

PRODUCTION OF HYALINE HAIRS BY INTERTIDAL SPECIES OF  
*FUCUS* (FUCALES) AND THEIR ROLE IN PHOSPHATE UPTAKE

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ABSTRACT

A field study to determine the precise times of year at which three intertidal species of *Fucus* start to produce hyaline hairs and cease producing such hairs was conducted on the Isle of Man, U.K. Hairs were first observed during February, and within 6 days of their initial appearance, all tagged plants of all species at all tidal heights on the shore possessed hairs. Hair production continued until the beginning of October, at which time *Fucus* plants growing at the lowest stations (+3.0 m) had glabrous apical growth. Hair production continued later into the year for plants growing higher on the shore, and it was not until mid-November that glabrous apical growth was observed in all plants.

Phosphate uptake rates of pilose (hairy) and glabrous (hairless) apical sections were measured in November 1988 for *F. spiralis* L. and in January 1989 for *F. spiralis* and *F. serratus* L., at phosphate concentrations ranging from 0.8  $\mu\text{M}$  (ambient seawater) to 9.0  $\mu\text{M}$ . In ambient seawater, pilose plants of *F. spiralis* removed phosphate 2-3 times faster than glabrous plants, whereas the uptake rates of pilose plants of *F. serratus* were about 50% greater than those of glabrous plants. The differences between uptake rates of pilose and glabrous plants of both species were smaller or nonsignificant at higher phosphate concentrations. The field and laboratory data are consistent with the hypothesis that hairs are formed in *Fucus* as a response to increased nutrient demand and that hairs facilitate the uptake of nutrients from seawater at concentrations typical of natural situations.

**Key index words:** *Fucus serratus*; *Fucus spiralis*; *Fucus vesiculosus*; glabrous; growth; hyaline hairs; Phaeophyta; phosphate storage; phosphate uptake; pilose; seasonal variation

Intertidal *Fucus spiralis* L., *F. vesiculosus* L., and *F. serratus* L. produce colorless, multicellular hyaline hairs, arising in tufts from cryptostomata on the

apical and midregions of their thalli (Fritsch 1945). The early development of cryptostomata is the same as that of the reproductive conceptacles in *Fucus*, from which cryptostomata are thought to be derived (Gardner 1922, Fritsch 1945, Powell 1957). In recent years, the hairs of *Fucus* have been largely ignored, except in occasional colorful descriptions in seashore guides (e.g. "soft silken hairs scattered thinly on the infertile ends"; Barrett and Yonge 1958), and their function is unknown. However, hairs produced by other algal species are known to enhance nutrient uptake (Whitton 1988).

Germings of *Fucus spiralis* produce a single, apical tuft of hairs in all seasons, except winter (Schonbeck and Norton 1979). In laboratory studies, the length of the apical hairs was found to increase with decreasing nutrient availability. These observations suggest that the apical hairs of germings serve to enhance nutrient uptake at low nutrient concentrations (Schonbeck and Norton 1979). Mature plants of *Fucus spiralis*, *F. vesiculosus*, and *F. serratus* on the Isle of Man (Irish Sea) also possessed hairs in the spring and summer, but hairs were absent in the winter when nutrient concentrations in the Irish Sea are maximal, implying a possible role in the acquisition of nutrients (Galvin 1988).

The goals of this study were to establish the precise dates upon which hair production in natural populations of *Fucus* starts and ends over 1 year and to test the hypothesis that the hyaline hairs of *Fucus* enhance phosphate uptake.

MATERIALS AND METHODS

Field experiments to determine the time of onset and cessation of hair production by intertidal species of *Fucus* were conducted on St. Michael's Island, off the east coast of the Isle of Man, U.K. (Ordnance Survey grid ref.: SC 674296), which has a maximum tidal range of 6 m. A permanent transect, running from low water to the uppermost limits of *Fucus spiralis*, was established on each of three shores: exposed (E), semisheltered (SS), and sheltered (S). Stations were marked at 0.5-m vertical intervals along each transect line by cementing a plastic marker at the appropriate place with Hawke Quick-Set cement. The height of each station above lowest astronomical tide was determined with a surveyors' level. Five stations were selected at sites E and SS: +3.0, +3.5, +4.0, +4.5, and +5.0 m. At site S, only two stations were marked,

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at +3.0 and +5.0 m, because a dense covering of *Ascophyllum nodosum* on the midshore prevented the growth of *Fucus* in this area.

