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Ecophysiology of Antarctic macroalgae: effects of environmental light conditions on photosynthetic metabolism

Ecofisiología de macroalgas marinas antárticas: efectos de las condiciones de luz sobre el metabolismo fotosintético

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ABSTRACT

Daylength is the major environmental factor affecting the seasonal photosynthetic performance of Antarctic macroalgae. For example, the "season anticipation" strategy of large brown algae such as *Ascoseira mirabilis* and *Desmarestia menziesii* are based on the ability of their photosynthetic apparatus to make use of the available irradiance at increasing daylengths in late winter-spring. The seasonal development and allocation of biomass along the lamina of *A. mirabilis* are related to a differential physiological activity in the plant. Thus, intra-thallus differentiation in O_2-based photosynthesis and carbon fixation represents a morpho-functional adaptation that optimizes conversion of radiant energy to primary productivity. In *Desmarestia menziesii,* reproductive phases show different photosynthetic characteristics. Small gametophytes and early stages of sporophytes, by virtue of their fine morphology, have a high content of pigments per weight unit, a high photosynthetic efficiency, very low light requirements for photosynthesis, and they are better suited to dim light conditions than adult sporophytes. This strategy ensures the completion of the life-cycle under seasonally changing light conditions. Low light requirements for growing and photosynthesizing are developed to cope with Antarctic seasonality and constitute adaptations to expand depth zonation of macroalgae. No differences in net P_{max} and photosynthetic efficiency (α) among algae growing at depths between 10 and 30 m, suggest a low potential for photoacclimation enabling algae to grow over a wide range of prevailing light conditions. However, shortenings in the daily period during which plants are exposed to saturation irradiances for photosynthesis (H_{sat}) and low carbon balance (daily P/R ratios) at depths close to or larger than 30 m negatively affect primary productivity. In general, photosynthetic rates of Antarctic macroalgae at 0 °C are comparable to those measured in species from temperate and cold-temperate regions. This clearly indicates a major physiological adaptation to the polar environment.

Key words: polar macroalgae, Antarctic, photosynthesis, daylength.

RESUMEN

Las variación estacional en la duración del día en los ambientes polares es el principal factor ambiental que regula la actividad fotosintética de las algas marinas. El aparato fotosintético de especies de algas pardas tales como *Ascoseira mirabilis* o *Desmarestia menziesii*, pertenecientes al grupo denominado "season anticipators", posee la habilidad de usar la radiación solar incidente durante el período de aumento de horas diarias de luz en el invierno tardío y primavera. El desarrollo estacional y la distribución de biomasa en el talo afectan también la actividad fisiológica de estas algas. De este modo, la diferenciación de la capacidad para fotosintetizar (medida como evolución de oxígeno y fijación de carbono) a través de la planta representa una adaptación morfo-funcional que optimiza la conversión de energía lumínica en producción primaria. En *Desmarestia menziesii*, las fases reproductivas tienen diferentes características fotosintéticas. Las micro-fases, gametofitos y estadíos tempranos de los esporofitos están mejor adaptados para usar niveles más bajos de luz que las plantas adultas (esporofitos), básicamente debido a un mayor contenido de pigmentos por unidad de biomasa, mayor eficiencia fotosintética y muy bajos requerimientos de luz para fotosíntesis. Esta estrategia asegura la consumación del ciclo de vida bajo condiciones variables de luminosidad. Las bajas demandas de luz para crecimiento y fotosíntesis no sólo posibilitan la supervivencia de macroalgas en escenarios lumínicos estacionalmente cambiantes, sino que paralelamente les permite expandir sus límites de distribución en profundidad. La inexistencia de diferencias en capacidad fotosintética máxima (P_{max}) y eficiencia fotosintética (α) de poblaciones de una misma especie habitando diferentes profundidades (entre 10 y 30 m) sugiere una baja fotoaclimatación, lo cual permitiría a estas especies ocupar amplios nichos lumínicos. Cuando disminuye el número de horas del día durante las cuales las plantas se encuentran lumínicamente saturadas (H_{sat}) y un bajo balance de carbono derivado de un bajo cuociente entre fotosíntesis versus respiración a profundidades cercanas a 30 m, la producción primaria puede ser limitada afectando la superviviencia. En general, las tasas fotosintéticas de algas antárticas medidas a 0 °C son comparables a los valores de producción primaria medidos en algas de regiones templadas, indicando una considerable adaptación al ambiente polar.

Palabras clave: macroalgas polares, Antártica, fotosíntesis, fotoperíodo.

INTRODUCTION

Eco-physiological studies focused on Antarctic macroalgae began relatively late. Drew (1977) described photosynthesis and respiration in the brown algae *Ascoseira mirabilis* Skottsberg, *Desmarestia anceps* Montagne and *Himantothallus grandifolius* (A. et. E.S. Gepp) Zinova from populations located in Signy Island, South Orkney Islands, with a particular emphasis on the effects of nutrients, ice-cover regime and light conditions (Drew & Hastings 1992). Further studies conducted in the area of Admiralty Bay, King George Island, included photosynthetic capacity, pigment contents and organic contents in species such as *Adenocystis utricularis* (Bory) Skottsberg and *Himantothallus* (Czerpak et al. 1981, Gutkowski & Maleszewski 1989). Morphogenesis and reproduction were investigated in *Desmarestia* spp. (Moe & Silva 1977, 1989), *H. grandifolius* (Moe & Silva 1981) and *Ascoseira mirabilis* (Moe & Henry 1982) which provided preliminary insights into the life history of Antarctic macroalgae.

