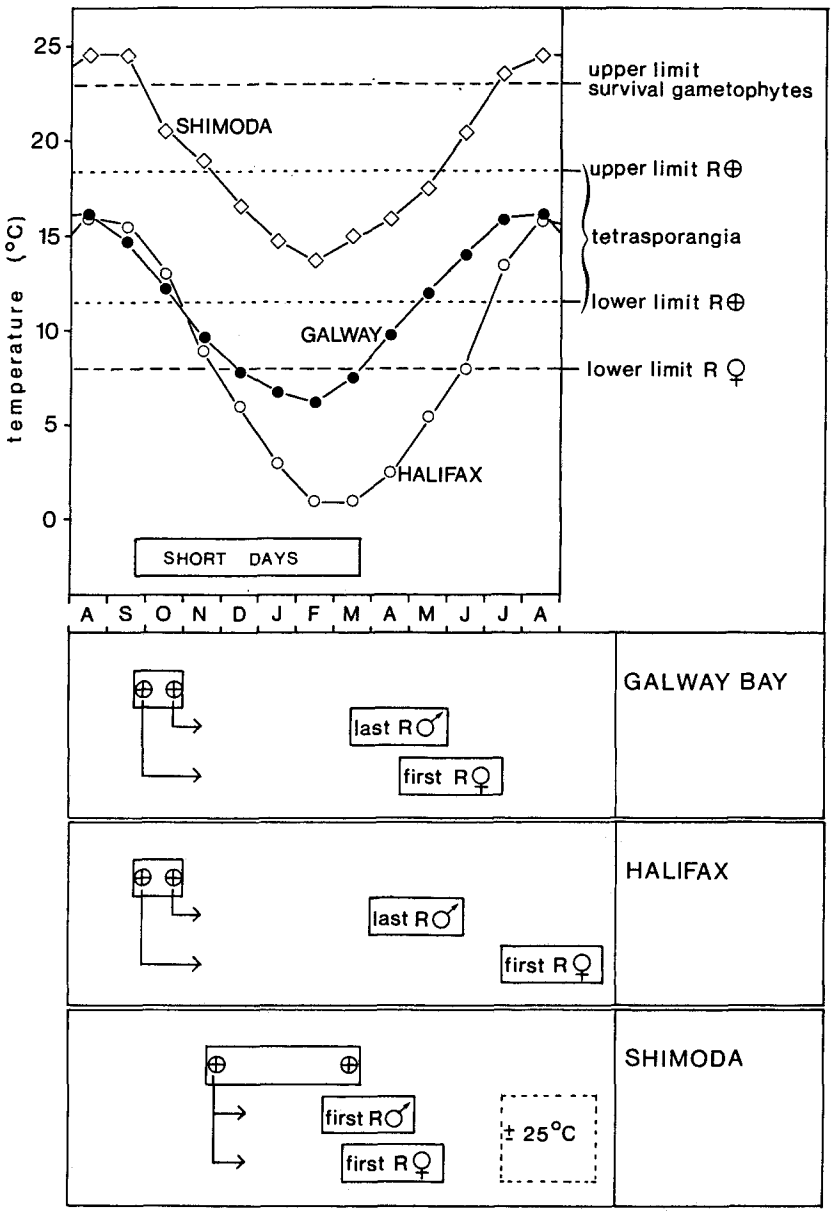

Fig. 8. *Bonnemaisonia hamifera*. Timing of reproductive events in relation to seawater temperatures in the eastern Atlantic (Galway), the western Atlantic (Halifax) and Japan (Shimoda). Temperature data based on Chihara, 1961 (Shimoda), Bird et al., 1983 (Halifax) and 10-year monthly means for Galway (Marine Shellfish Laboratory at Carna, unpublished). Experimentally determined temperature limits for reproduction of tetrasporophytes and female gametophytes and for survival of gametophytes in a normal growth form are indicated. See text for further explanation

it the cessation of growth, is induced in younger plants as a result of the more favourable temperature conditions. Thus, although the reproductive phenology was apparently quite similar in Japan and in Galway Bay, it was, in fact, regulated by a different temperature fluctuation regime (Fig. 8).

In summary, the physiological responses of *B. hamifera* make this species much better adapted to conditions in Japan than in the North Atlantic Ocean. This would seem to be additional evidence for a Japanese origin (Feldmann & Feldmann, 1942; Koch, 1949; Dixon & Irvine, 1977; West & Hommersand, 1981) of the Atlantic populations of this species. There may be several reasons for its enigmatic phenology in the Atlantic. In the first place, tetrasporangia will generally be present only during a brief period in autumn and may therefore pass unnoticed. Secondly, the induction of tetrasporangia, and the resulting crop of gametophytes for the following year, may be prevented during years in which unusually cold autumns occur. This would account for the sporadic occurrence of gametophytes in the northernmost part of the distribution range. Thirdly, male plants may reach reproductive maturity in winter when they are still in a juvenile stage, and then undergo senescence; this may account for their apparent absence in some regions. Finally, the onset of reproduction in female plants may be retarded by low temperatures in spring to such an extent that male plants have already senesced. This would account for the many reports of sterile pericarps in the North Atlantic Ocean.

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