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Aspects of carbon metabolism in relation to autumnal blade abscission in the kelp *Pleurophycus gardneri* (Phaeophyceae, Laminariales)

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ABSTRACT: Pre-abscission changes in the deciduous kelp *Pleurophycus gardneri* involve a gradual decrease in dry weight, mannitol and laminaran content. These carbon compounds decreased from about 18% (dry weight) to 4% prior to blade abscission, while the perennial structures, stipe and holdfast, showed a concomitant increase in mannitol and dry weight towards autumn. In November, at the time of new blade outgrowth, mannitol content peaked in stipe and holdfast with 12 and 18%, respectively. Laminaran accounted for less than 2% in all thallus parts and showed no measurable seasonal variation. Pigment levels of the blade increased with progressing senescence and were at maximum just prior to blade abscission. The photosynthetic performance of the blade revealed saturating irradiances of about 50 μE m^{-2} s^{-1} and a compensation irradiance of 2.5 to 3 μE m^{-2} s^{-1} measured in April. Light saturation of the stipe was at 38 μE m^{-2} s^{-1} and of the haptera at 23 μE m^{-2} s^{-1} while compensation irradiances were at roughly 8 μE m^{-2} s^{-1} for both perennial parts. It is suggested that new blade outgrowth requires light-carbon fixation. No acropetal translocation of the abundant carbon store of the perennial structures was observed. The deciduous habit of *P. gardneri* reflects a shade-adapted growth strategy. The perennial parts are involved in the overall physiology of the plant and have similar seasonal fluctuations in their constituents to those of the blade. The described growth strategy is novel among perennial kelp species.

INTRODUCTION

Perennial marine macroalgae usually generate new blade outgrowth in the darkest period of the year. Accumulation of reduced carbon compounds and the subsequent mobilization of these reserve products can be a necessary feature for a perennial growth strategy when the period for blade outgrowth occurs at a time when light is limited. The energy for new growth in autumn is generated at the expense of the major photoassimilates like mannitol and laminaran which enter glycolysis and form the substrate for light-independent carbon fixation (Schmitz et al. 1972, Lüning et al. 1973, Kremer 1981a, 1984). This metabolic strategy enables the circumpolar *Laminaria solidungula* to endure the arctic night period while producing a new blade and completing 90% of its annual linear growth (Chapman & Lindley 1980, Dunton et al. 1982, Dunton & Schell 1986). Similarly, the northwest Atlantic *L. hyperborea* depends on reserves of photosynthates accumulated in the old blade since irradiances are below compensation values at the time of new blade formation (Lüning 1971). In both species, the old lamina (or laminae as in *L. solidungula*) is necessary to act as a supply reservoir for photosynthates produced at the time when the photosynthetic rate exceeds the demands of growth and respiration.

In contrast to this growth strategy, little accumulation of reserve carbohydrates occurs in other perennial representatives of the family Laminariaceae, such as *Laminaria digitata* which exhibits continuous and rapid growth throughout the summer (Lüning 1979). Mannitol and laminaran of *L. saccharina* are synthesized during summer but are unnecessary for winter growth because

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the carbon fixed during winter covers the plant's energy requirement (Johnston et al. 1977). The northeast Atlantic *L. longicruris* – a species thought to be conspecific with *L. saccharina* (Bolton et al. 1983) – also showed a photosynthetic surplus throughout most of the autumn and winter and possessed a large annual assimilatory surplus that was not accounted for as stored material (Hatcher et al. 1977, Johnston et al. 1977, Chapman & Craigie 1978, Gagné et al. 1982). In Arctic waters, *L. saccharina* appears to complete nearly all of its annual growth during the relatively short period of ice-breakup when nutrients are still available and light begins to enter the water column (Dunton 1985).

In contrast, growth of the new blade in the deciduous kelp *Pleurophycus gardneri* (Laminariaceae) commences in the complete abscence of old blade tissue. This perennial kelp abscises the entire blade in autumn and within 2 wk new blade growth is generated at the distal stipe end (cf. Germann 1986a, b). In contrast to *Laminaria hyperborea* (Lüning 1969, 1986), the induction of new blade growth is independent of a photoperiodic signal in *P. gardneri* and is completely inhibited when cultured in darkness (Germann 1986b). Since the autumnal leaf abscission behavior of higher plants is coupled to carbohydrate metabolism (Addicott 1982), an attempt was made to monitor seasonal changes in dry weight, mannitol, and laminaran of all thallus parts. The photosynthetic performance was measured in April 1984 and pigment content was determined on a monthly basis, from May 1982 to May 1983.

MATERIAL AND METHODS

Site description. *Pleurophycus gardneri* was harvested at monthly intervals from a major wild stand in Barkley Sound (48° 50' 6" N, 125° 12' 18" W) Vancouver Island, British Columbia, Canada. The sporophytes were harvested from the upper to middle subtidal area from a boat or by SCUBA techniques. For a detailed description of the study area and environmental parameters see Germann (1988).