In mid-January 1986, the first 25 plants found growing to the right of the transect line at each station on all shores were tagged with plastic cable ties. At the time of tagging, no plants possessed hairs. Each station was then visited at 2–3-day intervals, and the number of plants with hairs were counted. In the following autumn, at a time when all plants still had hairs, the first 25 plants found growing to the left of the transect lines at each station were tagged. At this time, the number of plants that had stopped producing hairs (i.e. had glabrous apices) was recorded every 3–5 days.

Phosphate uptake rates were determined for pilose and glabrous plants of *Fucus spiralis* in November 1988 and of *F. spiralis* and *F. serratus* in January 1989. At these times, pilose and glabrous plants of these species occurred simultaneously in the field. Plants were collected from Port Kelly, Co. Down, a semisheltered rocky shore on the east coast of Northern Ireland (Irish grid ref.: J628467), at 3.1 m (*F. spiralis*) and 0.93 m (*F. serratus*) above chart datum. Collections were made between 0700 and 0900 the day before an experiment, and plants were transported to the laboratory within 10 min. Apical sections, of 0.5 g wet weight for *F. spiralis* and 1.5 g for *F. serratus*, were cut using a scalpel and cleaned of sand particles and epiphytes by rinsing under flowing seawater and wiping the thalli with tissue. The apices were pre-conditioned for 22–26 h in darkness at 12°C in aerated, filtered (Whatman GF/C) seawater containing ca. 0.8  $\mu\text{M}$   $\text{PO}_4$ . The rate of phosphate uptake from seawater with initial  $\text{PO}_4$  concentrations ranging from 0.8 to 9.0  $\mu\text{M}$  was measured over 2 h using the multiple flask method described by Hurd and Dring (1990).

The kinetic parameters,  $K$ , (half saturation constant) and  $V_{\text{max}}$  (maximum uptake rate), were calculated using the weighted regression of Wilkinson (1961). The advantages of this method are discussed by Hurd and Dring (1990). Curves were fitted to the data by substituting  $K$ , and  $V_{\text{max}}$  into the Michaelis–Menten hyperbolic equation. The uptake rate at 1  $\mu\text{M}$   $\text{PO}_4$  ( $V_1$ ) was also calculated. This parameter was used to compare the abilities of different species to take up phosphate at concentrations that were close to those in seawater during the winter months.

## RESULTS

At all sites, *Fucus serratus* was the dominant species at +3.0 m, whereas *F. spiralis* was dominant at +5.0 m. At sites F and SS, the dominant species growing at +4.0 m was *F. vesiculosus*, whereas mixed populations of *F. serratus*/*F. vesiculosus* and *F. vesiculosus*/*F. spiralis* were found at +3.5 and +4.5 m, respectively.

Hyaline hairs were first reported on tagged plants of *Fucus* on 24 February 1986. Within 6 days, 100% of tagged plants at each of the three sites and at all five tidal heights possessed hairs (Fig. 1). In autumn, plants with glabrous apical growth (i.e. in which hair production had stopped) were first recorded at +3.0 m on 30 September at all three sites (Fig. 2). The time taken from the start of the autumn experiment (22 September) for all tagged plants to exhibit glabrous apical growth was plotted against tidal height for each site (Fig. 3). In plants growing higher on the shore, the production of hyaline hairs continued later into the year (Fig. 3). A linear regression was fitted to data from the semisheltered and exposed sites. The slopes and intercepts of the regressions were tested, and no significant differences were