At the beginning of the 90's, the number of investigations addressing ecological and physiological processes of Antarctic macroalgae increased significantly as a consequence of improvements in the isolation and cultivation techniques as well as the use of simulated environmental conditions in the laboratory. Temperature requirements for growth and survival of different species were primarily documented by Wiencke & Tom Dieck (1989, 1990). For example, the endemic brown algal species *A. mirabilis*, *Phaeurus antarcticus* Skottsberg, *D. anceps* or *H. grandifolius* grow from 0 up to 5-10 °C with an upper survival temperature (UST) between 11 and 13 °C. Such UTS's are significantly lower than those determined for cold-temperate species from Southern Chile (Wiencke & tom Dieck 1990) or *Laminaria* species from the Northern Hemisphere (Bolton & Lüning 1980). Similarly, light requirements for growth and completion of the life-cycle as well as the development of different generations in species with an heteromorphic life-history are markedly low (see Wiencke 1990a, 1990b). It is now known that various of the reproductive- and life history events in Antarctic macroalgae are seasonally determined: microscopic gametophytes and early stages of sporophytes in *Desmarestia* (Wiencke et al. 1991, 1995, 1996), *Himantothallus* (Wiencke & Clayton 1990) and *P. antarcticus* (Clayton & Wiencke 1990) grow under limited light conditions during winter, whereas growth of adult sporophytes is restricted to late winter-spring. Culture studies under simulated fluctuating Antarctic daylength demonstrated that macroalgae exhibit two different strategies to cope with the strong seasonality of the light regime in the Antarctic (Wiencke 1990a, 1990b). The so-called "season responders" are species with an opportunistic strategy growing only under optimal light conditions mainly in summer, whereas the "season anticipators", grow and reproduce in winter and spring.

The idea that low temperature and low light requirements for growth of Antarctic macroalgae are based on adaptations in carbon metabolism, especially photosynthesis, has in the last time been particularly addressed. Preliminary surveys on selected Antarctic species, particularly brown algae, revealed photosynthetic rates and dark respiration measured at 0 °C comparable to rates of macroalgae from temperate regions (Thomas & Wiencke 1991) and very low light requirements for photosynthesis (Wiencke et al. 1993). In the light of this evidence, it was possible to argue that macroalgae are effectively highly adapted to the Antarctic environment (Kirst & Wiencke 1995, Wiencke 1996). However, aspects related to morphology and seasonality in the environmental factors were nor addressed during this first phase. Therefore, during the past 6 years research was conducted to address two major aspects: (1) the variation in physiological parameters in relation to morphology and biomass allocation patterns of macroalgae and (2) assessment of seasonal changes in daylength conditions and its impact on photosynthesis and light requirements of Antarctic macroalgae.

The present work is an overview of results from completed and ongoing investigations focused on photosynthetic metabolism of selected brown algae using cultured and field plants. Four main aspects will be considered. Firstly, I will address the structure of the thallus and its implications for photosynthetic performance in the brown alga *Ascoseira mirabilis*. A morpho-functional model is proposed on the basis of photosynthesis data (O_2 evolution and ^{14}C-assimilation) and biomass allocation patterns. Secondly, I will present physiological characteristics of different generations in *Desmarestia menziesii*, a species with a heteromorphic life history. In particular, I tested the hypothesis that the development of small gametophyes and young stages of sporophytes under dim light conditions during winter represents adaptations at the photosynthetic level. Thirdly, I studied the effects of seasonality of Antarctic light conditions on the photosynthetic characteristics of macroalgae. Growth rates, photosynthetic performance and pigment contents were measured in the brown algae *Ascoseira* *mirabilis* and *Desmarestia menziesii* cultivated under simulated fluctuating Antarctic daylength. Lastly, I examined the hypothesis that light availability is a key factor for depth zonation of Antarctic macroalgae by examining 36 species from Potter Cove (King George Island). Two brown algae, *Himantothallus grandifolius* and *Desmarestia menziesii*, and three red algae, *Palmaria decipiens*, *Kallymenia antarctica*, and *Gigartina skottbergii* were used to estimate metabolic carbon balance, photo-acclimation and other physiological adaptations in plants growing at depths between 10 and 30 m.

MATERIAL AND METHODS

Algal material

Algae were collected in King George Island, South Shetlands (62° 14' S, 58° 40' W). Cultures of *Ascoseira mirabilis* and *Desmarestia menziesii* used for growth and photosynthesis (O_2 and ^{14}C measurements) were originally isolated as spores/ zygotes from subtidal populations located near the Frei Station (Chile) during the Antarctic summers of 1985 and1986, and transported to the laboratory at the Alfred Wegener Institute in Bremerhaven (Clayton & Wiencke 1986). Field samples of species such as *A. mirabilis*, *Desmarestia menziesii*, *D. anceps*, *Himantothallus grandifolius*, *Palmaria decipiens*, *Gigartina Skottsbergii*, *Kallymenia antarctica* were collected in Potter Cove (Dallmann Laboratory-Jubany Station, Germany/Argentina) during spring/summer 1993-1994 and immediately used for photosynthesis measurements (see Gómez et al. 1995, 1996, 1997, Weykam et al. 1996 for more details on sites and sampling procedures).

Simulation of Antarctic daylength: a tool for determination of seasonal development

In general, field studies in Antarctic environments are hampered by considerable logistic difficulties, especially when physiological variables shall be examined on a seasonal basis. Cultured plants growing under controlled nutrient supply and irradiance allow a more accurate comparison of metabolic responses. The exposure of algae to simulated fluctuating Antarctic daylengths has revealed to be advantageous in seasonal studies of growth and reproduction. Other environmental variables in the Antarctic region (nutrients, salinity or temperature) are constant throughout the year and, hence, have no or only a slight effect on seasonal development (Wiencke 1990a, 1990b).

For the simulation of the Antarctic daylength, cultures were kept under light periods varying between 5 h light in winter and 19-20 h light during summer, which paralleled the light regime at King George Island. A constant irradiance of 10 to 13 µmol photon m^{-2} s^{-1} was provided by cool white fluorescence tubes (Osram L58/W19). Constant irradiances throughout the whole cultivation period were used in order to avoid possible synergistic and/or antagonistic effects with daylength regimes. Temperature was 0 ± 1 °C (average temperature at King George Island) and nutrients were maintained always at saturating levels of 0.6 mM nitrate and 0.025 mM phospate. The culture medium (Provasoli enriched seawater, 34 ‰ salinity) was changed every 15 days.

Determination of photosynthetic rates

Samples (thallus discs or fragments) were put into closed measuring Plexiglas chambers connected to Clark type-O_2 electrodes (Eschweiler and WTW, Gómez et al. 1995a, 1995b). In all cases, O_2 levels were adjusted to 50 % saturation before measurements. It is known that this O_2 concentration does not inhibit photosynthetic performance of macroalgae (Bidwell & Maclachlan 1985). The medium in the measuring chamber was additionally enriched with 3 mM $NaHCO_3$ and buffered with 8 mM Tris/NaOH (pH 8) to avoid C depletion during the experiments. This methodology was used during measurements of plants cultured under simulated daylength conditions in the laboratory as well as of samples collected directly from the field (Gómez et al. 1995a, 1995b).

