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Studies on the Recently Introduced Brown Alga *Sargassum muticum* (Yendo) Fensholt

IV. The Effect of Temperature, Irradiance and Salinity on Germling Growth

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Abstract

The growth rates of germlings of the large, introduced, brown alga *Sargassum muticum* (Yendo) Fensholt, collected from Bembridge, Isle of Wight, south coast of England, are described under different conditions of temperature, irradiance and salinity. The germlings showed a broad tolerance to all three environmental parameters, with growth recorded from 10 to 30 °C, 9 to 175 $\mu\text{E m}^{-2} \text{s}^{-1}$ (500 to 10 000 lux) and 6.8 to 34‰ salinity; optimum growth occurred at 25 °C, 44 $\mu\text{E m}^{-2} \text{s}^{-1}$ (2500 lux) and 34‰ salinity. These results are discussed in relation to aspects of the present and future ecology and geographical distribution of this invasive alga.

Introduction

As a consequence of its introduction to the British Isles and North Atlantic in the early 1970's (Farnham *et al.* 1973) the large, brown, invasive alga *Sargassum muticum* (Yendo) Fensholt has received particular attention from investigators. Aspects studied include its ecology (Critchley 1981; Jephson and Gray 1977), local and geographical spread and consolidation (Boalch and Potts 1977; Critchley and Morrell 1982, Critchley *et al.* 1983), life history (Fletcher and Fletcher 1975 a, Fletcher 1980) and vegetative plant growth (Fletcher and Fletcher 1975 b, Chamberlain *et al.* 1979, Gorham 1979, Kane and Chamberlain 1979). The primary objective of these studies was to provide a detailed understanding of the biology of the species which would, at most, provide a means of its eradication and control if required and, at least, predict its geographical spread and likely ecological impact on North Atlantic shores.

Fundamental to the success and spread of *Sargassum muticum* in the North Atlantic and beyond is its ability to tolerate and respond to environmental parameters. In this respect probably the most vulnerable growth stage in the life history are the young germlings. To date germling growth rates in relation to controlled physical factors have only been investigated in the *Sargassum* species *S. echinocarpum* J. Agardh, *S. obtusifolium* J. Agardh, *S. oligocystum* Montagne, *S. polyphyllum* J. Agardh (De Wreede 1976, 1978) and Pacific populations of *S. muticum* (Norton 1977). In the present paper results are presented of an investigation into the effect of temperature, irradiance and salinity on European *S. muticum* germlings.

Materials and Methods

Details of the three germling growth studies are listed in Table I. Healthy fertile plants were taken from the mouth of Langstone Harbour, Hampshire and cultured at 20 °C under continuous light until multicellular germlings were released. These germlings were stored in a 10 °C growth room at 50 $\mu\text{E m}^{-2} \text{s}^{-1}$ with

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Table I. Culture regimes used to investigate the influence of temperature, irradiance and salinity on *S. muticum* germling growth.

	Growth study 1 (Temperature variable)	Growth study 2 (Irradiance variable)	Growth study 3 (Salinity variable)
Temperature (°C)	10, 15, 20, 25, 30	20	20
Light intensity (lux)	4200	0, 500, 1000, 2500, 5000, 10 000	4200
Irradiance ($\mu\text{E m}^{-2} \text{s}^{-1}$)	74	0, 9, 18, 44, 88, 175	74
Salinity (‰)	34	34	0, 3.4, 6.8, 10.2, 13.6, 17.0, 20.4, 23.8, 27.2, 30.6, 34.0
Daylength (hours) (light:dark)	16:8	16:8	16:8
No. germlings at each regime	200	200	200
Start of experiment	November 1981	November 1981	November 1981
Period of culture (weeks)	4	4	4

regular seawater changes for two weeks and then used in the germling growth studies. Two hundred germlings were cultured in each regime and soon attached themselves to the base of the culture vessel. The mean germling length at the start of each study was 1.4 mm.

For the cultures 9 cm diameter glass crystallising dishes with glass lids were used throughout. Two dishes were used for each culture regime, with the germlings divided between them as equally as possible. Each culture dish contained 150 cm³ of von Stosch culture medium (von Stosch 1964). This volume was changed at three day intervals for the duration of the study. Different temperatures were maintained by placing the culture vessels in adjustable temperature water baths with thermostatic controls. Different irradiances were maintained by positioning the culture vessels at different distances from overhead cool white fluorescent tubes whilst different salinities were obtained by diluting von Stosch culture medium with distilled water. The germlings were introduced to the lower salinities by gradually passing them through a decreasing salinity gradient. An acclimation period of at least 3 hours was used at each of the salinities in this gradient.

Growth of germlings was recorded in terms of length and was measured at regular intervals using a dissecting microscope and an eyepiece graticule. The germling lengths excluded rhizoid measurement.