Photosynthesis-irradiance relationship. Experiments on photosynthesis and respiration were carried out on 7 sporophytes in April 1984 using an oxygen electrode (YSI, LN 3526) connected to a chart recorder. Fronds were collected by divers 1 d prior to the start of the experiment. Pigment extraction and photosynthesis measurements were conducted on separate tissues. Circular discs of 22 mm diameter were punched out of the midrib and wing about 10 cm distal to the transition zone; pieces of 27 to 30 mm in length were cut from the stipe apices, and pieces of 0.6 to 1.2 g fresh weight from newly grown, non-epiphytized haptera. The blade discs were preconditioned in running seawater for a minimum of 1 h and stipe and holdfast samples for a minimum of 2 h to minimize enhanced respiration due to wounding effects. The tissues were blotted dry, weighed and placed in a circular plexiglass chamber filled with 18 ml of filtered (0.45 µm) seawater. The chamber was equipped with a magnetic stirring bar and sealed with a polystyrene cover using silicon grease. The disc was held in the chamber on a fine glass capillary tip glued perpendicular to the polystyrene cover of the chamber (wounding effect of the capillary: 1 mm in diameter). The sealed, bubble-free chamber with inserted oxygen electrode was immersed in a water bath at 11 to 13 °C, using running seawater and ice as coolant. The temperature of the chamber remained between 11 and 12.5 °C. The oxygen electrode was calibrated both in air-saturated and oxygen-free (nitrogen-purged) seawater. Values for oxygen content in air-saturated seawater were taken from the tables presented by Green & Carritt (1967). Average nitrate concentrations of the seawater used for incubation were 2 µmol NO_3-N l^{-1}; average phosphate concentrations were about 0.5 µmol PO_4-P l^{-1} (analysing methods according to Strickland & Parsons 1972). Two Kodak Ektagraphic slide projectors equipped with Sylvania tungsten halogen lamps (CBA 500 W) were used as light sources, which illuminated the discs perpendicularly from each side. Net photosynthesis was measured at progressively increasing photon flux densities (PFD) (10, 20, 40, 70, 110, and 190 µE $m^{-2} s^{-1}$) using neutral density filters. Dark respiration was measured for about 5 min, or until a constant rate was achieved. In each light regime the tissue was allowed to accomodate to the different PFD until O_2 production was linear, usually within 10 min. The chamber was then flushed with 50 to 70 ml of filtered, nitrogen-saturated seawater via surgical tubing connected to the incubation chamber. Air-saturated seawater was used to measure respiration. After incubation, the discs were dried at 105 °C to obtain dry weights.

Maximum photosynthetic rates (P_{max}) were calculated after a Woolf plot linearization of the whole data set ($r \geq 0.95$). For linearization, rates of dark respiration and net photosynthesis were added to give gross photosynthesis. Photosynthetic efficiency, defined as the initial slope (α) of the P vs I curve, was calculated by linear regression analysis of the O_2-consumption and production rates of subsaturating photon flux densities (0, 10, 20, 40 µE $m^{-2} s^{-1}$). The saturation irradiance (I_k) was determined as gross P_{max}/α. The compensation irradiance (I_c) was graphically determined from the intersection of the initial slope of the P vs I curve with the *x*-axis.

Chemical analyses. Ten plants were analysed for dry weights and 3 to 5 plants were subjected to chemical analyses of mannitol and laminaran (for sampling

method see Germann et al. 1987; for analysing method see Germann 1988). Laminaran was obtained from a 0.2 *N* HCl extraction for 1 h, using an anthrone reagent (Yemm & Willis 1954) with D-glucose as a standard.

Discs (1.6 cm diameter) were punched from the blades with a copper corkborer and pieces 1 cm in length were cut from the stipe and haptera for pigment analyses immediately after harvesting. Average fresh weight of the extracted wing and midrib discs were about 0.1 and 0.3 g, respectively. The stipe tissues used weighed about 0.5 g and the holdfast tissue 0.3 g. Pigments were always subjected to analyses within 1 h of harvesting. Chlorophyll *a*, chlorophyll *c* and fucoxanthin contents were obtained following the DMSO-extraction procedure, described by Seely and coworkers (Seely et al. 1972) and modified by Wheeler (1980). Tissues were generally extracted until they were bleached. This was, however, sometimes not completely achieved in parts of the stipes and haptera. Chlorophyll *a* content of tissues adjacent to those used for photosynthetic rate measurements (April 1984) was obtained after acetone extraction according to the method of Arnon (1949).

There has been much dispute whether the use of tissue discs instead of whole plants is reasonable for physiological studies. Most photosynthetic measurements for *Laminaria* spp. have been made under laboratory conditions using blade discs under artificial light (e.g. Lüning 1971, King & Schramm 1976a, b, Küppers & Kremer 1978). Various other authors, however, employed whole plants and claimed differences in the physiological response (Hatcher 1977, Johnston et al. 1977, Gerard 1988). According to Gerard (1988), P_{max} and dark respiration determined for mature blade discs of *Laminaria saccharina* averaged 83 and 102 % of whole plant rates, respectively. In the present study, pigment content and photosynthetic performance were, for technical reasons, measured on tissue discs.