An important methodological factor often discussed in this type of studies is the use of thallus pieces or disc as wounding may add uncertainty to the photosynthetic data. Due to the space limitations imposed by the measuring chamber, experimentation with *A. mirabilis* included always the use of thallus pieces. Comparative data from discs "aged" for 48 h and non-incubated discs did not reveal significant differences in photosynthetic performance or in enhancement of dark respiration in *A. mirabilis*. Samples from cultured *Desmarestia menziesii* J. Ag. material were measured immediately. This was possible because wounding effects are more attenuated due to the branched thallus structure as compared with the leathery *A. mirabilis*.

Before determination of photosynthesis, respiratory activity was measured after exposure of 20 min to darkness. Samples were then consecutively exposed to increasing irradiances from 1 to approximately 800 µmol photon m^{-2} $s^{-1}$for 10 min each. Limiting (1, 3, 5, 10 and 27 µmol photon m^{-2} s^{-1}) and saturating (200, 250, 300, 400, 600 and 800 µmol photon m^{-2} s^{-1}) irradiances allowed reliable curve fitting and parameter calculations (Henley 1993). Exposures to each saturating irradiance just for 10 min avoided photoinhibition.

The photosynthetic parameters, saturated net photosynthesis (net P_{max}), photosynthetic efficiency (α),compensation (I_c), and saturation points of photosynthesis (I_k), and dark respiration were estimated using non-linear functions fitted to the data set. Two equations were preferentially used due to their versatility and good fit to the data (Nelson & Siegrist 1987, Henley 1993). The first equation describes an exponential curve:

$$P = P_{max} (1 - \exp^{\alpha I/P_{max}}) + R_{cal}$$

(Webb et al. 1974),

and the second is a hyperbolic tangent function:

$$P = P_{max} \tanh (\alpha I/ P_{max}) + R_{cal}$$

(Jassby & Platt 1976),

where P is the gross photosynthesis (range between the intersection with the Y axis and the saturated region of the curve), P_{max} is the saturated net photosynthesis, tanh is the hyperbolic tangent, I is the irradiance, a is the slope of the linear region, and R_{cal} is the estimated dark respiration.

Determination of ^{14}C-fixation in Ascoseira mirabilis

Rates of carbon assimilation were measured simultaneously with experiments of O_2-based photosynthesis (Gómez et al. 1995a, 1996). Photosynthetic C assimilation was determined in sample discs using saturating irradiances of 200 µmol m^{-2} s^{-1}after pre-incubating the sample discs for 15 min at the same irradiance. Samples were pre-incubated in the dark for 30 min was used for light independent carbon fixation. The algae were then incubated for 30 min with 9.1 KBq ^{14}C ml^{-1} as $NaH^{14}CO_3$ (Amersham Buchler GmbH). After incubation, samples were rinsed in unlabelled media and placed into liquid nitrogen. Samples were then solubilised with 200 µl of perchloric acid (70 %) and 500 µl of hydrogen peroxide (35 %). Radioactivity in the samples was measured in a Packard Tri-Carb 460C liquid scintillation counter adding 5 ml ionic Fluor scintillation cocktail. Quench corrections were made using an external standard.

RESULTS AND DISCUSSION

Longitudinal profiles of photosynthesis in Ascoseira mirabilis

The allocation of biomass within the thallus in *Ascoseira* was basically determined by the timing of the meristem activity. Punched-hole experiments carried out during two years under laboratory conditions (see Gómez et al. 1995a for details of cultivation) indicated that during the first year the blade was elongated longitudinally. In the second year, and due to the activity of the basal meristem, major changes in the blade shape become evident. Tissue formation from the meristem was bi-directionally oriented and increases in width were evident. After two months, the basal blade region increased in width three fold, but the total length did not change much. After five months, the total length of the plant had increased by only 10 %, whereas the basal blade region was 500 % wider. In the third year (second growth season), the basal region became wavy and the first signals of senescence (deterioration and erosion) of the oldest thallus parts in the distal region were evident.

The hypothesis that gradients of tissue composition in *A. mirabilis* involves differentiation at the metabolic level has been tested during three studies on photosynthesis and related parameters in different blade regions (Gómez et al. 1995a, 1995b, 1996). During the growing phase of plants cultured in spring, net photosynthetic rates (net P_{max}) on a fresh weight basis were slightly higher in the middle region as compared with the rates measured at the basal and distal regions (Fig. 1A). For plants measured in the field during September, this differentiation was more marked with middle regions having significantly higher net P_{max} rates (1.8 µmol O_2 cm^{-2} FW h^{-1}) than basal and distal tissues (1.2-1.25µmol O_2 cm^{-2} FW h^{-1}).

This pattern of physiological intra-thallus differentiation was similar to that previously found in *Laminaria* species, which intuitively underlines similar morpho-functional processes. In fact, architecture of thallus and tissue anatomy of adult plants of *A. mirabilis* resembles morphological organization of large kelps such as *L. digitata* (Clayton & Ashburner 1990). Figure 1B shows the longitudinal photosynthetic performance of the cold-temperate *L. longissima* Miyabe (Sakanishi et al. 1991) and that of the Arctic *Laminaria solidungula* J. Agardh (Dunton & Jodwalis 1988).