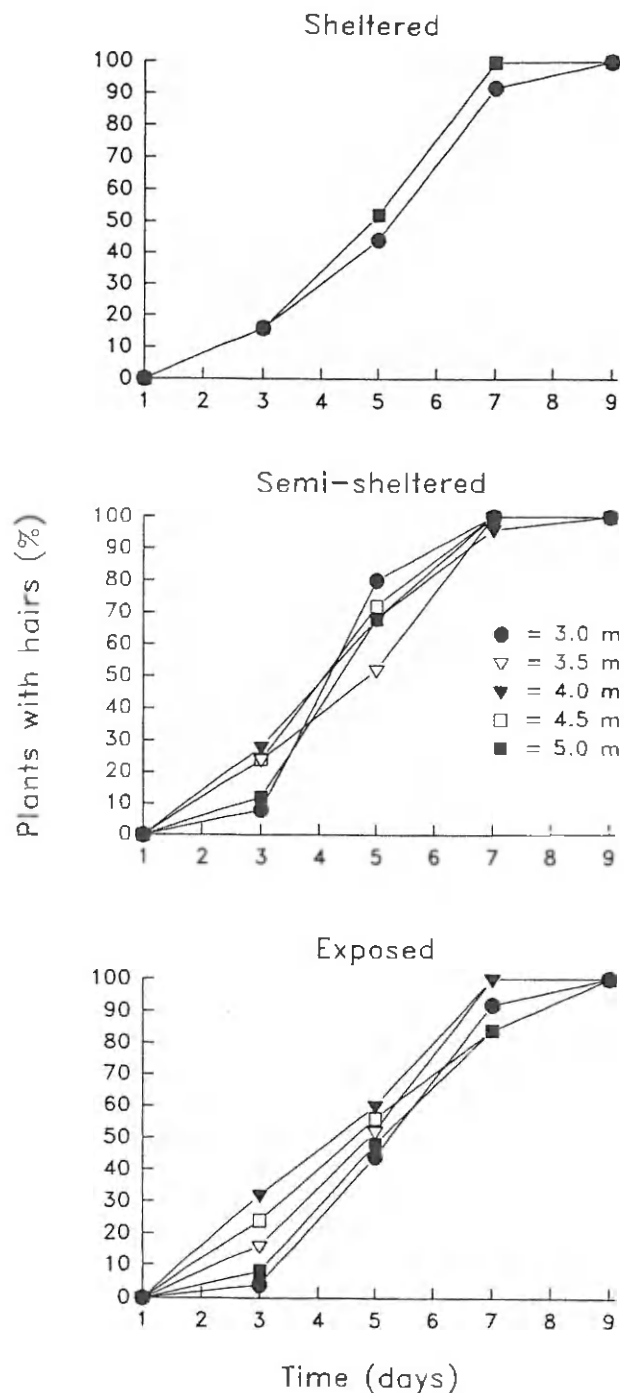


FIG. 1. Percentage of 25 *Fucus* plants with hyaline hairs at a range of tidal heights and on three shores with different degrees of exposure. Surveys were conducted on the Isle of Man; day 1 = 22 February 1986.

found ( $P > 0.05$ ). Thus, both the rates at which hair production ceased and the timing of this cessation were similar for plants growing at the same heights on different shores.

In November 1988, the rate of uptake of phosphate from ambient seawater (phosphate concentration 0.8–0.9  $\mu\text{M}$ ) by pilose plants of *F. spiralis* was