Results

Temperature and germling growth

Figure 1 shows an increase in germling growth with increasing temperature from 10 to 25 °C. In this range the relationship between germling growth (G) and temperature (T), after two weeks culture can be seen to fit the linear equation $G = a + b \cdot T$. There is a highly significant correlation between G and T, the

probability of unrelatedness being less than 0.1%. The descending part of the curve is fitted by eye and shows an inhibition of growth over the range 25 to 30 °C. Maximum growth during the first two weeks of culture occurred at 25 °C (0.21 mm day⁻¹) while growth at 30 °C averaged approximately 0.09 mm day⁻¹. At the end of this period the mean growth of germlings cultured at 10 °C was 1.3 mm while that of germlings cultured at 25 °C was 3 mm. The relationship between germling growth and temperature after four weeks culture may also be linear in the range 10 to 25 °C although in this case no 25 °C values were

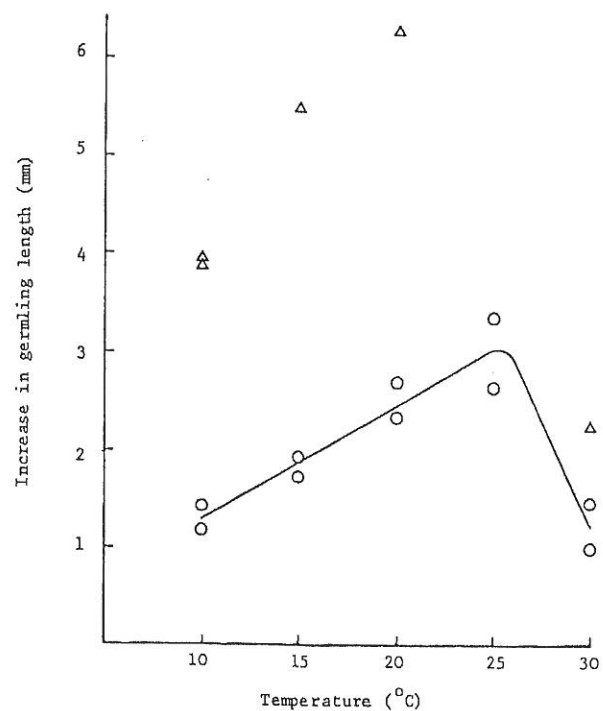


Fig. 1. The growth of *Sargassum muticum* germlings after 2 (○) and 4 (△) weeks culture at different temperatures. After 2 weeks culture the relationship between germling growth (G) and temperature (T) in the range 10 to 25 °C fits the linear equation, $G = 0.147 + 0.1151 T$ (6 d.f.; $r = 0.947$; $P < 0.001$)

available. At 30 °C the growth of germlings was still suboptimal after four weeks culture; after this period of time 95% confidence limits demonstrate a significant difference between growth at 20 and 30 °C.

Irradiance and germling growth

Figure 2 shows that germling growth occurred at all investigated irradiances in the range 9 to 175 $\mu\text{E m}^{-2} \text{s}^{-1}$ (500 to 10 000 lux). During the first two weeks culture, germling growth (G) can be seen to increase with irradiance (I) over the range 9 to 44 $\mu\text{E m}^{-2} \text{s}^{-1}$ (500 to 2500 lux). The relationship between the two variables fits the logarithmic equation $G = a + b \ln I$ and the probability of unrelatedness is less than 1%. This is a highly significant correlation. The four week curve and the descending portion of the two week curve are fitted by eye.

After 2 weeks culture maximum growth (0.28 mm day⁻¹) was evident at 44 $\mu\text{E m}^{-2} \text{s}^{-1}$ (2500 lux). High germling mortality occurred at 88 and 175 $\mu\text{E m}^{-2} \text{s}^{-1}$ (5000 and 10 000 lux) during these first two weeks of culture and growth was minimal at 175 $\mu\text{E m}^{-2} \text{s}^{-1}$ (10 000 lux). During the second two weeks of culture there was no further mortality and growth rates at all irradiances increased to more than 0.3 mm day⁻¹. Optimal growth occurred over a broader range of irradiance (18 to 88 $\mu\text{E m}^{-2} \text{s}^{-1}$) during this period.

The final mean lengths of germlings cultured at 9, 44 and 175 $\mu\text{E m}^{-2} \text{s}^{-1}$ were 6.2, 9.3 and 5.4 mm respectively. Germlings cultured in total darkness did not grow during the four week culture period.

Salinity and germling growth

Germlings grew in all investigated salinities except those of 0 and 3.4‰ (see Fig. 3). Growth increased with increasing salinity over the range 6.8 to 34‰; in the 6.8‰ cultures the mean germling growth rate was approximately 0.03 mm day⁻¹ but at full seawater salinity a value of 0.36 mm day⁻¹ was attained. After four weeks germlings cultured at 6.8‰ exhibited a mean extension of 0.95 mm while those cultured at 34‰ showed a mean extension of 10.6 mm. The relationship between germling growth (G) and salinity (S) in this range was found to fit logarithmic equations ($G = a + b \ln S$) after both two and four weeks culture. In each case there was a highly significant correlation between G and S, the probability of unrelatedness being less than 0.1%. Germlings were able to grow at very low salinities; the salinity at which growth ceased and death ensued appeared to lie between 3.4 and 6.8‰. All germlings exhibited a normal pattern of development except those cultured at the lowest end of the tolerance range (6.8‰) which developed a multibranched morphology.