RESULTS

Dry weight

The seasonal range in dry weight (as % fresh weight) of midrib and wings indicated minima of about 10 % and maxima of about 14 to 15 % (Fig. 1). The average values for seasonal dry matter were 26 % in the stipes and 21 % in the haptera, whereas they were 14 % in the midrib and 12 % in the wings. In contrast to the annual blade, seasonal maxima in dry weight of both perennial structures (stipe and holdfast) were recorded in the bladeless period. Dry weight of the stipe was greatest between September and January and peaked in January at ca 32 % dry matter. In the holdfast, the annual

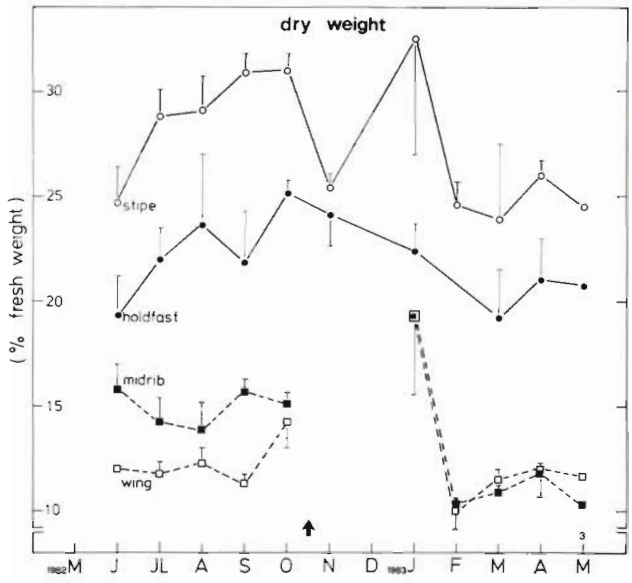

Fig. 1. *Pleurophycus gardneri*. Seasonal variation in mean dry weight (% fresh weight) of stipe, holdfast, midrib, and wing from May 1982 until May 1983. $n = 5$ except for May 1983 where $n = 3$. Standard deviation is shown if $n > 3$. Arrow denotes time of blade abscission

maximum of 24 % dry weight was obtained in November. Dry weight allocation of stipe and haptera was about 1 % dry matter d^{-1} in the bladeless period (not shown).

Mannitol and laminaran

Seasonal variation in mannitol content of *Pleurophycus gardneri* coincided with dry weight variation in both the annual and perennial structures whereas the polyglucan laminaran remained minimal throughout the whole study period (Fig. 2a, b). Mannitol content (as % dry weight) of the midrib was highest at 18 % in June and decreased with declining growth rates to about 4 % at the time of blade abscission. After blade abscission (Fig. 2a; November 1982), mannitol content reached its seasonal maximum in both stipe and holdfast with 12 and 17 % of dry weight, respectively. The increase in mannitol content thus coincided with the initiation of dry weight accumulation in the stipe and holdfast (Fig. 1). The variation in mannitol content was similar in the perennial parts and in the annual blade, but the maxima were at different times. With the onset of new blade outgrowth, mannitol content declined in stipe and holdfast. In January, when growth was apparently still light limited, the young blade already contained about 10 % mannitol, a value that corresponds with 86 % of the wing's seasonal mannitol maximum. Laminaran contributed, at most, 1.3 % of dry matter in the midrib and 0.5 % in all other thallus parts.

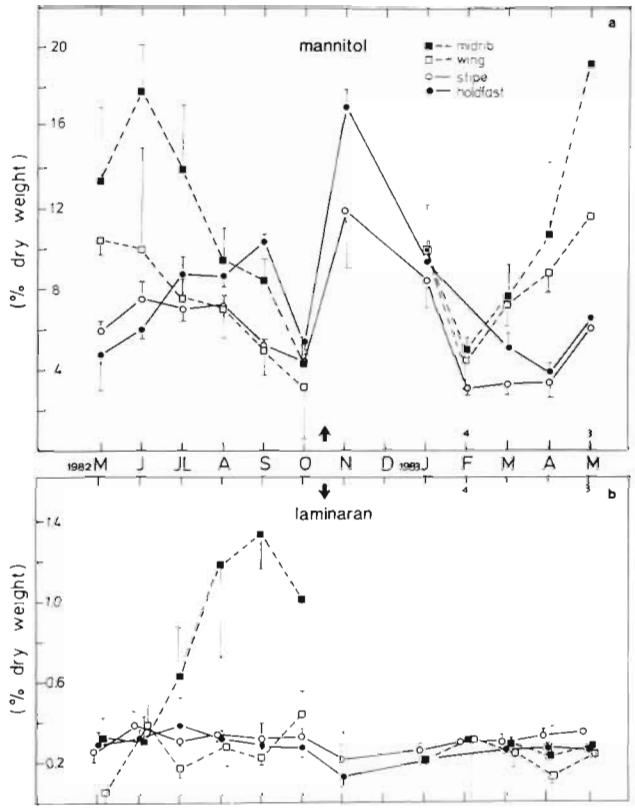

Fig. 2. *Pleurophycus gardneri*. Seasonal variation in (a) mean mannitol content and (b) mean laminaran content (% dry weight) of stipe, holdfast, midrib, and wing from May 1982 until May 1983. $n = 5$ except for May 1983 where $n = 3$. Standard deviation is shown if $n > 3$. Arrow denotes time of blade abscission

