

## Thermal tolerance of *Stypocaulon scoparium* (Phaeophyta, Sphacelariales) from eastern and western shores of the North Atlantic Ocean

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**ABSTRACT:** Isolates of *Stypocaulon scoparium* Kütz. were collected from the Gulf of St. Lawrence, Canada and compared in culture to isolates collected from the Atlantic and Mediterranean coasts of Europe. The Canadian isolates grew at temperatures ranging from  $-2^{\circ}\text{C}$  up to  $22^{\circ}\text{C}$ , with maximum rates of growth at  $10\text{--}15^{\circ}\text{C}$ ; in trials lasting 3 months they survived the lowest temperatures but died at  $22$  or  $25^{\circ}\text{C}$ . In contrast, for the European isolates, maximum growth occurred between  $10$  and  $27^{\circ}\text{C}$ , and they died only after several months at  $30$  or  $33^{\circ}\text{C}$ . At the low end of the temperature range, European plants suffered damage or died at  $5^{\circ}\text{C}$ . Only the northernmost isolate, from Brittany, could both survive at  $0^{\circ}\text{C}$  and remain undamaged at  $5^{\circ}\text{C}$  in short days. All European isolates died at  $-2^{\circ}\text{C}$ . Geographic distributions and the different thermal responses suggest that the eastern and western Atlantic populations are two different entities, the European plants being possibly of Tethyan origin, and the Canadian plants being possibly of north Pacific origin. The former would then have occupied the north Atlantic for the longest time, which may partly explain the occurrence of ecotypic variation among these isolates.

### INTRODUCTION

By considering the temperature regime at the geographic limits of a species, one can often predict the temperature limits for survival, growth or reproduction that keep a species within its geographic boundaries (van den Hoek, 1982a, b; Breeman, 1988). At times, however, one finds an anomalous pattern of distribution for which no workable hypothesis of limiting conditions is evident. Such is the case for the ampho-Atlantic brown alga known as *Stypocaulon scoparium* Kütz. or *Halopteris scoparia* (L.) Sauvageau.

In Europe, *Stypocaulon scoparium* is found in the outer Baltic Sea (Waern, 1952), the Black and Caspian Seas (Zinova, 1967), the Mediterranean and Red Seas (Menez & Mathieson, 1981), in West Agder in southern Norway (Rueness, 1977), along western Denmark (Christensen et al., 1985), around England, Ireland and all but the northeast of Scotland (Maggs, 1986) and from northern France south to Morocco and the Cape Verde Islands (Audiffred, 1985) or perhaps to Nigeria (Lawson & John, 1982). At its northernmost limit of distribution on the Norwegian coast it experiences an average temperature fluctuation of about  $6\text{--}14^{\circ}\text{C}$ , and in the Baltic of about  $2\text{--}16^{\circ}\text{C}$ . At the southern limit in the southern Mediterranean and Red Seas, temperatures range from about  $18$  to  $28^{\circ}\text{C}$ , while in Nigeria temperatures range from about  $24\text{--}28^{\circ}\text{C}$ .

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On the coast of North America, the species is confined to a relatively narrow range between northern Labrador and southern Nova Scotia in Canada (South & Tittley, 1986). Temperature ranges at the northern and southern limits are  $-2$  to  $10^{\circ}\text{C}$  and  $0$  to  $18^{\circ}\text{C}$ , respectively. There has been a single unsupported record from eastern Greenland (Kjellman, 1883).

In the North Atlantic Ocean, geographic limits of species are commonly set by low winter or low summer temperatures to the north, and high winter or high summer temperatures to the south (Breeman, 1988). *Stypocaulon scoparium* in the southern Mediterranean and south along the coast of Africa to Nigeria must tolerate several months of summer temperatures exceeding  $25^{\circ}\text{C}$ . At the southern limit of distribution on the North American coast, winter temperatures are relatively low and therefore, presumably not limiting, and summer temperatures do not exceed  $20^{\circ}\text{C}$ . One would expect the species to extend much farther south on the coast of North America, at least to North Carolina (where extensive sandy shores may form a barrier), but this is not the case. On the other hand, in winter, plants growing in the Gulf of St. Lawrence in Canada clearly tolerate months of sub-zero temperatures under a cover of ice. Why, then, do the European plants not extend much farther north along the relatively temperate coasts of Norway and southern Iceland where temperatures in both summer and winter are warmer than or equal to temperatures at the northern limit of distribution in eastern Canada?