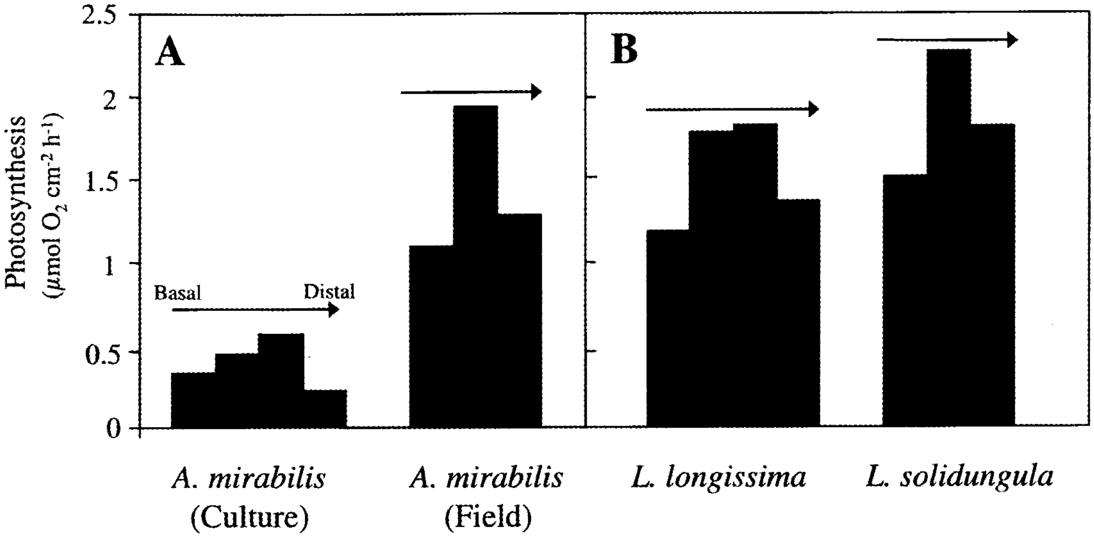

Fig. 1: Comparative longitudinal profiles of O_2-based net photosynthesis (net P_{max}) of the endemic Antarctic brown alga *Ascoseira mirabilis* and two different *Laminaria* species. Data for *Laminaria longissima* and *L. solidungula* were taken from Sakanishi et al. (1991) and Dunton & Jodwalis (1988), respectively.

Comparación de perfiles longitudinales de fotosíntesis neta medida como evolución de O_2 (P_{max} neta) de *Ascoseira mirabili* y dos especies de *Laminaria*. Los valores para *Laminaria longissima* y *L. solidungula* fueron tomados de Sakanishi et al. (1991) y Dunton & Jodwalis (1988), respectivamente.

Although these species show higher net photosynthetic rates on an area basis than *A. mirabilis*, longitudinal profiles resemble the highest values recorded at the middle regions of the blade. This pattern may be related to the age of tissues within the blade (i.e., photosynthetic activity increases with the age of tissues reaching a maximum, but then decreases with further aging). Interestingly, a considerable decrease in the distal photosynthesis was observed in those plants suffering apical erosion or senescence processes, particularly in *Laminaria* and cultured *A. mirabilis*. In field plants of *A. mirabilis* no signs of tissue deterioration were detected, which could be caused by removal of eroded, senescent blade portions in the field (Gómez et al. 1995b). In contrast, eroded tissues of cultured material remain attached for a longer time (Gómez et al. 1995a). This intrinsic pattern of biomass allocation can be found only in species with an intercalary meristem such as *A. mirabilis* or *Laminaria*. In contrast, species exhibiting apical growth (i.e., the oldest tissues located basally) such as *Fucus* or *Sargassum* show the highest photosynthetic capacities in the young apical regions (Küppers & Kremer 1978, Gao & Umezaki 1988, Gao 1991). Thus, the removal of apical tissues in species like *Fucus* sp. has a greater impact on primary productivity than in, for instance, *A. mirabilis*.

Photosynthetic C-fixation rates in highly differentiated brown algae show an intrinsic variation similar to that of O_2 production. Küppers & Kremer (1978) associated the increased ^{14}C-assimilation in the distal regions of *Laminaria* species to a higher activity of Calvin cycle's enzyme ribulose 1,5- bis-phosphate carboxylase-oxygenase (RUBISCO). Moreover, these authors demonstrated longitudinal profiles of light independent C-fixation in these species coupled to a high activity of the enzyme phosphoenolpyruvate carboxykinase (PEP-CK) in the growing regions (ß-carboxylation). Activities of these carboxylating enzymes respond, apparently, to the growing characteristics of *Laminaria*. In fact, *Laminaria* species from cold-temperate and Arctic regions grow in winter or under limited light conditions, which could prompt the development of an alternative carboxylating mechanism (Küppers & Kremer 1978). Beta-carboxylation measured as the activity of PEP-CK is also synchronized to energy requirements of these plants during the growing season. Light-independent carbon fixation provides C-skeletons (preferentially aminoacids or compounds of low molecular weight) for both biosynthesis and anabolic processes, thus compensating partially for C losses due to respiration during active growth. Particularly, in the meristematic region of *Laminaria* species, PEP-

CK metabolizes CO_2 gained in glycolysis of storage carbohydrates (e.g., mannitol), which are translocated from distal regions of the blade (Kremer 1981, Kerby & Evans 1983). Considering a carbon balance, ß-carboxylation appears to have important implications for primary productivity in these species: in *L. hyperborea* (Gunn.) Fosl., light-independent carbon fixation can account for more than 20 % of the total C-fixation in the growing region (Kremer 1981).

Carbon fixation in *A. mirabilis* exhibits also intra-blade variations. However, some differences with respect to patterns measured in species of *Laminaria* spp. were observed (Fig. 2). On the basis of profiles measured at eight sampling zones along the blade it was found that photosynthetic C-fixation increased with tissue age reaching a maximum in the middle blade. Values remain relatively constant in distal regions, supporting the statement that senescence in the oldest tissues affect carboxylation to a lesser extent than O_2 production (Küppers & Kremer 1978). Maximum light C-assimilation rates, close to 75 µmol C g^{-1} DW h^{-1} in *Laminaria digitata* (Huds.) Lamour. and *L. saccharina* (L.) Lamour., were higher than those measured in *L. hyperborea* (21 µmol C g^{-1} DW h^{-1}) and *A. mirabilis* (45 µmol C g^{-1} DW h^{-1}). In contrast to *Laminaria* species, light-independent C-fixation rates in *A. mirabilis* increased towards the distal oldest regions of the blade (maxima close to 26 µmol C g^{-1} DW h^{-1}), which may be related to the high dark respiration rates observed in distal blade regions as C fixed in the dark was 46 % compared to dark respiration (Gómez et al. 1995a, 1996). Whether light independent C-fixation in *A. mirabilis* may compensate for carbon losses due to respiration as suggested by Kremer (1981) for *Laminaria*, remains to be explored. In general, dark C-fixation represents between 24 (Gómez et al. 1995a) and 65 % (Gómez et al. 1996) of light C-fixation in the distal blade region in *A. mirabilis*. These values are comparable to ratios found in species of *Laminaria*. Growing regions of *L. digitata* and *L. saccharina* exhibit maximum light independent C-fixation rates close to 8 and 4 µmol C g^{-1} DW h^{-1}, respectively, which is close to 21 % of photosynthetic C-assimilation. Such values, however, can increase up to 67 % in the basal blade tissues of *L. hyperborean*. Thomas & Wiencke (1991), using various Antarctic marine macroalgae, did not conclusively demonstrate a relationship between light independent C-fixation and dark respiration. In general, dark C-fixation rates were between 4.9 and 31 % of dark respiration in five brown-and one red algae. In species such as *H. grandifolius* and *D. anceps*, low dark C-assimilation rates were coupled to high respiration rates. This situation was also found in *Ascophyllum nodosum* (L.) Le Jol. indicating that in the dark there was always a net carbon loss due to respiration (Johnston & Raven 1986).