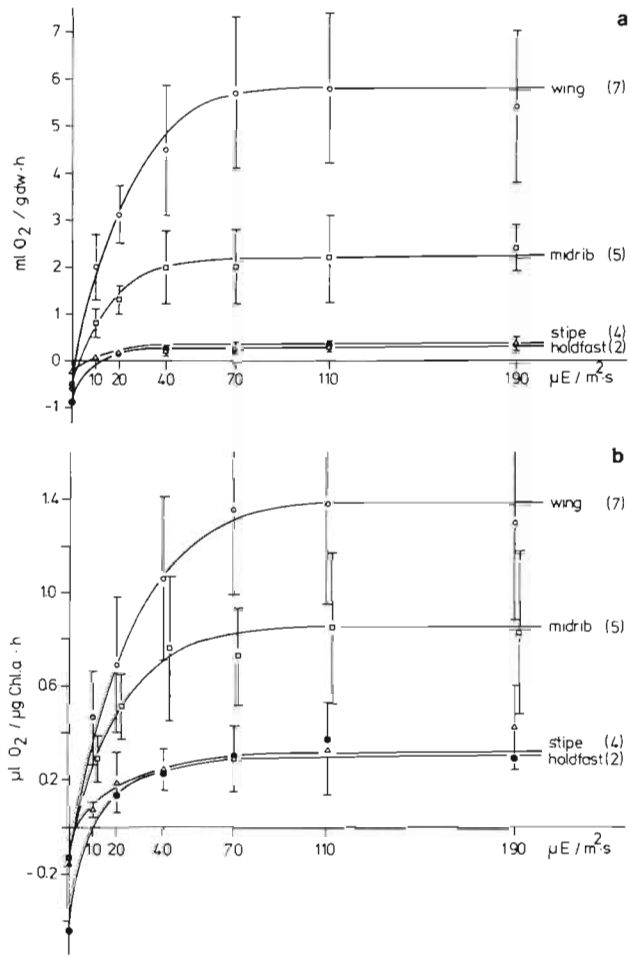

Fig. 3. *Pleurophycus gardneri*. Photosynthesis versus irradiance curves. Mean net photosynthesis (a) in ml oxygen produced g^{-1} dry wt h^{-1}, (b) in µl oxygen produced μg^{-1} chl *a* h^{-1} of stipe, holdfast, midrib, and wing. Vertical bars: SD; numbers in parenthesis: *n*. All measurements were made in April 1984, at 11 to 12.5 °C and 2 µmol NO_3-N l^{-1}. Curves were eye-fitted

Photosynthetic rates

The response of photosynthetic rate to light intensity in sporophytes of *Pleurophycus gardneri* was measured in April 1984, and curves were fitted by eye to P vs I data for different thallus parts (Fig. 3a, b). By analogy to enzyme kinetics, P_{max} was calculated by subjecting the whole data set to a Woolf plot linearization and by plotting irradiance/O_2 production vs irradiance (cf. Dowd & Riggs 1965). The eye-fitted and calculated P_{max} values are in close agreement. The calculated maximal photosynthetic rate (P_{max}) was highest in the wing reaching 5.9 ml (8.4 mg) O_2 g dry weight(dw)$^{-1}$ h^{-1}, while the midrib yielded 2.6 ml (3.7 mg) O_2 g dw^{-1} h^{-1}, which corresponds to 43 % of P_{max} of the wing (Fig. 3a). P_{max} of the holdfast was 0.32 ml (0.48 mg) O_2 g dw^{-1} h^{-1} and that of the stipe only 0.40 ml (0.57 mg) O_2 g dw^{-1} h^{-1}.

The difference in P_{max} on a chlorophyll *a* basis (Fig. 3b) was less pronounced between wing and midrib. Under saturating light conditions, O_2 production in the wing was about 5 times higher than in both stipe and holdfast.

The light intensity (I_k) at which light saturation occurs is usually taken as the intensity at which the initial slope and P_{max} of the P vs I curve intersect. This method is based on a linear regression analysis of the photosynthesis data obtained in the low range (subsaturating) of the applied irradiances (between 0 and 40 µE $m^{-2}s^{-1}$). The wing and midrib displayed saturating irradiances of about 50 and 47 µE m^{-2} s^{-1} ($r \geq 0.94$), respectively. I_k of the holdfast was about 23 µE m^{-2} s^{-1} and that of the stipe about 38 µE m^{-2} s^{-1} ($r \geq 0.80$).

Compensation irradiances (I_c) were found at about 2.5 to 3 µE m^{-2} s^{-1} for the wing and the midrib, whereas the stipe and holdfast indicated compensation irradiances of about 8 µE m^{-2} s^{-1}.

Pigments

As opposed to dry weight and mannitol content, chlorophyll *a* (chl *a*), chlorophyll *c* (chl *c*) and fucoxanthin contents of the blade (per area) increased from May until the time of blade abscission in October (Fig. 4). A steady increase in pigment content was also evident in the stipe between June and October in 1982, whereas the holdfast exhibited a decline (Fig. 5).

The assimilation area, chlorophyll *a*, and mannitol content of different ontogenetic stages of *Pleurophycus gardneri* are shown in Fig. 6. The adult thallus attained a maximal blade surface area on 23 June 1982, and produced highest levels of mannitol per unit area with 81 % of maximally measured chlorophyll *a* content. The senescent blade exhibited only 13.3 % of the maximal surface area, but reached maximal chlorophyll *a* concentrations while producing only 24 % of the June mannitol values. In contrast to senescent blades, very young blades contained double the amount of mannitol, 28 % less chlorophyll *a* per cm^2 and 13 % less surface area.

DISCUSSION

The autumnal leaf abscission behavior of higher plants involves major physiological changes and is highly related to the amount of carbohydrate reserves (Addicott 1982). High carbohydrate levels in a plant will contribute to the vigor of leaves and facilitate the synthesis of hormones required for growth, development and most importantly, inhibition of abscission. Moreover, abscission in higher plants is delayed if conditions for photosynthesis are favourable. Plants supplied with an abundance of amino acids and other nitrogenous compounds essential for active metabolism retain their leaves much longer than deficient ones.