To answer the questions posed by the distributions of *Stypocaulon scoparium* on the eastern and western sides of the North Atlantic, we have brought into culture isolates from both Canadian and European shores to study their thermal responses under controlled conditions.

#### MATERIALS AND METHODS

*Stypocaulon scoparium* was collected from sites listed in Table 1. Clones were propagated from vegetative apices, as no fertile material was seen in any collection. All isolates were incubated in a range of temperature conditions to determine rates of growth and long-term survival capacity. Incubations were done in growth cabinets ( $\pm 1-2^{\circ}\text{C}$ ) or

Table 1. Collection sites of isolates of *Stypocaulon scoparium*

Isolate	Location	Collector
CAN1	Bonne Bay, Nfld., Canada ( $49^{\circ}\text{N}$ , $58^{\circ}\text{W}$ )	E. Henry
CAN2	Rustico, P. E. I., Canada ( $46^{\circ}\text{N}$ , $63^{\circ}\text{W}$ )	J. McLachlan
CAN3	Rustico, P. E. I., Canada	J. McLachlan
CAN4	Rustico, P. E. I., Canada ( $46^{\circ}\text{N}$ , $63^{\circ}\text{W}$ )	I. Novaczek
EUR1	Roscoff, Brittany, France ( $48^{\circ}\text{N}$ , $4^{\circ}\text{W}$ )	I. Novaczek
EUR2	Calvi, Corsica, France ( $42^{\circ}\text{N}$ , $8^{\circ}\text{E}$ )	I. Novaczek
EUR3	Calvi, Corsica, France	I. Novaczek
EUR4	Canary Islands ( $28^{\circ}\text{N}$ , $15^{\circ}\text{W}$ )	E. Henry

water baths ( $\pm 0.5^\circ\text{C}$ ), under cool-white fluorescent light. For all cultures, sterile PES medium (McLachlan, 1973) based on North Sea water of 33‰ salinity, was used.

Isolates were maintained in stock culture at  $10^\circ\text{C}$ , long days (16 h light, 8 h dark). In preparation for experiments, plants were moved from stock culture toward the desired experimental temperature at a rate of no more than  $5^\circ\text{C wk}^{-1}$  and then acclimated to the experimental temperature for at least 5 days. All material to be tested at a particular light and temperature condition received the same acclimation and all available isolates were tested concurrently.

For growth studies, 5 apices, each about 3 mm long, were dissected from each isolate. Each apex was placed in a 50 mm diameter, sterile plastic Petri dish 3/4 full of medium and sealed with parafilm to prevent evaporation. The length of each apex was drawn at a standard magnification ( $7\times$ ) using a dissecting microscope fitted with a camera lucida. The culture dishes did not have to be opened, and the process was performed quickly to minimise temperature fluctuations. The drawings were later measured ( $\pm 1$  mm) using a Hewlett Packard digitiser (model 9835A). Drawings were made at intervals of 2 to 10 days, depending upon the rate of growth. Measurements were continued until a straight line could be fitted through at least three consecutive datum points plotted on semilog paper, indicating a steady, logarithmic rate of elongation. Where no growth was apparent, measurements were discontinued after 4 weeks or when the material was obviously dead. Apices damaged by transfer to a sublethal temperature were allowed to regenerate before measurements were begun. Quantum flux densities of 10 and/or  $40\ \mu\text{mol m}^{-2}\ \text{s}^{-1}$  were used at each temperature. All trials were conducted in long days, except at  $-2^\circ\text{C}$ , where short (8 h light, 16 h dark) days were employed. In general, experiments at sublethal high and low temperatures were performed at  $10\ \mu\text{mol m}^{-2}\ \text{s}^{-1}$ , to minimise damage (Cambridge et al., 1984; Yarish et al., 1984, 1986).