Estimations of photosynthesis (or dark respiration) using O_2-based techniques are generally not comparable to those using ^{14}C-fixation measurements as ^{14}C techniques do not detect carbon losses via respiration (Andersen & Sand-Jensen

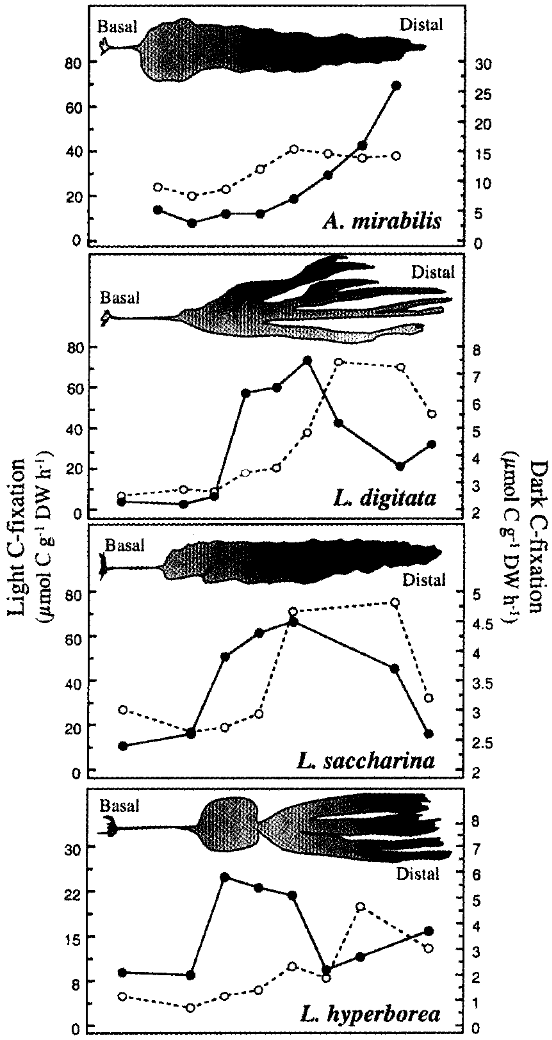

Fig. 2: Longitudinal profiles of photosynthetic carbon fixation (light-C fixation) and carbon assimilation in the dark measured in *Ascoseira mirabilis* and in three *Laminaria* species. Data for *Laminaria* were re-drawn from Küppers & Kremer (1978).

Perfiles longitudinales de fijación fotosintética de carbono (light C-fixation) y fijación de carbono en la oscuridad de *Ascoseira mirabilis* y en tres especies de *Laminaria*. Los datos para *Laminaria* fueron redibujados de Küppers & Kremer (1978).

1980, Williams 1993). Thus, only apparent photosynthetic quotients (O_2 produced: C assimilated or PQ) can be calculated, which do not always describe accurately photosynthesis in marine organisms (Laws 1991). Despite all these considerations, the findings that O_2-based photosynthesis and ^{14}C-fixation vary as a function of blade development in *A. mirabilis* add new evidence to a convergent morpho-functional evolution of this species with respect to large Laminariales. In this case not only morphological organization, but also a metabolic differentiation along the blade constitutes a common characteristic of both taxa.

Comparative photosynthesis rates of gametophytes and sporophytes of Desmarestia menziesii

Culture studies on all members of the Antarctic Desmarestiales indicate that life history depends strongly on seasonal changes in daylength. In general, the development of gametangia, fertilization (oogamy) and early stages of sporophytes take place in winter under short daylength in *H. grandifolius, P. antarcticus*, and *Desmarestia* spp., whereas growth of sporophytes begins with increasing daylength in late winter spring. In *D. menziesii*, reproduction, including gametogenesis and development of early sporophytes, occurs under daylengths shorter than 9 h in culture conditions. Irradiance levels of 5 μmol photon m^{-2} s^{-1} are necessary to induce gametogenesis and fertilization, whereas large sporophytes require higher irradiances (Wiencke et al. 1995). Apparently photon fluence rates of 10 to 13 μmol photon m^{-2} s^{-1} set the upper irradiance levels at which gametogenesis takes place in Antarctic Desmarestiales as it has been demonstrated in *Himantothallus grandifolius* (Wiencke & Clayton 1990) and *Desmarestia anceps* (Wiencke et al. 1996). In terms of