As in deciduous higher plants, photosynthetic reserves (mannitol and laminaran) are lowest (4 % of dry weight) just before blade abscission in *Pleurophycus gardneri* (Fig. 2). Pre-abscission changes included decreasing levels of dry weight in the annual blade coincident with dry matter accumulation in the perennial thallus parts. Thus, *P. gardneri* generally contained at least twice as much dry matter in the stipe and only about half the amount of dry matter in the blade compared with other Laminariaceae (Black 1954, Mann 1972). The meristematic region of *P. gardneri* contained less than half of the dry weight per cm^2 (not shown) of the corresponding region in *Laminaria hyperborea* and about 30 % less than *L. saccharina* (Küppers & Kremer 1978). Long-distance translocation of mannitol (review by Schmitz 1981) likely occurred just prior to blade abscission since mannitol content doubled in the haptera (Fig. 2a). However, most strikingly, mannitol increased in both perennial parts in *P. gardneri* during the bladeless period in October/November, when no major source for mannitol translo-

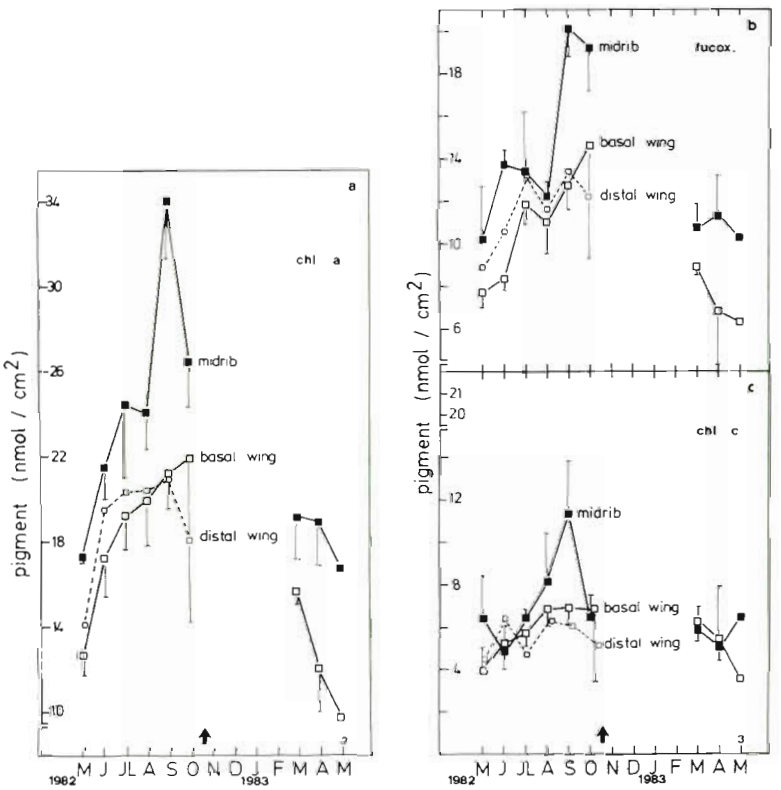

Fig. 4. *Pleurophycus gardneri*. Seasonal variation in mean pigment content (nmol cm^{-2}) of midrib, basal and distal wing regions from May 1982 until May 1983. (a) Mean chlorophyll *a* content, (b) mean fucoxanthin content, (c) mean chlorophyll *c* content. $n \leq 5$ except for May 1983 where $n = 3$. Standard deviation is shown if $n > 3$ for midrib and basal wing data. Arrow denotes time of blade abscission