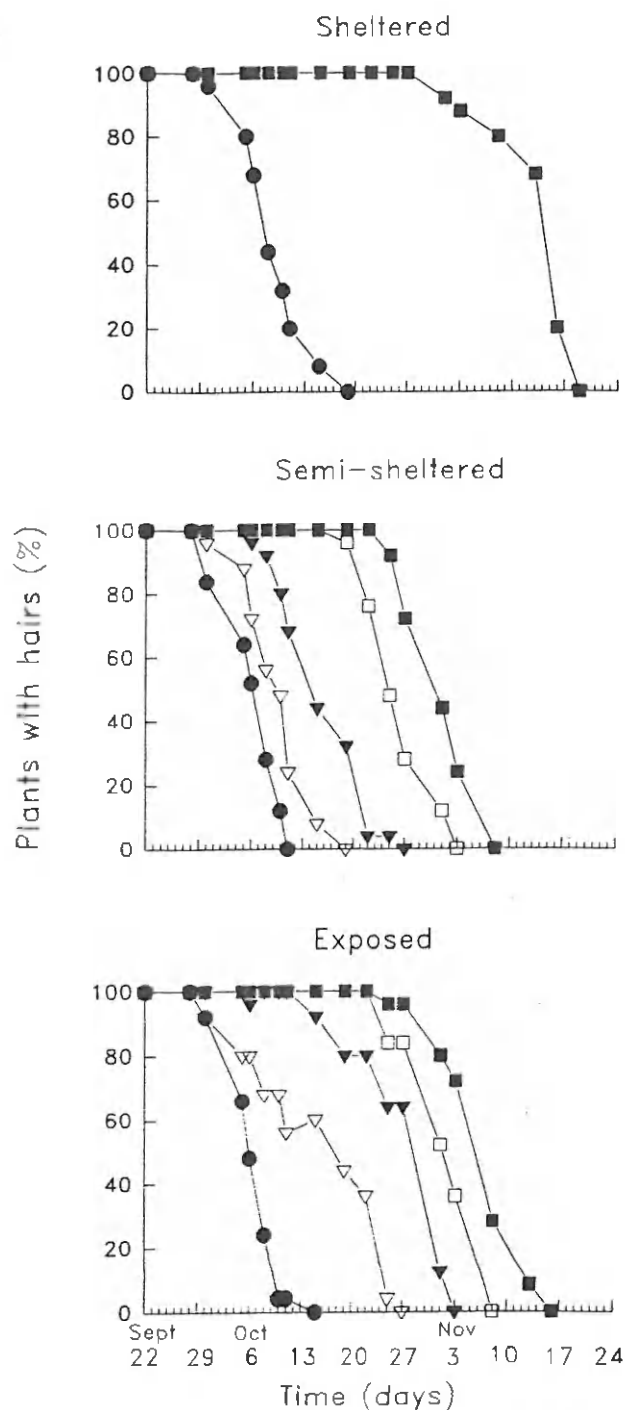


FIG. 2. Percentage of 25 *Fucus* plants with hyaline hairs at a range of tidal heights (symbols as for Fig. 1) and on three shores with different degrees of exposure. Surveys were conducted on the Isle of Man; day 1 = 22 September 1986. Plants that had stopped producing hairs were recognized by glabrous apical growth, although hairs were still observed on the older thallus.

3.5 times greater than that of glabrous plants (Fig. 4). However, there was no significant difference between the uptake rates of pilose and glabrous plants from seawater with higher phosphate concentra-

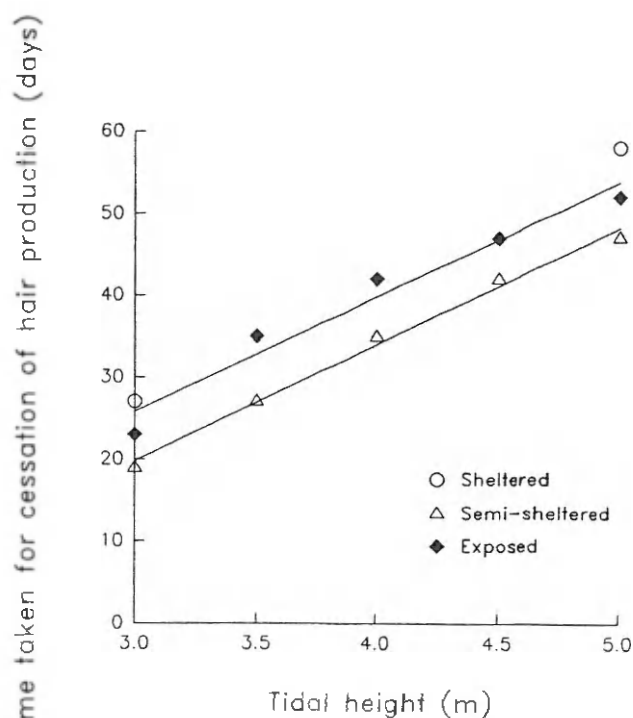


FIG. 3. Time taken, measured from 22 September 1986, for all 25 *Fucus* plants in samples, growing at different tidal heights above lowest astronomical tide, to cease hair production. Linear regressions were fitted to data from semisheltered and exposed sites. No significant differences were found between the slopes or intercepts ( $P > 0.05$ ).

tions (one-way ANOVA,  $P > 0.05$ ). In January 1989, the uptake rate from ambient seawater (phosphate concentration  $0.9 \mu\text{M}$ ) by pilose *F. spiralis* was 2.7 times greater than that of glabrous plants and, at all concentrations, the uptake rate of pilose plants was significantly greater than that of glabrous plants (1-way ANOVA,  $P < 0.001$ ). The rate of phosphate uptake from ambient seawater by pilose plants of *F. serratus* during the same period was 1.5 times greater than that of glabrous plants (Fig. 5), but there was no significant difference between the uptake rates of pilose and glabrous plants at the two highest phosphate concentrations used. At all concentrations tested, the uptake rates of pilose plants of *F. spiralis* were greater than those of pilose *F. serratus*.

