Seasonal growth and carbon and nitrogen content in canopy and first-year plants of *Laminaria hyperborea* (Laminariales, Phaeophyceae)

KJERSTI SJØTUN*, STEIN FREDRIKSEN AND JAN RUENESS

Department of Biology, University of Oslo, P.O. Box 1069 Blindern, N-0316 Oslo, Norway

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The seasonal growth pattern of canopy plants has been compared with that of first-year plants. Large, canopy-forming sporophytes grew between January and June. The seasonal variation in total carbon content of the lamina reflected the seasonal pattern of storage carbohydrates, with high content in the summer and autumn, and decreasing content after growth started in January. Vegetative and reproductive laminae contained similar percentages of carbon in dry weight in January, indicating that the process of sorus formation did not involve high consumption of stored carbohydrates in reproductive plants. The nitrogen content of the laminae of canopy plants was high during the growth period and low during the rest of the year. The high nitrogen content during spring may reflect storage in a period of excess ambient nitrate.

The first-year plants grew until the end of September, with the highest relative growth rate during July. During the summer the nitrogen dry weight content of the first-year plants was high (2-4%) compared to the canopy plants (about 1% in the lamina). Also, the C:N ratio of the first-year plants was low from May to October (<15), indicating that growth of the first-year plants was not nitrogen-limited during the summer. However, the low carbon content during the summer also contributed to the low C:N ratios of the first-year plants.

INTRODUCTION

Laminaria hyperborea (Gunnerus) Foslie forms extensive kelp forests along wave-exposed parts of the Norwegian coast. Individual plants may reach an age of 10–20 years (Kain 1971a; Sjøtun *et al.* 1993). There are no published data which describe seasonal growth in *L. hyperborea* from the Norwegian coast, but field observations corroborate the same seasonal growth pattern as described from the Isle of Man (Kain 1976a) and Helgoland (Lüning 1970).

Earlier studies of *L. hyperborea* have shown a seasonal variation in storage carbohydrates and protein in the lamina (Black 1950; Haug & Jensen 1954). Vegetative growth starts in mid-winter at the expense of carbohydrates accumulated during the summer (Lüning 1969), whereas luxury uptake of nitrate may occur in winter and spring (Black & Dewar 1949) when the nitrate concentration in the water is high. Recent experimental studies by Schaffelke & Lüning (1994) have demonstrated that the seasonal growth cycle of *L. hyperborea* is controlled by an endogenous circannual clock, with daylength as a synchronizer.

However, these studies have been carried out on large *L. hyperborea* plants. In *Laminaria bongardiana* Postels et Ruprecht (referred to as *Laminaria groenlandica* Rosenvinge by Druehl *et al.* 1987), Druehl *et al.* (1987) found a different growth pattern during the summer in first-year plants than in older plants during the summer. Also, the extent to which the seasonal growth pattern of *L. hyperborea* may be modified by environmental factors other than daylength has been little

studied. Several studies on kelp ecology have focused on growth in relation to nitrate availability. In *Laminaria longicruris* de la Pylaie reduced summer growth has been demonstrated due to nitrate limitation (Chapman & Craigie 1977). Lüning & tom Dieck (1989) postulated that although environmental signals such as daylength may be the triggering signal for growth in algae, nitrate availability may act as an additional factor modifying vegetative growth.

In the present study we measured growth and content of carbon and nitrogen in first-year and in canopy-forming *L. hyperborea* plants from a wave-exposed and a sheltered station on the west coast of Norway. The objective of the study was to examine whether juvenile and large plants showed a similar seasonal growth pattern. In both groups seasonal growth was related to the nitrogen and carbon content of the lamina.

MATERIALS AND METHODS

Seasonal growth of first-year plants

Gametophytes of *Laminaria hyperborea* were cultivated on sandpaper-rubbed Plexiglas plates ($6 \times 6 \text{ cm}^2$) in IMR/2 medium (Eppley *et al.* 1967) at 6° C in a 8:16 h L:D regime and a photon fluence of about 20 µmol m⁻² s⁻¹. In March 1993, plants were transferred to the sea (Station 1, Fig. 1). Eight replicate Plexiglas plates with a mixture of gametophytes and microscopic sporophytes (up to 160 µm long) were fixed to a stainless steel structure at 10 m depth.