Relative growth rate (RG) of each apex, expressed as % increase  $\text{day}^{-1}$ , was computed for the period of exponential growth, as follows:

$$\text{RG} = 100 (\ln L_2 - \ln L_1) / (T_2 - T_1) \quad (\text{Kain, 1987})$$

where  $L_2$  = final length,  $L_1$  = initial length,  $T_2$  = final time (d) and  $T_1$  = initial time. Five replicates were averaged to give the mean growth rate for each isolate. Differences among isolates were tested by a posteriori Student-Newman-Keuls (SNK) and Scheffe multiple range tests, using the Statistical Package for Social Sciences (SPSS).

To determine lethal limits, whole plants were incubated in 500 ml flasks at extreme temperatures for a period of 3 months. This relatively long incubation time was used in order to gain results relevant to survival over a summer or winter period in the field. Temperatures of  $-2$ , 0, 5, 20, 22, 25, 27, 30, 33 and  $35^\circ\text{C}$  were tested, in long and/or short daylengths. Because high quantum flux densities appeared to hasten death at extreme temperatures, all tests were conducted at about  $10\ \mu\text{mol m}^{-2}\ \text{s}^{-1}$ . Trials at  $0^\circ\text{C}$  were also performed in darkness. The medium was changed at 2–3-week intervals, using medium previously warmed or cooled to the appropriate temperature to avoid thermal shock. After 3 months, the cultures were transferred to 15 or  $20^\circ\text{C}$ , long days and observed for 1 month or until obvious growth had occurred. When test cultures appeared to be dead or dying in less than 3 months, portions were removed to test for recovery. All tolerance tests were performed on at least 2 separate occasions.

## RESULTS

Isolates of *Stypocaulon scoparium* from Canada differed markedly from European isolates both in their lethal limits (Table 2) and in their ability to grow over the range of temperatures tested (Figs 1–8). Whereas apices from plants from the western Atlantic not only survived but grew at 0 and  $-2^{\circ}\text{C}$  (Figs 1–4), these temperatures were lethal for apices of European isolates (Figs 5–8). In no instance did the Canadian isolates appear

Table 2. Thermal tolerance of isolates of *Stypocaulon scoparium* (whole plants) in culture. ++ = undamaged; + = alive but damaged; +- = dead or damaged; - = dead; nd = no data. Incubation time 3 months. S = short days; L = long days; D = dark

Isolate	Temperature ( $^{\circ}\text{C}$ ) and Daylength														
	-2S	OS	OL	OD	5S	5L	20S	20L	22L	25S	25L	27L	30L	33L	35L
CAN1	++	nd	++	nd	++	++	nd	+-	+-	nd	-	-	-		
CAN2	++	nd	++	nd	++	++	nd	+-	-	nd	-	-	-		
CAN3	++	nd	++	nd	++	++	nd	+	+-	nd	-	-	-		
CAN4	++	++	++	++	++	++	++	+	-	-	-	-	-		
EUR1	-	-	+-	++	++	+	++	++	++	++	++	++	+	-	-
EUR2	-	nd	-	nd	+-	-	++	++	++	++	++	++	+-	-	-
EUR3	-	nd	+-	nd	+-	+	++	++	++	++	++	++	+-	-	nd
EUR4	-	nd	-	nd	+	+	++	++	++	++	++	++	+	-	nd

damaged after transfer to low temperatures. Whole plants of European isolates suffered damaged apices or died when transferred to 5 or  $0^{\circ}\text{C}$  and all died at  $-2^{\circ}\text{C}$ . Results at 0 and  $5^{\circ}\text{C}$  varied depending on the combination of isolate and daylength (Table 2). EUR1, the northernmost isolate, survived  $0^{\circ}\text{C}$  only after acclimation for a month at  $5^{\circ}\text{C}$ , sustaining less damage at this temperature when in darkness. No amount of acclimation allowed long-term survival of the more southerly isolates at  $0^{\circ}\text{C}$ .