The kinetic parameters  $K_s$ ,  $V_{\max}$ , and  $V_i$  (Table 1) were calculated from the results in Figures 4 and 5. For *F. spiralis* in November and for both species in January,  $V_i$  values for pilose plants were between 1.5 and 3.3 times greater than those for glabrous plants (Table 1). The main contributor to the higher  $V_i$  values was  $K_s$ , which was consistently lower for pilose plants.  $V_{\max}$  values for pilose and glabrous plants were similar except for *F. spiralis* in January, in which pilose plants had rates 1.7 times higher than glabrous plants.

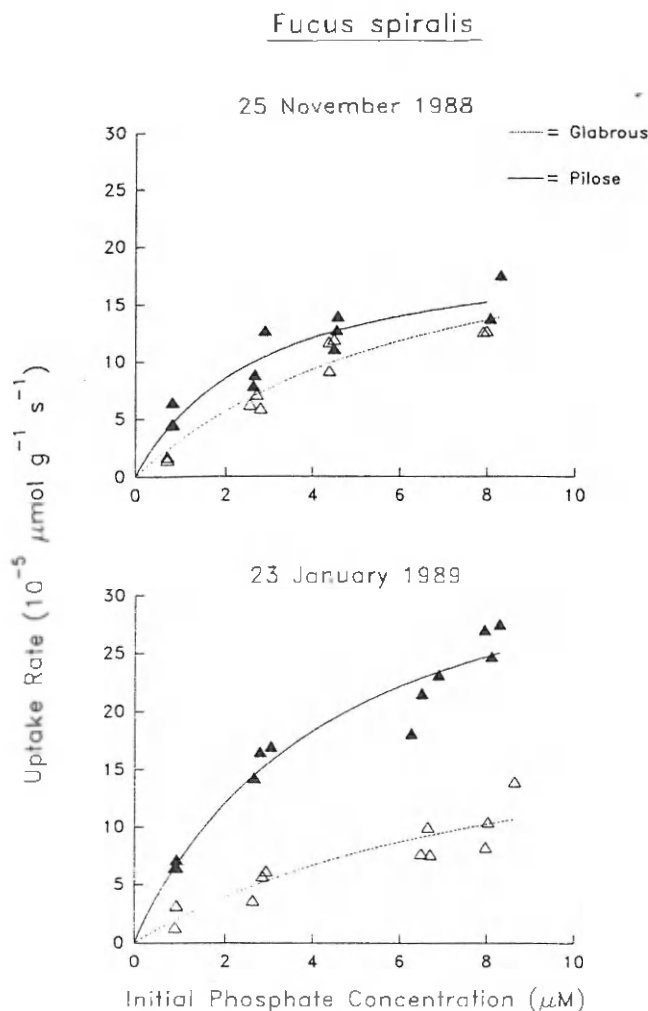


FIG. 4. *Fucus spiralis*. Phosphate uptake rate versus initial phosphate concentration for pilose and glabrous apical sections, measured using the multiple flask method in November 1988 and January 1989.

#### DISCUSSION

**Control of hair formation in the field.** The data presented here are the first to demonstrate the seasonal occurrence of hairs for any algal species and raise questions about the environmental control of hair formation in the field. The rapid appearance of hairs in all plants of all species at all three sites suggests that some environmental factor exerts precise control. Temperature and irradiance seem to be unlikely contenders for the controlling factor because plants high on the shore will be subjected to quite different light and temperature regimes from those low on the shore. Photoperiodic control is a possibility but, again, the precise daylength perceived by plants may be affected by their position on shore because of the variable depths of water overlying plants at dawn and dusk (see Dring 1984, Breeman and Guiry 1989). The variation in the timing of hair production between 1986 (first hairs, 24 February;