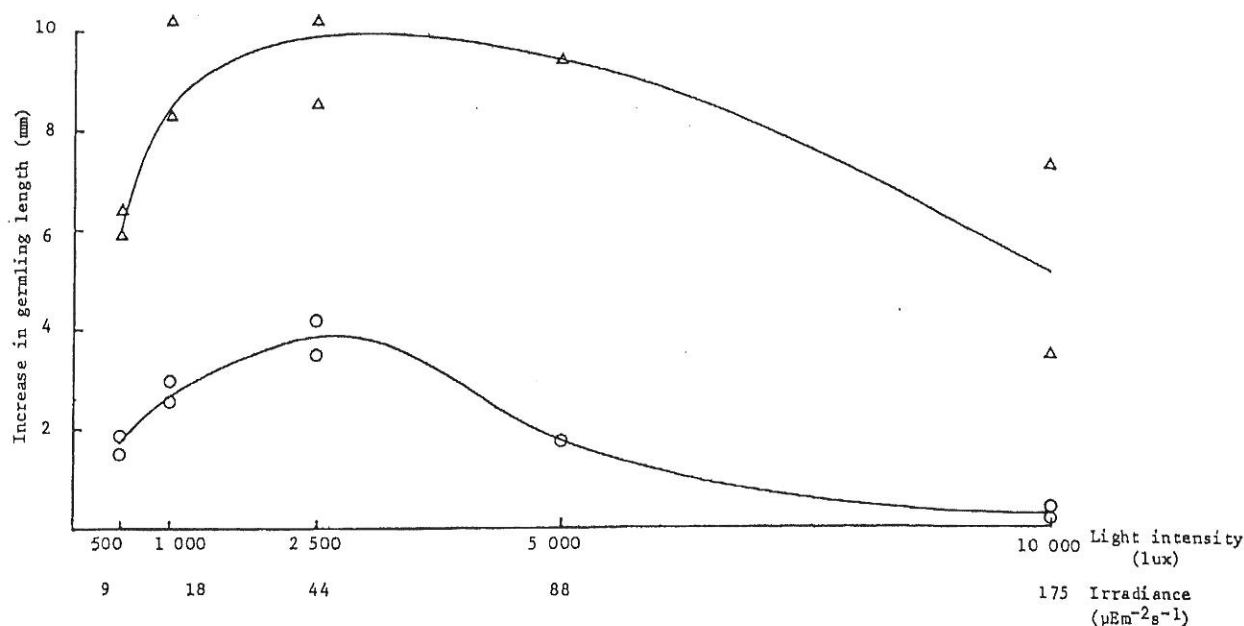


Fig. 2. The growth of *Sargassum muticum* germlings after 2 (○) and 4 (△) weeks culture at different irradiances. After 2 weeks culture the relationship between growth (G) and irradiance (I) in the range 9 to 44 $\mu\text{E m}^{-2} \text{s}^{-1}$ fits the logarithmic equation,
 $G = 1.1614 + 1.336 \ln I$
 (4 d. f.; $r = 0.957$; $P < 0.01$)