The plants were checked monthly from April to October 1993. The Plexiglas plates were divided into squares, each measuring 1 cm^2 ; during the first months some of the plants

^{*} Present address: Department of Fisheries and Marine Biology, University of Bergen, Bergen High Technology Centre, N-5020 Bergen, Norway.



Fig. 1. The location of Stations 1–3 on the west coast of Norway. The investigation of first-year plants was carried out at Station 1; tagged canopy plants were examined at Stations 2 and 3.

were removed from the Plexiglas plates in order to obtain a density of approximately one plant per square. This also made it possible to identify individual plants from their position on the plates. Lamina lengths of individual plants were measured from May to October. When laminae exceeded lengths of 5 cm, a small hole was punched at 2 or 5 cm from the transition zone between lamina and stipe, and the increase in that distance was measured at the next visit to the locality. The relative growth rate (R) (Kain 1982) was calculated as:

$R = (\ln x_2 - \ln x_1)/d$

where x_1 is the lamina length at the start and x_2 the total lamina length (x_1 plus lamina elongation) after d days.

Seasonal growth of canopy plants

Elongation of the lamina and stipe of tagged canopy plants (stipe lengths between 33 and 130 cm) was measured during 1991–1992 at a wave-exposed site (Station 2, Fig. 1). A dense kelp forest of *L. hyperborea* dominated the vegetation. In addition, during 1992 lamina elongation was measured in tagged plants at Station 3, a more sheltered locality (Fig. 1). At this site patches of *L. hyperborea* f. *cucullata* Svendsen et Kain

(1971) occurred within a bed of *Laminaria saccharina* (Linnaeus) Lamouroux. At both stations plants were tagged at 5 m depth (below Mean low water spring).

At the start of the seasonal growth period the total length of the new laminae was measured. In *L. hyperborea* meristem activity is not confined to the basal lamina area as in most *Laminaria* species, but shifts to the middle and slightly more distal part of the lamina as the lamina grows larger (Kain 1976b). As the new laminae grew larger, holes were punched at 10 and 20 cm from the transition zone between stipe and lamina, and the length added to the new laminae was measured at each visit to the locality.

Lamina content of carbon and nitrogen

Parallel to the growth measurements, a total of 15 randomly chosen canopy plants were collected in the vicinity of the tagged plants at Station 2, except in January and March, when a higher number of plants were collected. A lamina sample of each plant was dried at 70°C and homogenized. The carbon and nitrogen contents were then analysed in a Carlo Erba Elemental Analyzer, model 1106 (Instrument-Teknikk Scandinavia A/S). Each sample consisted of pooled subsamples



Fig. 2. Laminaria hyperborea. Average relative growth rate (with 95% confidence limits) of laminae of first-year plants from May to October 1993; *n = 7, otherwise n = 22-30. (\downarrow) indicates when the plants were transferred to the sea.

taken from randomly chosen positions of the lamina, except in January and March when the subsamples of old laminae were taken exclusively from the medium part of the lamina in order to compare the carbon and nitrogen content of tissue carrying sori and vegetative lamina tissue. The number of subsamples in each sample varied between 1 and 10, depending on the size of the lamina.

For carbon and nitrogen analyses of first-year sporophytes, one sample consisting of between 6 and 15 pooled plants was collected at each visit to Station 1.

Environmental factors

Samples of surface seawater were collected at Stations 1–3 during 1991–1993 and analysed for nitrate in a SAN plus segmented flow analyser (Skalar, Delft, The Netherlands). Daylength and global radiation in 1991–1993 were calculated from Den Norske Almanakk (1994) and Radiation Yearbook Nos. 27–29 (1991–1993), respectively.

RESULTS

First-year plants

In the first-year plants, the laminae grew during the whole summer (Fig. 2). From June to September a number of new macroscopic sporophytes developed on the Plexiglas plates. This was not due to natural recruitment of *Laminaria* spp., as *Laminaria* sporophytes were not observed on the structure carrying the Plexiglas plates. The successive development of new macroscopic plants, together with variable growth rates, resulted in total lamina lengths varying from 1 to 23 cm in October. Stipe growth was small; the largest plants measured had stipes of 1–1.5 cm in October.