Over the range of 5 to  $15^{\circ}\text{C}$ , growth rates of the European isolates were not, as a group, significantly different from those of the Canadian isolates. However, at  $5^{\circ}\text{C}$ , two Canadian isolates grew significantly faster ( $p < 0.05$ ) than the European isolates. All European isolates grew at rates significantly higher than all Canadian isolates ( $p < 0.05$ ) at temperatures of  $20^{\circ}\text{C}$  or more. The maximum growth rates of European plants were consistently higher than those of Canadian isolates.

The differences in upper lethal limits and in growth at high, sublethal temperatures were dramatic (Table 2; Figs 1–8). Apices of Canadian isolates grew at 20 and  $22^{\circ}\text{C}$ , but always at a slower rate than at 10 or  $15^{\circ}\text{C}$  (Figs 1–4). When incubated for a long period at  $20^{\circ}\text{C}$ , whole plants were damaged and appeared unhealthy. At  $22^{\circ}\text{C}$  all the Canadian isolates died or were severely damaged after 3 months. At  $25^{\circ}\text{C}$  all died completely after 1 month (Table 2). In contrast, the European isolates all had a broad range of optimal growth temperature from 10 to 27 or  $30^{\circ}\text{C}$  (Figs 5–8). Growth rate was most markedly reduced at  $30^{\circ}\text{C}$  in the isolate from Brittany (EUR1, Fig. 5), whereas the Canary Islands isolate grew well at this temperature (EUR4, Fig. 8). All four isolates were damaged by long-term incubation at  $30^{\circ}\text{C}$  but were able to regenerate after 3 months at this

temperature. They were all killed by prolonged exposure to 33°C but even at this extreme temperature the Canary Islands clone (EUR4, Fig. 8) was able to grow well for a number of weeks before showing signs of damage, and grew at a rate significantly higher ( $p < 0.05$ ) than that of other isolates.