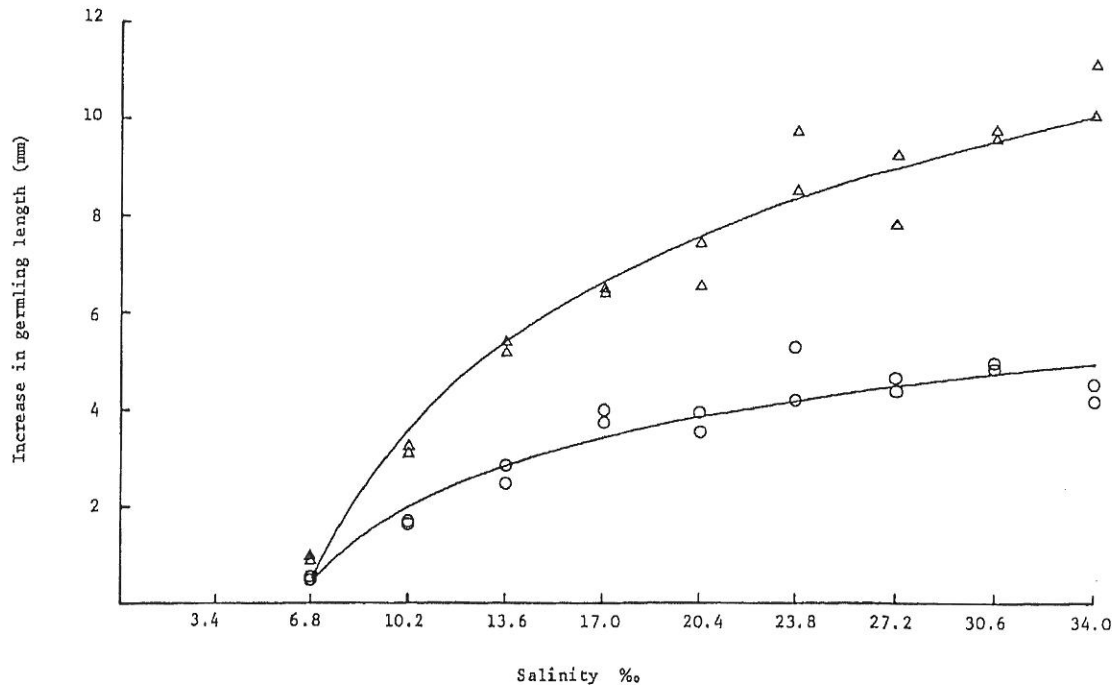


Fig. 3. The growth of *Sargassum muticum* germlings after 2 (○) and 4 (△) weeks culture at different salinities. After 2 and 4 weeks culture the relationships between germling growth (G) and salinity (S) fit the following logarithmic equations:

2 weeks: $G = -1.0552 + 1.766 \ln(S-4.5)$
(18 d. f.; $r = 0.959$; $P < 0.001$)

3 weeks: $G = -3.7615 + 4.0593 \ln(S-4)$
(18 d. f.; $r = 0.979$; $P < 0.001$)

Discussion

The effect of temperature on germling growth

The germling growth studies demonstrate that *Sargassum muticum* is able to tolerate and develop under a wide range of temperatures between 10 and 30 °C. The cultured material continued to grow at both ends of this temperature gradient suggesting that the thermal tolerance of the alga exceeds the 20 °C range used in the investigations. Norton (1977) investigating North American *S. muticum* populations has similarly demonstrated a tolerance range of at least 20 °C (from 5 to 25 °C) for vegetative lateral branches and germlings (see below). The broad thermal tolerance illustrated in these laboratory experiments is also demonstrated by the species' wide geographical distribution. In its native Japan, *S. muticum* is influenced by the warm waters (20 to 28 °C) of the Kuroshio current (Yendo 1907) experiencing an annual temperature range from 5–28 °C (Anon 1975). It is also present in the warm waters of the Mediterranean (Knoepffler-Peguy *et al.* 1985) and occupies sheltered habitats in southern California where the temperature never drops below 14 °C and can be as high as 30 °C (Nicholson *et al.* 1981). These warm habitats contrast with the relatively cold waters inhabited by *S. muticum* near Vancouver Island, British Columbia (annual

range approximately 6–15 °C, Anon 1970), in southern Alaska (annual range approximately 3–10 °C, Anon 1970) and in the Solent, southern England (annual range approximately 3–20 °C); the species' eurythermal nature is also demonstrated in its ability to colonise these temperate waters for it is in such marine habitats that the largest annual temperature range (spanning 10 to 15 °C) is known to occur (Dring 1982). Colonisation of tide pools in which temperature fluctuation is both greater and more rapid than in the sea is also made possible by the alga's broad thermal tolerance. This tolerance is comparable with that displayed by truly intertidal algae such as *Fucus spiralis* L. and *F. vesiculosus* L. (Niemeck and Mathieson 1978) which, unlike *S. muticum*, can tolerate considerable periods of emersion.

The presence of attached *Sargassum muticum* in the English Channel and in the Mediterranean suggests that it will also be able to colonise sheltered shores of intermediate temperature on the Atlantic coasts of France, Spain and Portugal. North-west Brittany is the southern limit of distribution for many European algae with a growth optimum of 10 °C but most species having a wide optimum of 10 to 15 °C have more southerly limits such as the Loire/Gironde area (*Fucus serratus* L.), north-west Spain (*F. vesiculosus*,

Chondrus crispus Stackh.), or Morocco [*F. spiralis*, *Petalonia fascia* (O. F. Müll.) O. Kuntze], (Hoek and Donze 1967). *S. muticum* has a higher optimum growth temperature (25 °C) than the above species and could be expected to penetrate even further south. It may spread to parts of the North African Atlantic coast as it presently occupies similar latitudes on the Mexican Pacific coast (Fletcher and Fletcher 1975 a).

Although *Sargassum muticum* has a wide distribution on the south coast of England no attached plants have been found on the west coast and only one on the east coast (at Sheringham, Critchley *et al.* 1983). The question arises as to whether *S. muticum* will be able to colonise sites lying further north. Germling growth rates have been shown to be substantial at 10 °C in laboratory culture (Fig. 1) and since vegetative *S. muticum* segments are able to mature at temperatures as low as 10 °C. (J. M. Hales and R. L. Fletcher, unpublished) it is probable that the species will increase its northerly distribution. The Gulf Stream has a warming influence upon the west coast of England so that winter temperatures are approximately the same as those of the south coast. The 15 °C mean sea surface isotherm for July lies so that the south coast of Ireland and most of the west coast of England are surrounded by waters at or above this temperature (Lumb 1961); the rest of the Irish coast lies between the 13 and 14 °C sea surface isotherms for July. January and July sea surface isotherms for the east coast of England show that winter and summer temperatures are generally a few degrees below those of the south coast (Lumb 1961). Jones (1981), however, has shown that the highest mean monthly temperatures recorded for several east coast sites are comparable with those recorded for south coast sites. Craig (1958) published sea surface temperature maps for Scotland which show that, although winter temperatures may be low, most of the coast is surrounded by water in excess of 13 °C in mid-July; the waters of the Moray Firth, much of the Firth of Forth and most of the western sea lochs lie at or above 15 °C at this time. These summer temperatures may well permit successful growth should *S. muticum* plants reach Scottish waters.