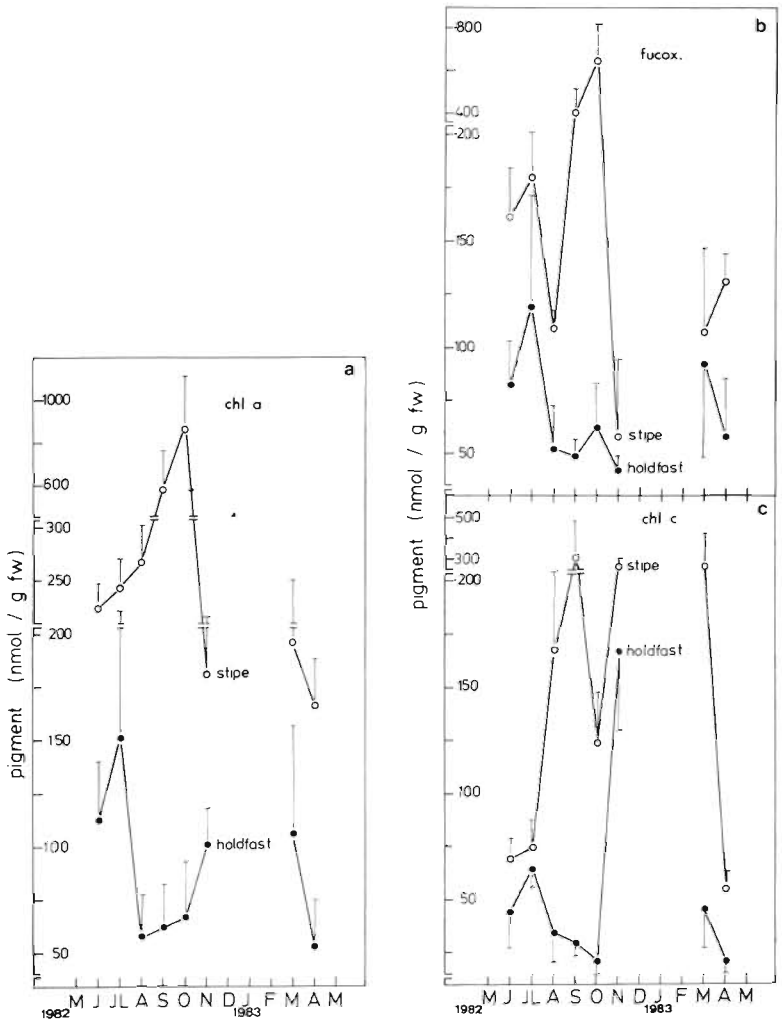

Fig. 5. *Pleurophycus gardneri*. Seasonal variation in mean pigment content (nmol g^{-1} fresh weight) of stipe and holdfast from May 1982 until May 1983. (a) Mean chlorophyll *a* content, (b) mean fucoxanthin content, (c) mean chlorophyll *c* content. Means of $n = 5 \pm SD$

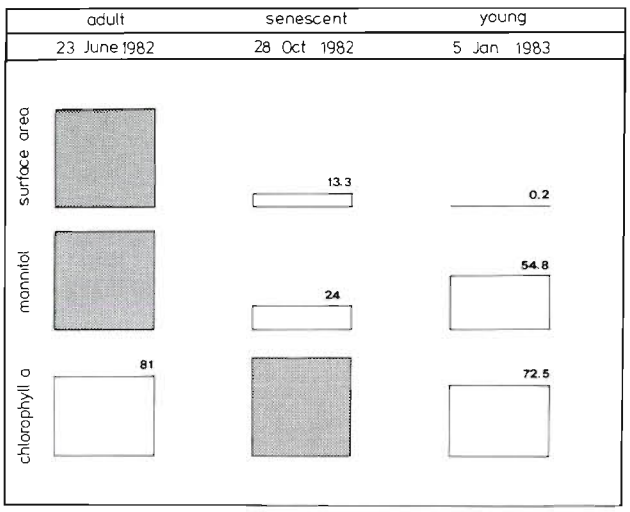

Fig. 6. *Pleurophycus gardneri*. Relative surface area (cm^{-2}), relative mannitol (mg cm^{-2}) and relative chlorophyll *a* content (μg cm^{-2}) in an adult, a senescent, and a young blade. Hatched areas denote the 100% reference and numbers indicate percentage to this reference

cation existed. Although there was a considerable amount of stored mannitol available in holdfast and stipe (18 and 12%, respectively), *P. gardneri* was unable to produce any outgrowth when cultured in complete darkness (Germann 1986b). This suggests that new growth is totally dependent on the acquisition of newly fixed carbon. These high levels of stored carbon in the perennial parts of *P. gardneri* may compensate primarily for respiratory losses and are apparently not utilized for the biosynthesis of new tissue via beta-carboxylation. As noted previously, the major physiological role of mannitol is to provide fixed carbon for respiratory pathways (Kremer 1979a).

According to Kremer (1979b), light-independent carbon fixation in *Pleurophycus gardneri* averaged 5.3% of photosynthesis during August/September – a value well within the range of the dark fixation potential of other members of the Laminariales. As demonstrated in a previous study, thallus regions with highest dark fixation rates and maximal phosphoenolpyruvate carboxykinase (PEP-CK) activity also appeared to have

highest total nitrogen content (Küppers & Kremer 1978). The large amount of total nitrogen content (mainly as ninhydrin positive substances) present in the stipe and haptera of *P. gardneri* throughout the growth cycle, independent of the ontogenetic stage (Germann et al. 1987), suggests that light-independent carbon fixation might be quite effective in these perennial parts. Chlorophyll *a* concentration in the holdfast is only half of the maximal levels measured in autumn (Fig. 5). This may indicate an increasing importance of light-independent carbon assimilation towards autumn, which would allow the plant to enter a resting period, without a major supporting photoassimilatory organ, during a period of light limitation. The observation that no growth was produced in those sporophytes cultured for several month in complete darkness raises the question whether beta-carboxylation is confined to the light period in this particular ontogenetic stage, perhaps due to a lack of substrate availability. Beta-carboxylation of phosphoenolpyruvate is generally not restricted to dark periods, but also occurs concomitant with photosynthesis and results in a more effective net gain of carbon (Kremer 1981b, Weidner & Küppers 1982). According to Kremer (1984), the substrate for beta-carboxylation originates only in the dark from the dissimilation of mannitol, whereas in the light, the substrate of PEP-CK is preferentially provided by 3-phosphoglycerate from the reductive pentose phosphate cycle. In *Laminaria hyperborea* and *L. saccharina* (Schmitz et al. 1972, Lüning et al. 1973, Kremer 1981a), mannitol stored in the stipe in autumn (7 % of dry weight in the case of *L. hyperborea*: Haug & Jensen 1954) is not used for translocation in the reverse, acropetal direction. A similar lack of such an upwardly directed translocation can also be presumed in *P. gardneri*.