## DISCUSSION

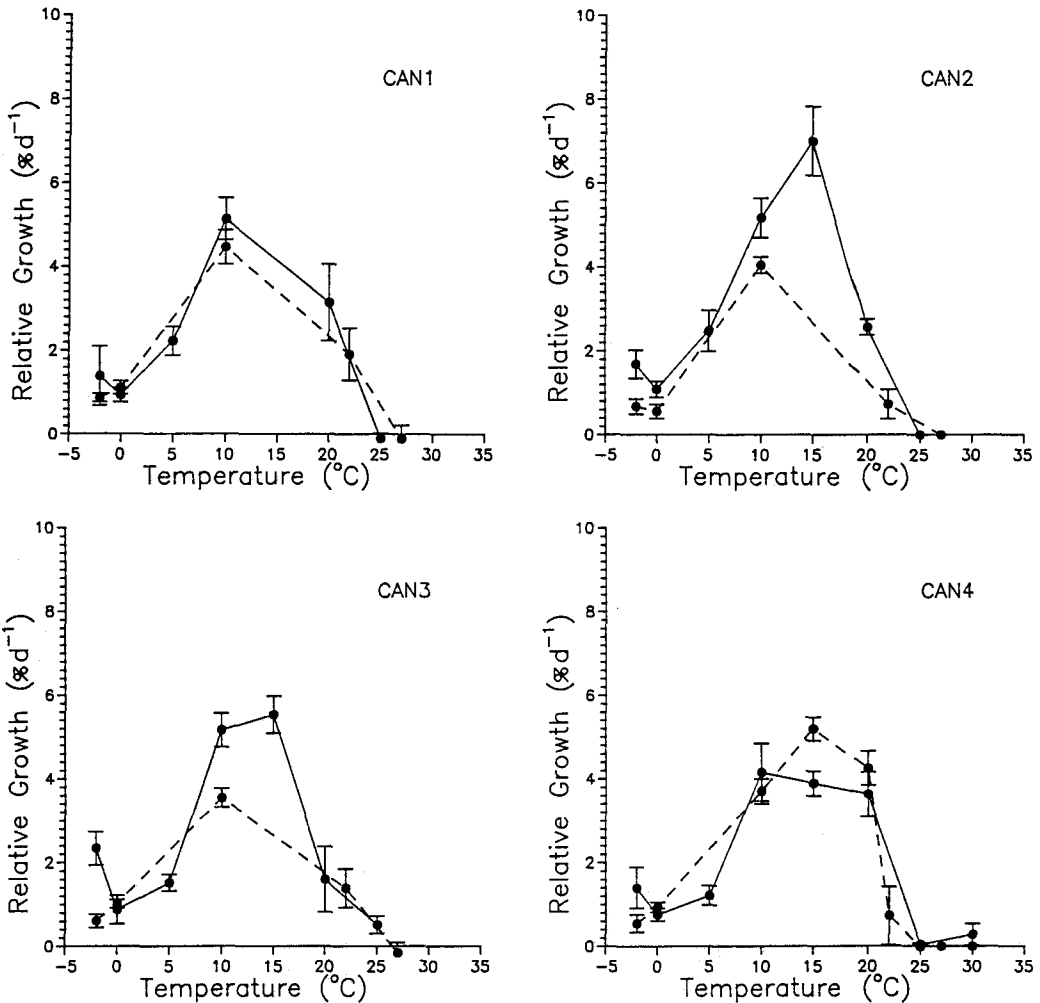
Culture experiments have shown that the apparent anomalies in the limits of geographic distribution of *Stypocaulon scoparium* in the North Atlantic Ocean are owing to the very different thermal tolerances of plants on the eastern and western sides of the ocean. European isolates resemble warm-temperate to tropical species (Cambridge et al., 1987). They do not tolerate sub-zero temperatures and suffer damage or die even at 5°C, but grow well above 25°C and sustain damage only at 30°C. One would expect such plants to occur in the tropics, making the Nigerian record entirely believable. In contrast, Canadian isolates resemble Arctic to cold-temperate species such as *Devaleraea ramentacea* (L.) Guiry and *Phycodrys rubens* (L.) Batt. (Novaczek & Breeman, unpubl. obs.) in that they tolerate -2°C and even grow at this temperature, while being unable to tolerate or grow at temperatures much above 20°C. The southern boundary of *Stypocaulon* in the western Atlantic coincides with the 18°C summer isotherm, making this boundary defined by an upper lethal limit.

Among the European isolates there was evidence of ecotypic variation. The northernmost isolate, EUR1, was least able to grow at high temperatures while the southernmost isolate, EUR4, grew better than all others at 30 and 33°C. A relative disadvantage at low temperatures accompanied the better high temperature tolerance. Whereas EUR4 died completely at 0°C and was severely damaged at 5°C, EUR1 was undamaged or able to regenerate from surviving cortical cells after exposure to these low temperatures (Table 2). There were no differences in tolerance among the Canadian isolates (Table 2) nor were there distinct differences among short-term growth rates at either end of the temperature scale.

In general, thermal ecotypes that have different absolute survival limits appear to be rare in morphologically well-defined species of marine algae (Novaczek & Breeman, unpubl. obs.; Bolton & Luning, 1982; Guiry et al., 1987; Breeman, 1988), even in cases where there are variations in the thermal response with respect to reproduction (Novaczek, 1984), morphogenesis (tom Dieck, 1987; Rietema & van den Hoek, 1984) or growth (see refs. in Breeman, 1988). When they do occur, variations in upper lethal limits are only of 1–3°C (Novaczek & Breeman, unpubl. obs.; Lüning et al., 1987; Breeman, 1988; Gerard & DuBois, 1988). One apparent anomaly is the case of the cosmopolitan "species" *Ectocarpus siliculosus* (Dillw.) Lyngb. (Bolton, 1983). This taxon probably encompasses a number of species, as there are both morphological differences and degrees of intersterility among the isolates tested (Müller, 1976, 1979). Similarly, differences have been documented between eastern and western Atlantic isolates of *Callithamnion tetragonum* (Withering) S.F.Gray (Whittick & West, 1979; Yarish et al., 1986), but taxonomic controversy suggests that more than one species is involved. Short-term photosynthetic measurements at extreme temperatures have shown differences between plants that have had different histories of acclimatization (Mathieson & Norall, 1976) but these do not indicate genetic variation, nor can the results be extrapolated to predict long-term growth