Figure 1 illustrates that the optimal temperature for germling growth in *Sargassum muticum* is 25 °C. Maximum growth occurred at the same temperature when vegetative lateral branches and germlings of North American *S. muticum* were cultured in the laboratory (Norton 1977). Some *Sargassum* species appear to have higher temperature optima for growth; *S. pteropleuron* Grunow from Southern Florida, for instance, undergoes maximum growth in the summer when mean maximum and minimum water tempera-

tures are 33 and 28 °C respectively (Prince and O'Neal 1979). Other *Sargassum* species have a temperature optimum very similar to that of *S. muticum*; *S. filipendula* C. Agardh, for example, taken from its northernmost geographical extension along the North American coast (Cape Cod, Massachusetts), grows optimally in culture at 25 °C (Prince 1974). Similarly the winter fertile Hawaiian species *S. echinocarpum*, *S. obtusifolium*, *S. oligocystum* and *S. polyphyllum* display maximum growth at 24 °C (De Wreede 1976, 1978). Many Japanese *Sargassum* species may also resemble *S. muticum* in their thermal tolerances and optima. They may therefore, have a similar capacity for aggressive colonisation should they be introduced into American or European waters.

The optimal temperature for *S. muticum* germling growth (25 °C) may reflect an adaptation to the warm conditions imposed by the Kuroshio current (20 to 28 °C) on the Japanese coast; it is less suited to the summer water temperatures of southern England which rarely exceed 20 °C. Optimal temperatures for the growth of germlings of British macroalgae are correspondingly lower. An increase in germling growth at temperatures up to 20 °C has been demonstrated for *Ascophyllum nodosum* (L.) Le Jol. (Sheader and Moss 1975) and for *Halidrys siliquosa* (L.) Lyngb. (Moss and Sheader 1973) a species with which *S. muticum* is often closely associated. Lower optima of 10 and 12 °C have been indicated for germlings of *Himanthalia elongata* (L.) S. F. Gray (Moss *et al.* 1973) and *Fucus vesiculosus* (Munda 1977) respectively. *S. muticum* has nevertheless formed many large dense populations on the south coast of England. The species' vigour is partly attributable to the germlings' ability to grow at reduced but substantial rates at low temperatures (Fig. 1); Norton (1977) has demonstrated germling growth at temperatures as low as 5 °C and it is probable that such growth proceeds for most of the cold winter period.

Another factor contributing to the success of *S. muticum* as a competitive immigrant species is the rapid growth rate of its young germlings which ranges from 0.2 to 0.36 mm day⁻¹ under favourable culture conditions (see Figs 1, 2 and 3). This is several times faster than the maximum growth rates recorded for several other British marine macroalgae including *Ascophyllum nodosum* (0.02 mm day⁻¹, Sheader and Moss 1975), *Halidrys siliquosa* (0.03 mm day⁻¹, Moss and Sheader 1973) and *Fucus vesiculosus* (0.035 mm day⁻¹, Munda 1977). Rapid initial germling growth rates may contribute to the success of *S. muticum* in its competition with other algal germlings and may also help to minimise the time during which the very young plants are susceptible to faunal micrograzing.

The effect of irradiance on germling growth

The initial growth of *S. muticum* germlings was inhibited or terminated at irradiances of 88 and 175 $\mu\text{E m}^{-2} \text{s}^{-1}$ (5000 and 10000 lux) but the ability to tolerate and utilise these high photon flux densities increased as early development proceeded (Fig. 2); thus during the first two weeks of culture at 175 $\mu\text{E m}^{-2} \text{s}^{-1}$ (10000 lux) the mean germling length increased by 0.3 mm while during the second two weeks of culture the mean length increased by 4.9 mm. This increasing utilisation of high irradiances during the four week culture period suggests that the optimal irradiance for growth may increase as the young *S. muticum* plant develops. In seeming contradiction to this view is the 33 $\mu\text{E m}^{-2} \text{s}^{-1}$ optimal irradiance for primary lateral branch extension reported by Lewey and Gorham (1984), which is lower than the 44 $\mu\text{E m}^{-2} \text{s}^{-1}$ optimum for germling extension demonstrated in the present study. Primary lateral branch extension, however, may not be particularly representative of the growth of the *S. muticum* plant; Lewey and Gorham (1984) have observed considerable morphological variation between plants grown under different irradiance regimes which suggests that the primary lateral branch and its subtending secondary lateral branches respond differently to the same range of photon flux densities. The measurement of final dry weight may give a more meaningful estimation of the optimal irradiance for the growth of the *S. muticum* frond; Lewey and Gorham (1984) found that the final dry weight of primary lateral branches was maximal at an irradiance of 128 $\mu\text{E m}^{-2} \text{s}^{-1}$. If the optimal irradiance for *S. muticum* growth does increase as the plant develops it is appropriate that this optimal value (128 $\mu\text{E m}^{-2} \text{s}^{-1}$) for 1° lateral growth should be intermediate between the optimal values recorded for germlings in the present study (44 $\mu\text{E m}^{-2} \text{s}^{-1}$) and for receptacles (at or above 175 $\mu\text{E m}^{-2} \text{s}^{-1}$; J. M. Hales and R. L. Fletcher, unpublished).