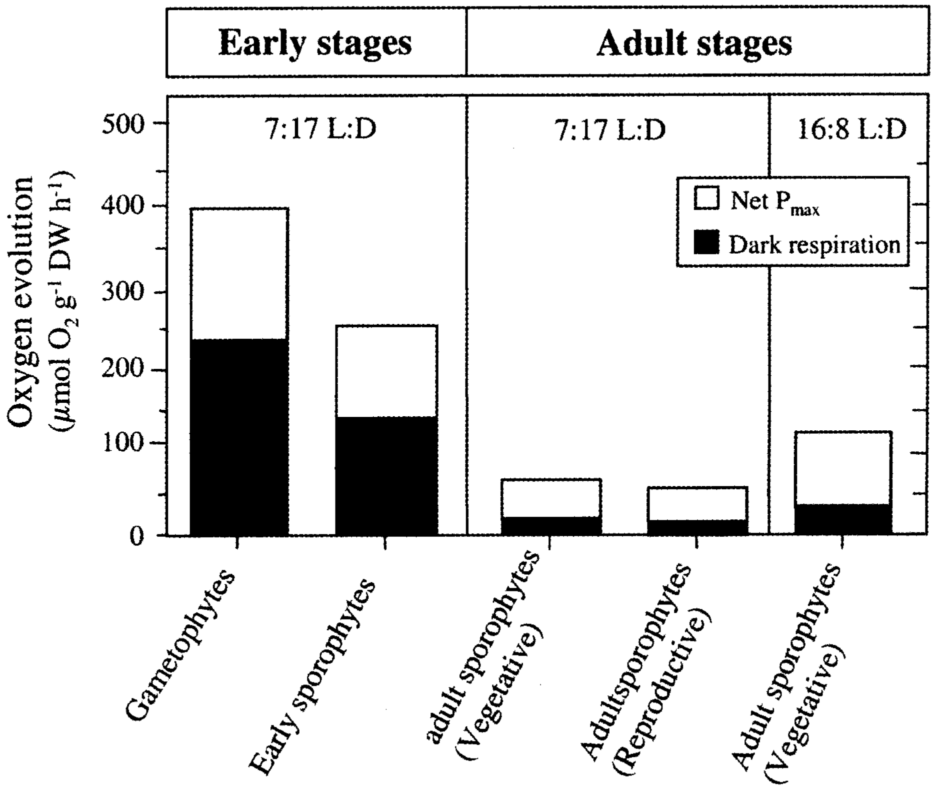

Fig. 3: Comparison of photosynthetic performance (net P_{max}) and dark respiration estimated on a dry weight basis between gametophytes and sporophytes at different developmental stages of the Antarctic brown alga *Desmarestia menziesii*. The daylength regime of the cultures at the time of the measurements is indicated.

Comparación de las tasas de fotosíntesis (P_{max} neta) y de respiración en la oscuridad entre gametófitos y esporófitos en diferentes estadios de desarrollo de la macroalga antártica *Desmarestia menziesii*. Se indica el fotoperíodo para crecimiento de los cultivos al momento de las determinaciones.

ecological significance, the development of gametophytes, or at the least their reproductive capacity, appears to be constrained at high light conditions suggesting that development of gametophytes in winter lies partly on a differentiation of light requirements for photosynthesis among different life-history components.

Gametophytes and small, uncorticated sporophytes show significantly higher gross photosynthetic rates in short days (7:17 L:D) than adult sporophytes, particularly when data are expressed on a dry weight basis (Fig. 3). This situation demonstrates that seasonality of daylength plays an important role in the photosynthetic metabolism of sporophytes (see below), and emphasizes that gametophytes and early stages of sporophytes are photosynthetically more active than adult plants during winter. Data on photosynthetic performance of gametophytes grown under long daylength are not available so far for any of the Antarctic algae and thus it is not possible to infer comparative advantages of this generation in spring-summer conditions.

Dark respiration rates were very high in gametophytes and young sporophytes (Fig. 3) indicating an increased metabolic activity. In contrast, adult sporophytes were characterized by a low respiratory activity relative to net P_{max}. The high dark respiration rates of the uncorticated sporophytes may be explained by a high growth activity as plants were measured in August under daylengths of 7:17 L:D. During this period, major morphogenetic processes take place, including an increase of size and number of cells, the formation of the cortex, and the formation of intercalary meristems in primary lateral branches (Wiencke et al. 1995). Such processes require relatively high amounts of energy, which may be supplied via anabolism. Interestingly, the high respiration rates of gametophytes can not be related to biomass formation processes because these plants have a limited growth. Instead, reproductive rather than growth processes may explain the high respiration rates. The fact that a relatively important fraction of the cellular mass in the dioecious gametophytes during reproductive periods is constituted by oogonia or spermangia (Wiencke et al. 1995) supports this idea. In contrast, the low proportion of reproductive tissues relative to the total cell mass in adult reproductive sporophytes may account for the scarce effect of reproduction on the net P_{max} and dark respiration in these plants.

The hypothesis that gametophytes of *D. menziesii* are better suited to live under low light conditions than adult sporophytes was also tested using data on photosynthetic efficiency (α) and light requirements for saturation (I_k) and compensation (I_c) for photosynthesis. Alpha-values computed for gametophytes and juvenile stages of sporophytes (Fig. 4) show a five times higher photosynthetic efficiency than adult sporophytes. In contrast to net P_{max}, α values of adult sporophytes growing under a daylength of 16:8 L:D were low and similar to those of plants grown in short days. This indicates that, comparatively, the α parameter is more strongly affected by the thallus morphology than net P_{max}. The proportion between photosynthetic to non-photosynthetic tissues underlies also differences in the assimilatory pigment content per unit weight or thallus surface area, which may be directly related to the light harvesting efficiency at low irradiance (Ramus 1981). In filamentous or thin-sheet like thalli, pigment-dependent photosynthetic O_2 production follows a linear curve, whereas photosynthesis in thick morphologies, characterized by several cell layers and low ratios of photosynthetic to non-photosynthetic tissues, becomes uncoupled of the pigment content due to a greater attenuation of light within the thallus (Ramus 1978).

Light requirements for compensation of photosynthesis (I_c) are strongly determined by dark respiration and α. Because of their high respiration rates, I_c in gametophytes and small sporophytes did not significantly decrease, whereas light required for saturation (I_k) strongly increased in adult sporophytes due to low α values. Photosynthesis of adult sporophytes was saturated at significantly higher irradiances (30 µmol photons m^{-2} s^{-1}) than photosynthesis in gametophytes or young sporophytes (16 µmol m^{-2} s^{-1}). Although low I_k values have been claimed to reflect an inefficient use of high irradiance rather than an efficient use of low light (Henley 1993), the results found for *D. menziesii* confirmed that low I_k of gametophytes and early sporophytes may be a good indicator of shade adaptation as irradiance was similar (10-13 µmol photon m^{-2} s^{-1}) for all the phases in cultures. On the other hand, the low I_c (5-12 µmol photon m^{-2} s^{-1}) may be related to the low irradiance required by these plants during growth. Sporophytes and gametophytes from several Antarctic Desmarestiales show light saturation of growth at irradiances close to 10 µmol photons m^{-2} s^{-1} (Wiencke 1990a, Wiencke & Fischer 1990). According to Markager & Sand-Jensen (1992), high photosynthetic efficiencies at low light, and low respiration rates are adaptations for growing and survival of macroalgae under low light conditions. Despite this, gametophytes and uncorticated sporophytes of *D. menziesii* exhibited high respiratory activities. As photosynthetic compensation points normally