and survival in the field at extreme temperatures. Longer term experiments have also indicated differences in thermal tolerance of about 2°C that are attributable to seasonal acclimatization (Lüning, 1984) but again these do not indicate the genetic difference required for the recognition of an ecotype. It has been documented that in some species, short-term exposure to lethal temperature may result in faster average growth rather than in mortality (Stromgren, 1977, 1983). When attempting to test the genetic component of thermal tolerance, therefore, acclimation procedures must be thorough and standardized.

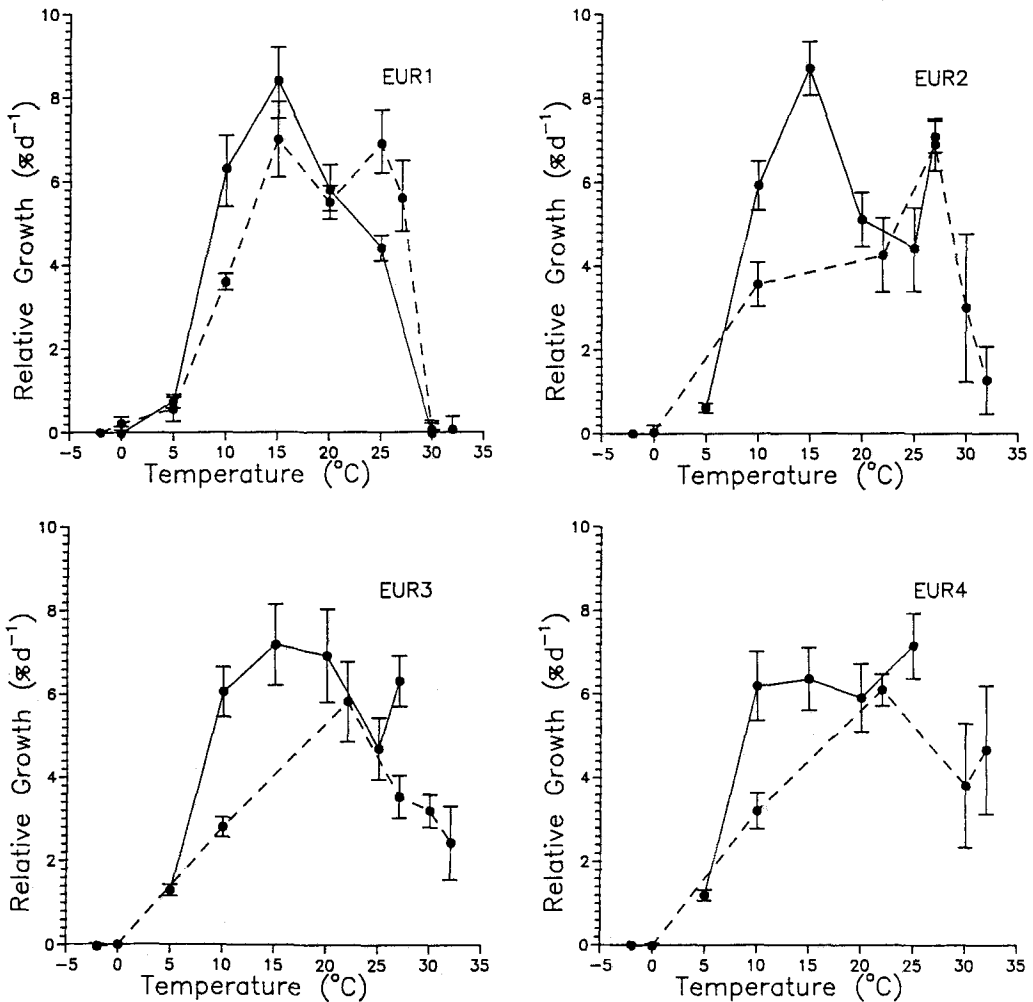
Slight differences in thermal response have been found between haploid and diploid phases of some monomorphic species (Novaczek et al., 1987; Yarish et al., 1986), and also