The tolerance of high irradiance levels enables *S. muticum*, primarily a sublittoral species, to occupy intertidal rockpools and shallow lagoons where there is comparatively little attenuation of incident radiation. In the harbours of the Solent, southern England, *S. muticum* is often attached to floating pontoons so that its buoyant fronds lie just beneath the water surface at all times and thus receive maximum irradiance. The dark brown fronds of early summer often become golden brown in midsummer on account of a decrease in pigment concentration. This may result from dilution due to rapid extension growth or may be due to pigment photobleaching (Lewey and Gorham 1984). The receptacles also become less pigmented but continue to grow throughout the fertile

summer season. The absence of *S. muticum* from intertidal sites where there is any but the briefest emersion is probably more a consequence of its inability to withstand desiccation and wave action than a reflection of any inability to withstand high irradiance levels.

The broad irradiance tolerance of *S. muticum* enables the alga to grow at low as well as high irradiances. At a photon flux density of 9 $\mu\text{E m}^{-2} \text{s}^{-1}$ (500 lux) the germlings exhibited a mean growth rate of 1.5 mm per week (Fig. 2). No growth occurred in the absence of light and viability at the end of the culture period was not assessed. Critchley (1981), however, has demonstrated that *S. muticum* germlings, like those of *Ascophyllum nodosum* (Sheader and Moss 1975) and *Halidrys siliquosa* (Moss and Sheader 1973), are able to withstand several weeks of total darkness and resume growth when returned to the light. This enables the germlings to survive temporary shading by the parent canopy or fronds of other species. It also permits survival during winter periods when daytime irradiances may fall below the level required to attain the germling compensation point. Tolerance of long periods of total darkness has also been demonstrated for meiospores and gametophytes of three *Laminaria* species (Kain 1979) and for young filaments of *Ectocarpus confervoides* (Kütz.) Batt. [= *E. siliculosus* (Dillw.) Lyngb. (Boalch 1961)]. De Wreede (1980) demonstrated that overwintering portions of *S. muticum* in the Strait of Georgia, British Columbia, receive insufficient light for the compensation point during December and concluded that they must depend on stored photosynthates during this period. The subsequent period of rapid spring growth is maintained by photosynthesis and levels of stored polysaccharide actually increase at this time (Gorham and Lewey 1984).

The optimal irradiance for *S. muticum* germling growth is initially 44 $\mu\text{E m}^{-2} \text{s}^{-1}$ (2500 lux) but appears to increase as development proceeds. Germlings of many other sublittoral species have been reported to grow optimally at lower irradiance levels. Thus sporelings of the sublittoral red algae *Naccaria wiggii* (Turn.) Endl., *Bonnemaisonia asparagoides* (Woodw.) C. Ag. and *Halarachnion ligulatum* (Woodw.) Kütz. exhibit growth optima at or below 1000 lux (Jones and Dent 1970) and germlings of *Himanthalia elongata* reach their saturation point between 636 and 1272 lux at 10 °C (Moss *et al.* 1973). *Laminaria* gametophytes have been shown to be light saturated at approximately 1000 lux (Lüning and Neushul 1978) and *L. digitata* (Huds.) Lamour. germlings of up to 10 mm in length have been reported to grow optimally between 4.5 and 9 Wm^{-2} (approx-

mately 1000 to 2200 lux) (Cosson 1973). Kain (1965) has demonstrated that temperature may modify light requirements for growth; *Laminaria* sporelings were light saturated at about 350 lux at 10 °C whereas at 17 °C saturation values lay between 1000 and 2000 lux. In the present study an optimal irradiance was recorded for *S. muticum* germlings cultured at 20 °C but optimal irradiances at lower temperatures may be reduced to values similar to those reported for the above mentioned sublittoral algae.