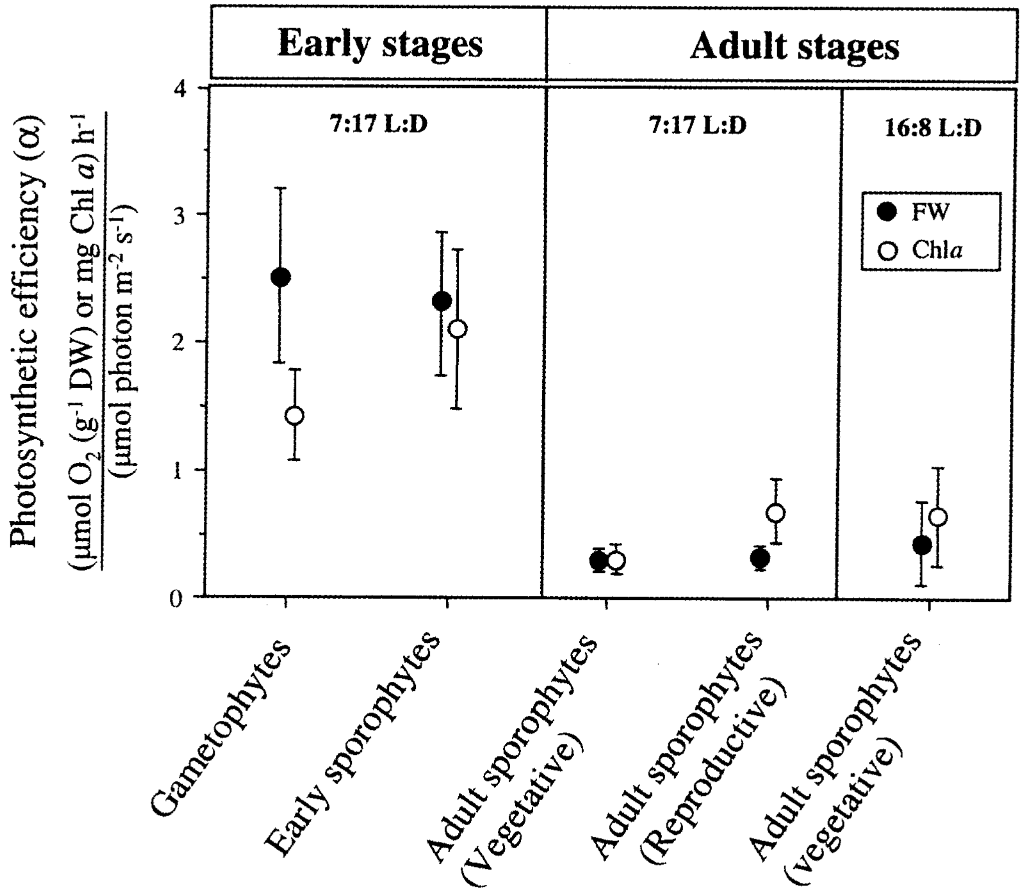

Fig. 4: Comparison of photosynthetic efficiency at limiting irradiances (α) between gametophytes and sporophytes of the Antarctic brown alga *Desmarestia menziesii* expressed on a fresh weight (FW) and chlorophyll a (Chl a) basis. The daylength regime for growth at the time of the measurements is indicated.

Comparación de eficiencia fotosintética (α) entre gametófitos y esporófitos de *Desmarestia menziesii* expresada en base a unidad de peso fresco (FW) y clorofila a (Chl a). Se indica el fotoperíodo para crecimiento de los cultivos al momento de las mediciones.

do not agree with minimum light requirements for growth of macroalgae (Markager 1993, Markager & Sand-Jensen 1992), results in gametophytes of the *D. menziesii* suggest that culture irradiances of 10 to 13 μmol photon m^{-2} s^{-1} are substantially higher than compensation irradiances for growth, and thus plants were not constrained by high dark respiration.

The ability of gametophytes and uncorticated sporophytes to grow and photosynthesize under low light conditions may be considered as adaptive, and allows the algae to survive under seasonally changing Antarctic light environments. During winter, when incident irradiance is low and daylength is short, high photosynthetic rates and growth of gametophytes and uncorticated sporophytes are favored by virtue of their fine morphology (high surface-area/volume ratio), higher pigment content and more efficient light use. In contrast, large sporophytes require higher irradiances for carbon assimilation and probably to compensate for tissue losses due to herbivory or ice-disturbance. The question whether heteromorphic phase expression in Antarctic Desmarestiales is also dependent on herbivory, substrate modifications, or ice-abrasion remains to be answered.

Seasonal photosynthetic performance and dark respiration

Photosynthesis is closely linked to changes in growth as carbon assimilation supplies the necessary substrates for biomass formation. However, such a widely accepted relationship