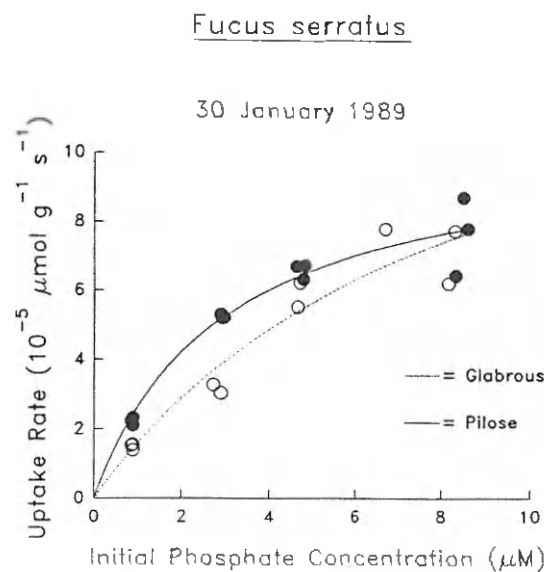


FIG. 5. *Fucus serratus*. Phosphate uptake rate versus initial phosphate concentration for pilose and glabrous apical sections, measured using the multiple flask method in January 1989.

Fig. 1) and 1989 (hairs present, 23 January; Fig. 4) also argues against precise photoperiodic control. The environmental variable that is likely to be most uniform at all levels on the shore at any given time is, therefore, the nutrient content of the ambient seawater. The control of hair formation by falling nutrient availability would fit with the positive influence of hairs on nutrient uptake that has been demonstrated in this study, as well as with previous observations with other species that high nutrient concentrations inhibit hair formation (DeBoer and Whoriskey 1983).

Because the concentrations of nitrate and phosphate in the Irish Sea are maximal in January/February

TABLE 1. *Fucus spiralis* and *Fucus serratus*. Kinetic parameters  $K_i$  and  $V_{max}$  for phosphate uptake, and rate of phosphate uptake at  $1 \mu\text{M}$   $\text{PO}_4$  ( $V_i$ ) for pilose and glabrous plants in November 1988 and January 1989. Uptake was measured using the multiple flask method, and kinetic parameters were estimated according to Wilkinson (1961).

Species	Kinetic parameters		
	$K_i$ ( $\mu\text{M}$ )	$V_{max}$ ( $10^{-5} \mu\text{mol g}^{-1} \text{s}^{-1}$ )	$V_i$ ( $10^{-5} \mu\text{mol g}^{-1} \text{s}^{-1}$ )
November 1988			
<i>Fucus spiralis</i>			
Pilose	2.81	20.47	5.37
Glabrous	7.07	25.63	3.18
January 1989			
<i>Fucus spiralis</i>			
Pilose	4.26	37.82	7.19
Glabrous	9.15	21.94	2.16
<i>Fucus serratus</i>			
Pilose	2.95	10.44	2.64
Glabrous	8.51	15.21	1.60

ruary (Slinn 1974), however, it is unlikely that hair formation in *Fucus* is triggered directly by the ambient concentrations of these nutrients. Another possibility is that hair formation is a physiological response to an increased demand for nutrients that results from increased photosynthesis and growth. In western Scotland, laminaran and mannitol contents of all three *Fucus* species measured in the field (Black 1949) were lowest in January but increased rapidly from February to June. Both the timing and the rate of increase of these storage products was similar for all three species. Growth rate of *Fucus* species from different areas of the North Atlantic were also minimal between November and January but, from late January, growth rate rapidly increased to a maximum, which was maintained until July or August (Niemeck and Mathieson 1976, Schonbeck and Norton 1980, Carlson 1991).