Also of interest is the ability of the germlings to grow in irradiances as high as $175 \mu\text{E m}^{-2} \text{s}^{-1}$ (10 000 lux). A number of British algae which also occupy both tidepools and the sublittoral exhibit lower irradiance tolerances. The growth rates of *Palmaria palmata* (L.) O. Kuntze and *Dilsea carnosa* (Schmidel) O. Kuntze, for instance, decrease above 6620 and 2690 lux respectively (Jones and Dent 1970), while *Griffithsia flosculosa* (Ellis) Batt. can only be maintained in the laboratory at light intensities under 600 lux (Filho and Jones 1973). Such algae may survive in shallow waters by occupying shaded positions but the buoyant fronds of *S. muticum* which can grow to several metres in length often reach highly illuminated surface waters and therefore require a greater light tolerance. This high tolerance may also reflect the species' ability to withstand the higher irradiance levels which prevail on the more southerly coasts of its native Japan.

Germlings of certain littoral British algae grow optimally at irradiances which exceed the optimal value for initial *S. muticum* germling growth ($44 \mu\text{E m}^{-2} \text{s}^{-1}$ or 2500 lux). Germlings of *Halidrys siliquosa*, for instance, approach a saturating illuminance at approximately 6000 lux (Moss and Sheader 1973) while those of *Dumontia incrassata* (O. F. Müll.) Lamour. (Jones and Dent 1970) and *Ascophyllum nodosum* (Sheader and Moss 1975) display maximal growth at approximately 10 000 lux. Fortes and Luning (1980) have demonstrated that the growth of the sublittoral species *Ulva lactuca*, L. *Porphyra umbilicalis* (L.) J. Ag. and *Chondrus crispus* is not inhibited by exposure to 12 500 lux for one week, while in *Plumaria elegans* (Bonnem.) Schmitz light saturation for growth is reached at 22 000 lux (Boney and Corner 1962). The maximum growth of four *Fucus* species has been shown to occur between 5000 and 10 000 lux under laboratory culture (McLachlan *et al.* 1971) and net photosynthesis in *Fucus spiralis* and *F. vesiculosus* was found to be optimal between 200 and $300 \mu\text{E m}^{-2} \text{s}^{-1}$ (Niemeck and Mathieson 1978). In another littoral species, *Ascophyllum nodosum*, Chock and Mathieson (1979) have demonstrated a requirement of $205 \mu\text{E m}^{-2} \text{s}^{-1}$ for optimal growth. *S. muticum* therefore appears to exhibit a broad irradiance tolerance at all

stages of its life history except that of very early germling development. The species' optimal irradiance requirements alter during development and, when considered together, are intermediate between those of typically sublittoral and littoral British algae. This is perhaps appropriate in an immigrant species which has shown itself capable of occupying new niches in a variety of positions including the upper sublittoral zone and permanently submersed sites of the littoral zone.

The depth to which *S. muticum* will be able to colonise any portion of coast will depend primarily upon turbidity and light quality as well as the nature of the substratum and potential biological competition. The present study demonstrates growth at irradiances as low as $9 \mu\text{E m}^{-2} \text{s}^{-1}$. Norton (1977) has demonstrated that *S. muticum* grows well at only 6.696 Wm^{-2} in culture (approximately 1600 lux in daylight) and points out that this irradiance occurs in August at depths below 25 m, in the open waters off San Juan Island, Washington. Nicholson *et al.* (1981) found *S. muticum* at depths below 12.2 m off the Californian coast but noted that the plants had drifted to these positions and consequently had imploded air vesicles. In the turbid waters of the Solent, Southern England, *S. muticum* grows profusely but is confined to relatively shallow waters; clearer waters off the nearby Bembridge coast, Isle of Wight, permit growth to approximately 8 m below extreme low water spring tides. It is probable that *S. muticum* will become established at greater depths as it encounters still clearer European waters though grazing by sea urchins, competition with Laminarian species and a diminished spectral range may impose limitations. Nicholson *et al.* (1981) note that *Macrocystis* limits the distribution of *S. muticum* on the Californian coast but that *S. palmeri* Grun. and *S. muticum* coexist with little mutual detriment, the two having different growth seasons. It remains to be seen whether Mediterranean *S. muticum* populations will impinge upon the habitats presently occupied by *S. vulgare* C. Agardh and *S. hornschurchii* C. Agardh which grow to depths of 30 and 100 m respectively (Campbell and Nicholls 1977).

The effect of salinity on germling growth

The present study demonstrates maximal growth of *S. muticum* germlings at full seawater salinity (34‰). In an earlier study Norton (1977) demonstrated the same optimal growth at 34‰ but no germling survival below 20‰. The germlings' greater tolerance of lower salinities in the present study may be due to the use of slightly older germlings, the use of enriched sea-

water, or a more gradual salinity acclimation procedure. There could alternatively be a genuine difference in the tolerance of low salinity by germlings of the respective American and European *S. muticum* populations. The results of the present study correspond quite closely with those of Khfaji and Norton (1979) who demonstrated germling growth from 34 to 8.5‰ in *Fucus vesiculosus* and *F. ceranoides* L.