Figs 1–4. Relative growth rates (mean  $\pm$  standard error) of all isolates (see Table 2) of *Stygocaulon scoparium* at different temperatures. Solid line = quantum flux density 40  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ; broken line = 10  $\mu\text{mol m}^{-2} \text{s}^{-1}$ . Fig. 1. Isolate CAN1; Fig. 2. Isolate CAN2; Fig. 3. Isolate CAN3; Fig. 4. Isolate CAN4

between plants at different morphogenetic stages (Lüning, 1984). In these cases the various plants either tolerated a lethal temperature for different lengths of time or, if there was a difference in lethal limits, it was of only a few degrees. The only large differences (over 5°C) in thermal tolerance that have been recorded are those between micro- and macrothallic phases of heteromorphic brown algae (Novacek et al., 1986; Novacek, 1987).

It seems that, for any particular morphological phase of an algal species, thermal tolerance is a highly conservative genetic feature. Indeed, some modern methods of estimating phanerozoic ocean temperatures depend upon the assumption that fossil phytoplankton had the same range of thermal tolerance as morphologically identical



Figs 5-8. Relative growth rates (mean  $\pm$  standard error) of all isolates (see Table 2) of *Stypocaulon scoparium* at different temperatures. Solid line = quantum flux density  $40 \mu\text{mol m}^{-2} \text{s}^{-1}$ ; broken line =  $10 \mu\text{mol m}^{-2} \text{s}^{-1}$ . Fig. 5. Isolate EUR1; Fig. 6. Isolate EUR2; Fig. 7. Isolate EUR3; Fig. 8. Isolate EUR4

extant species. In general, the conclusions drawn from studies based on this assumption have been supported by conclusions drawn by other means (Lamb, 1977). The few exceptions to this are of interest, as they indicate that there may be a link between shifts in low temperature tolerance and potentially mutagenic events such as the reversal of the earth's magnetic field (Kennett, 1968, 1970).

In the case of *Dictyota dichotoma* (Huds.) Lamour., where a large difference in thermal tolerance had been noted between eastern and western Atlantic populations (Biebl, 1962), recent research has shown that the plants of the North American coast are a different species from those of the European coast (Schnetter et al., 1987). In the case of *Stypocaulon scoparium*, the large differences in thermal tolerance indicate that in this case, too, the plants on the eastern and western sides of the Atlantic are of two separate entities.

*Stypocaulon scoparium* is not limited to the Atlantic Ocean but is also recorded in the northwest Pacific and in the Caspian Sea. Its occurrence in the Caspian Sea indicates that the European populations are probably descended from an ancient species that entered the developing North Atlantic Ocean from the warm, equatorial Tethys Sea. The Caspian Sea was once an arm of the Tethys. A Tethyan origin is consistent with the present-day thermal tolerance of the European plants, which places them in the group of warm-temperate to tropical species.

Patterns of variation in thermal response may provide clues to evolutionary history. Species of Tethyan origin will have been in the Atlantic since it was first formed over 150 million years ago. Ecotypic variation, resulting from evolution in the face of changing temperature regimes, may be more evident in Tethyan algae than in species more recently introduced to the ocean. For instance, southern Atlantic and presumably Tethyan populations of *Ectocarpus siliculosus* encompass many ecotypes and probably several species having distinctive thermal responses. In contrast, *Laminaria saccharina*, which is thought to be a more recent introduction from the north, has developed thermal ecotypes only at the southernmost boundary of distribution, where populations experience the most extreme selective pressure from high summer temperatures (Bolton & Lüning, 1982; Gerard & DuBois, 1988). In this study we found that the European, presumably Tethyan, species of *Stypocaulon* did encompass populations having different abilities to grow and survive at both extreme high and extreme low temperatures.