Relative growth rates were maximal in July and decreased from August to October (Fig. 2). Individual relative growth rates were not positively correlated with lamina size of the examined plants (Pearson's product-moment, p > 0.05).

Percentage nitrogen in dry weight of first-year plants ranged from 2 to 4.3% of the dry weight from May to October, with



Fig. 3. Laminaria hyperborea. Content of total nitrogen (\bigcirc) and total carbon (\bigcirc) (A) and atomic C:N ratio (B) in first-year plants from May to October 1993. One sample was taken per month, containing 6–15 plants. (\downarrow) indicates when the plants were transferred to the sea.

the highest values observed in June and July (Fig. 3A). Percentage carbon in dry weight of the first-year plants increased from about 24% of the dry weight in May to about 33% in October (Fig. 3A). The atomic ratio between carbon and nitrogen did not exceed 15, and values below 10 were observed in June and July (Fig. 3B).

Canopy plants

In canopy plants, the new annual lamina appeared in January at both stations (Fig. 4). Lamina growth was high until June, with the period of most rapid elongation from March to April evident at Station 2. At the end of the growth season, the average lamina length was similar at the two stations. Very little growth occurred in summer and autumn (Fig. 4). The average increase in stipe length of the measured plants was about 20 cm from January to June at Station 2 (Fig. 4).

The total nitrogen content of the laminae was low during the summer and autumn, increasing in January, with maximum occurrence in March and April (Fig. 5A). This pattern was evident both on a dry weight and a fresh weight basis.

The percentage of carbon in dry weight of the lamina showed a seasonal pattern opposite to the percentage of nitrogen in dry weight, with maximum values in late summer and autumn and minimum values during late winter and spring



Fig. 4. Laminaria hyperborea. Length of new laminae $(\bigcirc, \triangle, n = 15-90)$ and stipes $(\oplus, n = 18-21)$. Average measurements with 95% confidence limits of plants from the exposed Station 2 (circles) and the sheltered Station 3 (triangles). (\downarrow) indicates start of lamina measurements at Station 2.

(Fig. 5B). Percentage carbon contents in dry weight of the 1991 laminae were compared in a one-way analysis of variance. A significant difference among the means was found (p < 0.05), and in an unplanned comparison among the means (Tukey-test) the carbon content of old laminae in March and April 1992 was found to be significant lower (p < 0.05) than the carbon content from July 1991 to January 1992 (Fig. 5B).

The overall seasonal variation in the C:N ratio of the canopy plants was large, with maximum values from 28 to 55 between June and October and minimum values from 9 to 15 between January and April at Station 2 (Fig. 5C). In March and April the C:N ratio was about 10 (Fig. 5C).

In January no difference was found in total nitrogen and carbon content of vegetative and fertile laminae (Table 1). By March most of the reproductive plants had emptied their sporangia. The carbon contents in dry weight of vegetative tissue and emptied sori tissue were similar, but tissue from plants which failed to develop sori during the winter had a higher content of nitrogen and lower C: N ratio than tissue from emptied sori (Table 1). A one-way analysis of variance on arcsine-transformed values of the nitrogen content gave a significant result, and in a Tukey-test of the means the nitrogen content of vegetative tissue in March was found to be significant higher (p < 0.05) than that of emptied sori (Table 1).

Environmental factors

The nitrate concentration of the seawater was low from April to September in both 1992 and 1993 (Fig. 6). In September

1991 an elevated nitrate concentration was found. Maximum values of between 5 and 6.5 μ mol nitrate were measured during January and March (Fig. 6).

The mean global radiation was generally very low from November to January and high from May to July (Fig. 7). In 1993 the global radiation in July was about the same as in August, and low compared to the preceding years (Fig. 7). The day lengths increased from c. 6 h in December to a maximum of c. 19 h in June (Fig. 7).

DISCUSSION

First-year plants

Laminaria hyperborea is reproductive from September to April, with a peak in January (Kain 1975). Water samples collected in a kelp forest from December to February contained the highest density of spores in January (Fredriksen *et al.* 1995). Under optimum conditions in the laboratory it takes about 10 days from liberation of spores to the formation of zygotes (Kain 1971a). Under *in situ* conditions in winter, with suboptimal light conditions or light saturation during part of the day only, it probably takes longer before the gametophytes become fertile. This suggests that the first-year plants transferred to the sea in mid-March corresponded in developmental stage and size to naturally recruited plants from spores liberated during February.