The time of hair formation observed in our investigation coincides, therefore, with seasonal increases in photosynthesis and growth reported by other workers and is consistent with the hypothesis that hairs are formed in *Fucus* as a response to increased metabolic activity and increased nutrient demand. The factor controlling the onset of hair formation may, therefore, be the internal concentrations of nutrients such as nitrogen or phosphorus. Total tissue phosphorus and/or nitrogen of *Fucus* species in the field have been measured by Larsen and Jensen (1957; *F. serratus*, Norway), Kornfeldt (1982; *F. serratus*, Sweden), Asare and Harlin (1983; *F. vesiculosus*, eastern U.S.), and Carlson (1991; *F. vesiculosus*, Sweden). Typically, internal nutrient concentrations were highest between January and April and decreased from mid-April to reach a minimum in June. Since no decline in internal nutrient levels was detected during the period of rapidly increasing photosynthesis and growth rates, we suggest that nutrient uptake rates increase parallel to the increase in metabolic rates at this time and that nutrient reserves in the thalli are not depleted until mid-April, when seawater nutrient concentrations are lower. Therefore, the appearance of hairs may enable plants to maintain their reserves at a time of increasing nutrient demand. A more detailed survey of internal nutrient concentrations during the period when hairs first appear is needed to test the hypothesis that such concentrations trigger hair formation.

*Cessation of hair formation in autumn.* Growth and photosynthetic rates of *Fucus* decrease during September and October (Black 1949, Niemeck and Mathieson 1976, Carlson 1991), so that the plants' requirements for phosphate and nitrate are likely to decrease. The increase in tissue phosphorus and nitrogen levels after September, which has been observed by several workers (Larsen and Jensen 1957, Kornfeldt 1982, Asare and Harlin 1983, Carlson 1991), also indicates that the supply of these nutrients during this period is greater than their rate of

utilization. The cessation of hair production in the autumn may, therefore, occur in response to the increase in the internal concentration of nutrients, effectively reversing the situation in spring.

Although the first appearance of hairs in spring was closely synchronized among plants at all levels on the shore, the cessation of hair production was spread out over a longer period. Plants growing at low tidal heights stopped hair production earlier in the season than those growing progressively higher on the shore. The resulting prolongation of the period with hairs for upper shore plants may have been due to the shorter submersion times for these plants, which would prolong the period of nutrient limitation. However, the cessation of hair formation could be detected only when the new growth was seen to be glabrous. Therefore, the observed timing of cessation must be related to growth rate, and the earlier cessation of hair formation by plants low on the shore may result from faster growth in these plants, compared to plants higher on the shore. These possible explanations of the variable timing of the cessation of hair formation at different shore heights need to be tested by more detailed surveys of growth rate and internal nutrient concentrations of plants at different tidal heights during the period when hair formation ceases.

*Influence of hairs on rate of phosphate uptake.* The curves generated by the Michaelis-Menten model for pilose and glabrous plants of both *Fucus* species provide a good fit to the data and help us to understand the physiological processes involved in phosphate uptake. However, the Michaelis-Menten parameters ( $K_s$  and  $V_{max}$ ) obtained are all higher than typical concentrations of phosphate in seawater, so that these parameters can tell us little about the ecological role of the hairs. The rate of uptake ( $V_i$ ) from seawater containing  $1 \mu\text{M PO}_4$  was, therefore, calculated and used to evaluate the influence of hairs on the rates of phosphate uptake by plants in the field. On the basis of the  $V_i$  values for pilose and glabrous plants, we conclude that hairs enhance the ability of plants to take up phosphate from natural seawater.

The enhancement of phosphate uptake could result from the increased surface area available for catalysts of active uptake. However, Raven (1981) suggests that the main factor limiting the rate of uptake of a nutrient is the rate of its diffusion through the boundary layer, rather than the number of uptake sites at the plasmalemma. Thus, the primary effect of the hairs may be to project parts of the plasmalemma through the boundary layer surrounding the thallus. Although the hairs, themselves, will have a boundary layer associated with them, this layer will be much thinner than that surrounding the main thallus (Raven 1981). In addition, the hairs may cause a certain amount of turbulence at the surface of the plant, which would reduce the thickness of the boundary layer associ-



ated with the thallus. These ideas on how hairs might increase nutrient uptake are not new. They were first proposed exactly 100 years ago by Oltmanns (1892).

Many other species of brown algae produce hyaline hairs similar to those reported here (e.g. *Undaria*, *Sacchoriza*, *Alaria*, Fritsch 1945; *Petalonia*, *Scytosiphon*, Lüning and Dring 1973; *Sargassum*, *Dictyota*, Littler et al. 1989), and it seems probable that such hairs influence nutrient uptake in a similar way. There is, therefore, considerable scope for laboratory-based investigations of the factors controlling hair formation in brown algae and for field studies of their seasonality in relation to ambient nutrient concentrations.

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