The question has to be asked whether the complex polysaccharides, such as laminaran, are another source of respiratory substrates, although they are usually of secondary importance (Bidwell 1967, Kremer 1975). It is assumed that mannitol and laminaran are interconvertible in a manner analogous to sucrose and starch in higher plants (Percival & McDowell 1967). The present study found that *Pleurophycus gardneri* does not store laminaran at levels comparable to other investigated *Laminaria* spp. where it can range from less than 2 % up to 34 % of the dry weight (Powell & Meeuse 1964). Even among *Laminaria* spp. in which a carbohydrate reserve was not found to play a major role for new autumn/winter growth, 25 % laminaran (of dry weight) was obtained in *L. digitata* (Black 1948b) and 30 % in distal blade regions in *L. saccharina* (Black 1954). However, the amount of laminaran in the stipe of *P. gardneri* was comparable to the laminaran content in the stipes of *L. hyperborea, L. digitata* and *L. saccharina* (Haug & Jensen 1954). Maximum tissue density (% dry weight of fresh weight) was also related to laminaran content in many *Laminaria* species (Black 1947a, b, Haug & Jensen 1954, Chapman & Craigie 1978, Küppers & Weidner 1980). Fluctuations in laminaran in *P. gardneri,* however, cannot account for the variation in dry weight.

In summary, stored carbon in the perennial parts is not used for new blade outgrowth and the formation of a new blade is dependent on carbon assimilated directly from photosynthesis in *Pleurophycus gardneri.* Evidence in support of highly effective photosynthesis is provided by the high amount of mannitol (86 % of the seasonal maximum) obtained in the very young blade in January (Fig. 6). Moreover, the photosynthetic performance of *P. gardneri* measured in April revealed rather low saturating irradiances (I_k) of about 50 $\mu E\ m^{-2}\ s^{-1}$ and a low compensation irradiance of around 3 $\mu E\ m^{-2}\ s^{-1}$ of the lamina (Fig. 3). Photosynthetically active radiation required to saturate photosynthesis in *Laminaria* spp. ranges from 150 to 200 $\mu E\ m^{-2}\ s^{-1}$ and compensation irradiances from 5 to 8 $\mu E\ m^{-2}\ s^{-1}$ (for review see Lüning 1981). Saturation irradiances seem to vary distinctly between tissue areas of different age as demonstrated in *L. solidungula* (Dunton & Jodwalis 1988). In this arctic kelp species, I_k averaged 38 $\mu E\ m^{-2}\ s^{-1}$ in adult and 46 $\mu E\ m^{-2}\ s^{-1}$ in young plants, suggesting high photosynthetic performance during the summer period of ice-breakup. Compensation irradiances of extremely shade-adapted red algae were about 2 $\mu E\ m^{-2}\ s^{-1}$ (Lüning 1981). These measurements support the idea that *P. gardneri* can grow with minimal light, typical of a shade-adapted plant.

Laminaria hyperborea, which depends on stored carbon compounds for new outgrowth in autumn, grows much deeper in the sublittoral than *Pleurophycus gardneri* and is characterized by having saturating irradiances (I_k) between 50 and 70 $\mu E\ m^{-2}\ s^{-1}$ (Lüning 1971). O_2-production at saturating irradiances on a chlorophyll basis is the same in *L. hyperborea* as in *P. gardneri* although pigment levels in *P. gardneri* are much lower. This may indicate that the number but not the size of the photosynthetic units is the same in these 2 species (Dring 1982). The wings of *P. gardneri* exhibited the same O_2-production as the old frond in *L. hyperborea* (1.6 $\mu l\ O_2\ chl\ a^{-1}\ h^{-1}$: Drew 1983) and the stipe and holdfast each produced as much O_2 as the new blade of *L. hyperborea* (0.7 $\mu l\ O_2\ chl\ a^{-1}\ h^{-1}$).

The maximal photosynthetic rates (P_{max}) of *Pleurophycus gardneri,* an indication of the overall activities of the carboxylating enzymes, may reflect levels which are suboptimal in the course of the seasons, since nitrate concentrations were only about 50 % of seasonally occurring maxima. The experimental temperature was also about 4 °C higher than ambient at

the time of measurements. However, P_{max} (per dry weight) of the midrib compares with the perennial *Laminaria digitata* (King & Schramm 1976a) whereas P_{max} of the more fragile wings is in the range of annual species which tend to be more productive than perennials (Darley 1982). It would be necessary to assess P vs I properties of *P. gardneri* on a seasonal basis in order to get a more accurate picture of the photosynthetic performance during the blade renewal process.

Table 1 gives an estimate of seasonal underwater photon flux densities (PFD) (no facilities were available for in situ measurement of PFD). Assuming that the study site corresponds to Jerlov coastal water type 9 (Jerlov 1976), which is probably a light-deficient estimate of the actual situation, 2 to 5 % of surface irradiances (cf. Fig. 12 in Lüning & Dring 1979) would reach the *Pleurophycus* stand at its depth of 4 m. Water transparency (Secchi disk depth) seasonally peaked at 12 m in October/November (Germann 1986a) and improved the light conditions of the habitat at the time of new outgrowth. This suggests that compensation irradiances of the blade and stipe of *P. gardneri* are met year-round. The molar ratio of fucoxanthin:chlorophyll *a* generally varies from 0.3 to 0.4 in brown algae and from 0.5 to 0.6 in diatoms (Dring 1982 and literature cited therein). The fucoxanthin:chlorophyll *a* ratio in stipe and holdfast of *P. gardneri* averaged about 0.6 and lies well in the range of diatoms which suggests a typical shade habit of these perennial structures. This particular photosynthetic efficiency probably enabled *P. gardneri* to invade southern Californian waters, where quite large populations were recently found at a remarkable depth of 27 m (VanBlaricom et al. 1986). Although mainly northerly distributed, this kelp avoids prevailing temperature conditions in southern California by isothermal submergence (Briggs 1974), which in turn requires a highly efficient photon harvesting apparatus. The upper survival temperature of *P. gardneri* was shown to be 15 °C (Germann 1986b).