In the present study, first-year L. hyperborea grew until



Fig. 5. Laminaria hyperborea. Content of total nitrogen (A), carbon (B), and atomic C:N ratio (C) in laminae of canopy plants from Station 2. Continuous line: dry weight; dotted line: fresh weight. Filled symbols: 1991 lamina; open symbols: 1992 lamina. n = 10-43. In (B) groups of significantly different means of 1991 lamina are enclosed in brackets (Tukey-test, p < 0.05).

September, about 3 months longer than the canopy plants. Long days have been shown to promote growth rate reduction in older plants (Schaffelke & Lüning 1994), but do not seem to have the same influence on summer growth of small first-year plants. Lüning (1979) found first-year *L. hyperborea* growing until July in Helgoland, which was about one month longer than for older plants. The first-year plants used in Lüning's study were 5–25 cm long when transplanted to 2–7 m depths in the sea in February (Lüning 1979). Those plants were therefore larger than the plants used in the present study. Apparently small first-year plants have a potential for growth throughout the summer, whereas the seasonal growth pattern changes with increasing size or age of the plants.

The relative growth rate of the first-year plants varied considerably from May to October. The reduction in growth rate during late summer can be due to an endogenous clock, or alternatively, growth could be limited by environmental factors. *Laminaria hyperborea* shows maximal growth at 15°C

Table 1. Contents of total nitrogen and carbon (% of dry weight) in lamina samples of canopy plants in January and March 1992. The samples were taken from nonreproductive plants (vegetative tissue), tissue carrying sori, and tissue with empty sori. n.s = means not significantly different, s = significantly different means (Tukey-test, p < 0.05); n = 8–12

Tissue	January			March		
	% N	% C	C:N	% N	% C	C : N
Vegetative Sori	2.1 2.2	35.0 35.8	16.7 16.3	2.9	27.4	9.5
Empty sori				2.3	27.3	11.9
Tukey-test	n.s	n.s	n.s	s	n.s	s

(Bolton & Lüning 1982). On the outer coastal area of west Norway the seawater temperature is normally in the range of $11-18^{\circ}$ C during the summer (Kain 1971b). It is therefore unlikely that temperature limited the growth in the period investigated. On the other hand, the nitrate concentration at the locality was very low from May to October, and light (global radiation) varied considerably.

Carbon-to-nitrogen ratios of 10–15 have been found to be critical in several algae, with lower values indicating storage of nitrogen and higher values nitrate-limited growth (Hanisak 1983). The C:N ratio of first-year plants was below 15 all summer, indicating that growth was not nitrogen-limited. Also, the nitrogen content was high in the first-year plants compared to the canopy plants during the summer. The first-year plants therefore may have a high potential for uptake of nitrogen. Faster uptake rates of nutrients in first-year plants than in older plants have been demonstrated in *L. bongardiana* (referred to as *L. groenlandica*) (Harrison *et al.* 1986). Juvenile *L. hyperborea* have thin laminae with a higher surface area-to-volume ratio than mature plants. A high surface area-to-volume ratio has been correlated with high uptake rates of nutrients in algae (Rosenberg & Ramus 1984).

However, during the first part of the summer the carbon content (percentage of dry weight) of the first-year plants was low compared to the canopy plants. This could be due to both low content of structural polysaccharides of the cell walls and low storage of carbohydrates in the first-year plants compared to the canopy plants. The ash content was not measured in the plants, and the composition of the rest of the dry matter is unknown. The low carbon content also contributed to the low C: N ratios in first-year plants. In addition, it is not known if a high nitrogen content reflects nitrogen storage in juvenile plants. Wheeler & North (1980) found that high nitrogen content of first-year plants of Macrocystis pyrifera (Linnaeus) C. Agardh was not due to intracellularly stored nitrate, and that growth of the plants was a linear function of tissue nitrogen. Thus, in spite of the high nitrogen content and the low C:N ratio in the first-year plants, growth may have been nitrogenlimited during the summer or part of the summer. From August to October the growth rate decreased concurrently with decreasing values of irradiance and day lengths, suggesting that growth was light-limited or reduced because of shorter day lengths during this period.