In the Pacific, *Stypocaulon scoparium* is recorded from the shores of northern Japan and the Sakhalin Peninsula of the USSR. When grown in culture, plants from Japan resemble the Canadian *Stypocaulon* in that they produce a basal disc (H. Kawai, pers. comm.). In contrast, European plants are only known to be attached by rhizoids (Prud'homme van Reine, pers. comm.; Novaczek, unpubl. obs.). The southern limit of distribution of Pacific *Stypocaulon* lies near the 18°C summer isotherm, suggesting that in physiological terms, also, these plants are closer to Canadian populations than to European ones. A second, poorly known species, *Halopteris dura* Rupr., which closely resembles *S. scoparium* (Ruprecht, 1851), has been recorded in far northern Pacific waters, overlapping in distribution with *S. scoparium* and extending north into the Bering Sea. Tokida (1931) considers *H. dura* to be conspecific with *S. scoparium*. Unfortunately, the type specimen lacks a holdfast (Prud'homme van Reine, pers. comm.) and the written descriptions of this northern entity (Ruprecht, 1851; Perestenko, 1980) do not indicate definitively whether it is closely allied to the species found in Canada.



The Canadian species, with its cold-temperature to Arctic type of thermal response, may have evolved from the Tethyan stock in response to cooling temperatures. On the other hand, the existence of one or two sister species in the northwestern Pacific suggests that the ancestors of Canadian populations entered the Atlantic from the north. The ancestral stock may have been part of the flora of the present-day Arctic basin at the time when it became separated from the Pacific Ocean by the Bering land bridge. The species could then have entered the north Atlantic about 55 or 40 million years ago when the rifting process that formed the Atlantic Ocean severed Greenland from Norway, allowing Arctic water to flow in (Lüning, 1985). Alternatively, the ancestral stock may have invaded more recently from the north Pacific following the opening of the Bering land bridge, which once again allowed the confluence of Pacific and Arctic waters, in the late Pliocene (McKenna, 1983). The present-day absence of the species from the Arctic indicates that if the plants migrated through these northern waters, they must have done so prior to the deterioration of polar temperatures during the ice ages.

Considering the possible introduction of the Canadian species from the north, and its present ability to tolerate sub-zero temperatures, it is then surprising that populations are not found farther north than southern Labrador on the Canadian coast. Summer temperatures in embayments north of this point can approach 10°C, which is more than adequate for vigorous growth. Even the European plants might be expected to grow farther north along the coast of Norway, as they tolerate more severe winters in the Baltic than on the coast, and also can grow at the summer temperatures of this coast (roughly 10°C). However, even for the hardiest thermal ecotype, winters in which the temperature drops below 5°C for more than 3 months would be very stressful if not fatal. The length of winter, rather than any particular low lethal temperature, may therefore determine the northern geographic boundary in Europe. It is possible that competition from other algae or herbivory play a part, but these factors have never been shown to control large-scale distribution (Breeman, 1988). Alternatively, the northern boundaries of both eastern and western Atlantic populations may be explained by a requirement for some particular condition for reproduction which is not met under current northern climatic regimes. This might be a need for high summer temperatures or for some particular temperature-daylength combination. The requirements for reproduction in *Stypocaulon* are enigmatic, as the plant has never reproduced in culture (Novaczek, pers. obs.; Henry, pers. comm.) and no detailed field observations have been published. From present northern boundaries, a requirement for a minimum of 10°C is suggested for Canadian plants, and of 14°C for European plants. However, other thermal requirements may prevail if the plants have a daylength response.

Before a choice can be made from the various possible phylogenetic relationships among the disjunct populations currently included in *Stypocaulon scoparium*, more information is required. Knowledge of the thermal responses of the Pacific taxa and a more thorough understanding of their morphological variation are needed. Modern methods of genetic analysis could also be employed to determine how closely related each taxon is to the others.

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