Despite the broad salinity tolerance exhibited by *S. muticum* in the laboratory, field populations have only been found within a relatively narrow range of salinities (70 to 100‰ normal seawater salinity). On the North American Pacific seaboard *S. muticum* has been found growing at salinities of 24 to 25.5‰ (Druehl 1967), 27 to 35‰ (Kjeldsen and Phinney 1972) and 30 to 21‰ (Widdowson 1965). Phillips and Fleenor (1970) note the absence of *S. muticum* from an area of the Hood Canal, Washington, where snow-melt run-off in spring lowers the salinity of the upper 6 m to 8.64‰ but the alga extends from 6–10 m depth in the same region. At Chesil Fleet on the south coast of England *S. muticum* has been found at salinities ranging from 25 to 34‰ (W. F. Farnham, personal communication) and in the south west Netherlands attached populations are present in brackish water habitats at 27.1 to 30.7‰ (15 to 17‰ Cl⁻, Nienhuis 1982). On the basis of salinity tolerance under laboratory culture *S. muticum* might be expected to grow at field salinities lower than those recorded so far. If *S. muticum* continues its European spread and if seasonal temperatures permit, it will be interesting to see if the species is able to colonise sites on the eastern Danish and southern Swedish coasts where salinities are intermediate between those of the North Sea (34‰) and the Baltic (10‰).

Kjeldsen and Phinney (1972) measured *S. muticum* photosynthetic rates using a Gilson respirometer and noted no marked inhibition of photosynthesis unless salinity was reduced below 20‰. They presented data showing optimal photosynthesis at 22‰ at 10, 15 and 20 °C. Many studies use the rate of photosynthesis as a measure of the ability of an alga to function at a given salinity. The results may correspond with those of salinity studies which use survival and growth as a measure of algal functions; this is particularly so when optimal salinities are being recorded. At suboptimal salinities, however, the results of the two different methods may give differing indications of algal salinity tolerance. The discrepancy arises because photosynthetic measurements are generally made after the tested algal material has acclimatised to a new salinity for only a few hours whereas growth measurements are made after an acclimatisation lasting several days or even weeks.

Although *S. muticum* salinity tolerances have been investigated under laboratory culture and in the field, very little comparable data is available for other *Sargassum* species. It is probable that different members of the genus exhibit a range of tolerances and optima as in other genera. In the genus *Fucus*, for example, *F. ceranoides* has been shown to be successful in estuaries but absent from fully marine situations; growing thallus tips exhibited growth in culture at salinities down to 1‰ (Khfaji and Norton 1979). *F. vesiculosus* var. *spiralis* Farlow is similarly tolerant extending into tidal tributaries where extensive floodings occur and no other fucoid algae grow (Niemeck and Mathieson 1978). *F. distichus* L. emend Powell subsp. *edentatus* (de la Pyl.) Powell appears to be less tolerant of reduced salinity than *F. vesiculosus* (Munda 1977) which together with *F. spiralis* has a broad estuarine distribution (Niemeck and Mathieson 1978). Yarish *et al.* (1979) studied two estuarine red algae and demonstrated that a euryhaline algal species may consist of a number of salinity ecotypes each with some potential for physiological adaptation to salinity changes. Genetic differences controlling salinity tolerance may exist between the many isolated *S. muticum* populations of the European coast; the populations may have each developed from a small quantity of fertile drift material and hence from different initial gene pools.

Total available carbon appears to be particularly relevant to the photosynthesis of marine plants and may be more important than the absolute concentration of salts or the osmotic pressure of a culture medium. Dissolved carbon dioxide (CO₂), bicarbonate ions (HCO₃⁻) and carbonate ions (CO₃⁻) all contribute to the total carbon dioxide which is potentially available to a marine alga. Gordon *et al.* (1980) used 200 mg l⁻¹ NaHCO₃ as a supplement in the preparation of different salinities for a study of salinity tolerance in the green alga *Cladophora albida* (Huds.) Kütz. They demonstrated some suppression of photosynthesis at 0.2 and 60‰ but little effect over the range 10 to 40‰. Chock and Mathieson (1979) used a NaHCO₃ buffer in a similar investigation of *Ascophyllum nodosum* and demonstrated a maximum photosynthetic efficiency at 0 to 30‰. In *Ulva*, *Porphyra* and *Gelidium* the photosynthetically inhibitory effect of diluting culture media has been largely negated by maintaining high NaHCO₃ levels and normal salinity has been shown to have no positive benefit in the absence of available carbon (Ogata and Matsui 1965). Hammer (1969) demonstrated that chloride ions can be replaced by available bicarbonate ions in the 'apparent free space' of seaweeds and this may account for sustained photosynthesis at low salinities. It would be interesting to investigate the effect of bicarbonate ion

supplements on *S. muticum* photosynthesis at a range of salinities. High available carbon levels may increase the salinity range over which the alga is able to photosynthesise normally as has been demonstrated in the above mentioned species. If such treatment could also increase survival and growth in more prolonged culture experiments, like those described in this paper, the findings would be particularly relevant to the interpretation of the salinity distribution of *S. muticum* in the field.

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