It is possible that environmental influence on growth varies with the size of the first-year plants. Gametophytes and microscopic sporophytes grow within the laminar boundary layer



Fig. 6. Nitrate concentration in surface water from the area investigated.

(Neushul 1972), which may reduce the nutrient uptake of the plants. This may lead to low growth of the microscopic sporophytes, and increased growth as they grow out of the laminar boundary layer. This can explain the development of new macroscopic sporophytes on the Plexiglas plates throughout the summer. On the other hand, Kain (1965) found that growth of small sporophytes of *L. hyperborea* was logarithmic. Variation in the size of the microscopic stage in a batch of plants

will therefore lead to considerable variation in size and high bias towards small plants after a period of time.

Canopy plants

Canopy plants grow from January until June. Such growth pattern has previously been reported for *L. hyperborea* from Helgoland (Lüning 1970) and the Isle of Man (Kain 1976a).



Fig. 7. Day lengths (bold line) and average monthly global radiation at the stations in (\bullet) 1991, (\triangle) 1992, (\Box) 1993.

The results from the present study support Kain's (1976a) observation of a maximum elongation rate of lamina in March and April. In contrast, in Iceland, Gunnarsson & Ólafsson (1992) observed maximum growth in May and a slow summer decline in both lamina and stipe growth, indicating that some variations in the growth pattern of *L. hyperborea* exist.

The seasonal pattern of total carbon content of laminae coincides with the annual variation of mannitol and laminaran content observed in *L. hyperborea* by Black (1950) and Haug & Jensen (1954). A build-up of mannitol and laminaran takes place during the summer when growth has terminated, whereas the onset of the growth period in early winter takes place at the expense of stored carbohydrates (Lüning 1969). In the present study a rapid decline in total carbon content of old laminae was found from January to March, a period with low light and increasing lamina and stipe elongation. The carbon content of the old lamina was lowest in April, indicating that carbon reserves were depleted before the laminae were shed.

Although the overall carbon content of dry lamina tissue decreased considerably from January until March, similar carbon contents of vegetative and reproductive laminae were found in each of the two months. By January, sorus formation is completed in most plants (Kain 1975). Thus, compared to the reduction in carbon content which accompanied increased vegetative growth during winter and early spring, the results indicate that little stored energy is allocated to the process of sorus formation in *L. hyperborea*. In March a lower content of nitrogen was found in the empty sori compared to vegetative tissue, which suggests that some nitrogen is lost from the plants with the liberation of spores.

The total nitrogen content of laminae was high during the period of growth and low when growth was minimal, and followed the seasonal pattern of protein found in *L. hyperborea* (Black 1950; Haug & Jensen 1954). However, the pattern of high versus low nitrogen content may also indicate storage of nitrate in a period of high ambient nitrate concentration (Black & Dewar 1949). Asare & Harlin (1983) found that values exceeding 1% nitrogen content of tissue dry weight represented intracellular stored nitrate in *L. saccharina.* If this also applies to *L. hyperborea*, it suggests that nitrate is being stored in the plants from January to April. The concentration of nitrate in the seawater decreased to minimum levels during April and was low until September.

The nitrogen content and the growth rate of the plants decreased simultaneously in the spring. Thus, the reduced growth in the summer could be due to nitrate limitation. However, Lüning (1979) concluded that the seasonal growth rate reduction in July in L. hyperborea from Helgoland was not a result of nitrate limitation. Schaffelke & Lüning (1994) found that the seasonal growth pattern of L. hyperborea was due to an endogenous circannual cycle, on which long days acted as a signal to cease growth. In that study, day lengths of 12 h permitted a free-running growth cycle, whereas 16 h induced ceasation of growth in the laboratory. At the locality of the present study daylength is about 16 h at the beginning of May. Because ambient nitrate is reduced to minimum values shortly before and internal nitrogen probably depleted at about the same time as the plants are exposed to a daylength of 16 h, it was not possible to separate the possible effects of low nitrogen availability and long days in this study. However, it is probable that stored nitrogen can support growth during a

period in the spring, before the daylength signal induces ceasation of growth. At the most wave-exposed locality a considerable part of the total lamina elongation took place from the beginning of April until June. The high nitrogen content and low C:N ratio in the plants in March and April suggests that the plants were not nitrogen-limited during early spring, and that enough nitrogen was stored in the plants to support growth until May.

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