Table 1. Monthly mean photon flux densities (PFD) at the surface at Carnation Creek, a site in Barkley Sound near Bamfield in 1981 and 1982. Surface PFD data were taken from Fig. 2 in Wheeler at al. (1984). Data from January to September are means of PFD measured at the surface. Daylength data were taken from the Smithsonian Meterological Tables (1951) valid for Seattle (48° N). PAR: photosynthetically active radiation

Month	Light d^{-1} at 48° N (h)	Surface PAR ($\mu E\ m^{-2}\ s^{-1}$)	1 % of surface PAR ($\mu E\ m^{-2}\ s^{-1}$)	2–5 % of surface PAR ($\mu E\ m^{-1}\ s^{-1}$)
Jan	9	308.6	3.1	6.2–15.5
Feb	10.6	381.3	3.8	7.6–19.0
Mar	12.2	626.1	6.3	12.6–31.5
Apr	14	685.5	6.9	13.8–34.5
May	15.4	775.0	7.8	15.6–39.0
Jun	16	753.0	7.5	15.0–37.5
Jul	15.4	766.6	7.7	15.4–38.5
Aug	14	784.7	7.8	15.6–39.0
Sep	12.2	724.5	7.2	15.4–36.0
Oct	10.6	452.6	4.5	9.0–22.5
Nov	9	359.3	3.6	7.2–18.0
Dec	8.3	300.0	3.0	6.0–15.0

Since light is apparently not limiting to photosynthesis year-round, this may explain the lack of reserve accumulation in *Pleurophycus gardneri*. It has been demonstrated that the light availability in a given habitat may exert some control over the accumulation of reserve material (Lüning 1979). *Laminaria digitata* growing in the upper subtidal transfers more energy into growth in the second half of the year than does *L. hyperborea*, and hence accumulates less reserve products in the blade towards autumn. If *L. digitata* were transplanted to a deeper (more light-limited) habitat in the subtidal area, the accumulated reserves could not compensate for the lower light regime. Thus, the ability to invest in reserve accumulation may be genetically fixed and relates to light-limited growth phases.

With progressing blade senescence, concentrations of chlorophyll *a* (on an area basis) increased, as did, to a lesser extent, the accessory pigments chlorophyll *c* and fucoxanthin. Seasonal pigment levels in the midrib were highest in the old lamina, just before blade abscission. Moreover, the measured pigment content increased enormously in the stipe up to October (Fig. 5a, b). Chlorophyll *c*, however, increased in the perennial parts only in November, after the blade had been abscised (Fig. 5c). This is in contrast to pre-abscission changes in higher plants where a gradual decline and disappearance of chlorophyll and an eventual breakdown of all the pigments can be observed (Addicott 1982). The increase in pigment concentrations towards autumn can possibly compensate for the decrease in irradiance (Ramus et al. 1977). Old tissues of *Macrocystis integrifolia* contained pigment concentrations intermediate between young and mature tissues (Smith et al. 1983) and the oldest tissue of *Nereocystis luetkeana* had on average 42 % more chlorophyll *a* and 56 % more fucoxanthin (per unit area) than the young proximal tissue (Wheeler et al. 1984). Hence, senescence and pigment concentration decrease are not necessarily correlated in these brown macroalgae. In *Fucus virsoides* (Zavodnik 1973) and in the red alga *Hypnea musciformis* (Durako & Dawes 1980) thallus degradation occurred when pigment and protein levels were low. It has been suggested that a high pigment content provides a large reservoir of amino-N that can be used to buffer the seaweed against a temporary reduction in N supply (Chapman et al. 1978, Probyn 1982, Smith et al. 1983) and that accessory pigment concentrations are

responsive to light as well as to ambient nitrogen (Shivji 1985). In *Pleurophycus gardneri,* however, the senescent blade contains a higher amount of photon-trapping chlorophyll *a* per unit area than the young blade, but produces only half the amount of mannitol (Fig. 6). This means either that the photosynthetic machinery is exhausted (inactivated chlorophyll), or that respiration readily consumes copious amounts of mannitol, or that the senescent tissue exudes this low-molecular weight compound (Moebus & Johnson 1974). Hence, abscission of the senescent blade appears to have an advantage over its maintenance, especially considering high photosynthetic efficiency of the stipe and holdfast.

In conclusion, blade abscission in *Pleurophycus gardneri* involves (1) the reduction of total dry weight in the blade and a subsequent translocation of mannitol and laminaran to the perennial parts (stipe and holdfast); (2) an increase in pigment levels in blade and stipe during blade senescence; (3) the generation of a new blade requiring light-carbon fixation, where beta-carboxylation is assumed to be coupled to the light phase. The deciduous habit of *P. gardneri* reflects a rather shade-adapted growth strategy with a high photosynthetic performance of blade and perennial parts. Both perennial parts are involved in the overall physiology of the plant. This growth strategy is novel among perennial kelp species.

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