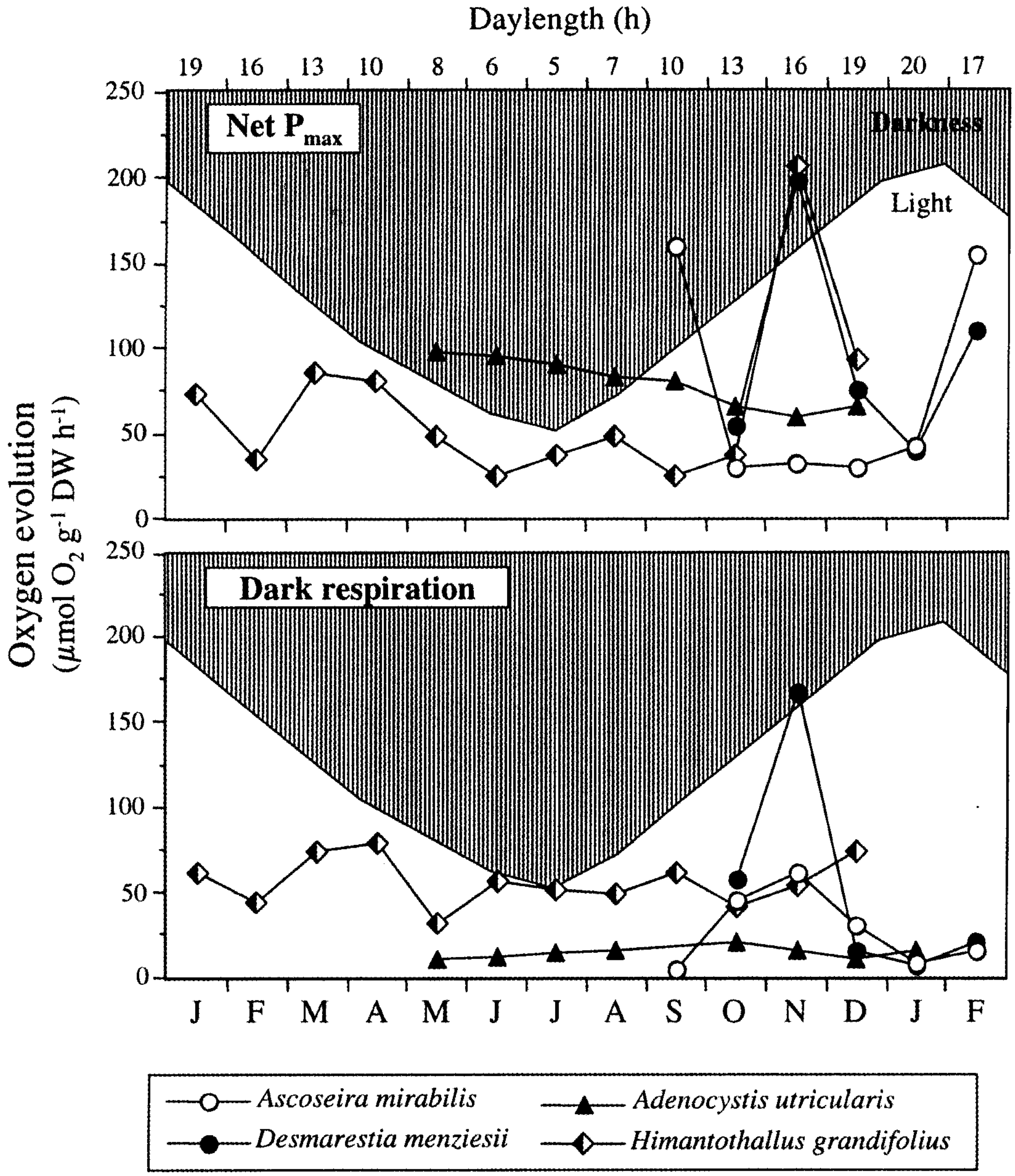

Fig. 5: Seasonal changes in photosynthetic performance (net P_{max}) and dark respiration of Antarctic macroalgae from King George Island and Signy Island (South Orkney Islands) in relation to daylength variations. Data for *Adenocystis utricularis* and *Himantothallus grandifolius* were taken from Gutkowski & Maleszewski (1989) and Drew & Hasting (1992), respectively.

Variación estacional en las tasas de fotosíntesis (P_{max} neta) y de respiración en la oscuridad de macroalgas antárticas recolectadas en la Isla Rey Jorge (Shetlands del Sur) y Signy (Orcadas del Sur) en relación a los cambios en la duración del día. Los datos para *Adenocystis utricularis* y *Himantothallus grandifolius* fueron tomados de Gutkowski & Maleszewski (1989) y Drew & Hasting (1992), respectivamente.

becomes complicated in polar macroalgae since frond elongation and carbon assimilation via photosynthesis are restricted generally to a short period (i.e., when favorable conditions of daylength or light intensity are available). As outlined above, the acquisition of an optimal size as rapid as possible appears to be a major adaptation in species of *Laminaria* and Antarctic macroalgae, which requires synchronized thallus elongation and carbon assimilation processes. For example, maximum rates of growth and photosynthesis in the Arctic *Laminaria solidungula* occur in different seasonal periods: growth under darkness in winter and photosynthesis during the spring-summer open water (Dunton & Schell 1985). This pattern contrasts clearly with the seasonal strategy observed in Arctic populations of the Arctic-cold temperate *Laminaria saccharina*, whose growth is entirely powered by photosynthesis from late-winter spring onwards (Dunton 1985, Dunton & Jodwalis 1988, Henley & Dunton 1995).

Figure 5 shows the variations in net P_{max} measured to field plants of the "season anticipators" *A. mirabilis*, *D. menziesii* and *H. grandifolius*. For comparative purposes, a "season responder", *Adenocystis utricularis* is also included. Net P_{max} in *Himantothallus* decreases between March and June (autumn), but peaks strongly in November decreasing again in December (Drew & Hastings 1992). Increased net P_{max} in November is also observed in *Desmarestia menziesii* (Gómez et al. 1997b), but not in *A. mirabilis*. In this latter species, maximum net P_{max} values are recorded in September and February (no data available between February and September, Gómez et al. 1995b). Data for *Adenocystis utricularis*, whose net P_{max} values gradually decrease from autumn onwards (Gutkowski & Maleszewski 1989), indicate no seasonality of net P_{max}, contrasting with the situation in the other species whose photosynthetic capacities increase with increasing daylength. However, α-values in field plants of *A. utricularis* show a clear seasonal pattern with higher values in late winter-spring than in summer (Gutkowski & Maleszewski 1989).

These findings of high respiration rates in *A. mirabilis* and *D. menziesii* during late winter-spring are reported for the first time for Antarctic brown algae and suggest an active growth in this period (Gómez et al. 1995b,1997b). Interestingly, high respiration rates were also found in *Himantothallus*, and they exceed net P_{max} (P/R ratios < 1) after some months. Using models of carbon accretion, Drew & Hastings (1992) predicted more carbon losses in winter-early spring than carbon gains. However, and when the annual carbon balance is calculated, a positive carbon budget is obtained. As outlined above, field plants need to achieve rapid thallus elongation during a short time period in late winter-spring, which implies a high respiratory activity. If respiration exceeds assimilation, then, plants necessarily utilize other mechanisms to optimize metabolic balance for supporting growth.

High respiration rates exceeding net P_{max} during late-winter spring are not only found in large field plants. In cultured macroalgae (Fig. 6), P/R ratios close to 1 are observed in July for *D. menziesii*, and in June for *D. anceps*. In *Himantothallus*, low P/R ratios were observed between December and June. Assuming an adequate nutrient supply, non limiting light for photo-synthesis, constant temperature and absence of simulated ice-cover, then a negative C balance in the thallus is certainly the result of high growth rates. In the case of *D. menziesii*, it was clearly demonstrated that net P_{max} peaks occur earlier than peaks of dark respiration and growth rates (Gómez & Wiencke 1997a) which optimizes the use of photoassimilates, i. e. photosynthesis supplies the substrates for anabolism and biomass formation. The direct relation between high growth rates and elevated dark respiration is observed when both species of *Desmarestia* are compared. In fact, *D. menziesii* shows significantly lower weight-based growth rates than *D. anceps*, which, however, exhibited dark respiration and net P_{max} rates almost two times higher than *D. menziesii* (Gómez 1997). Differences in plant age between both species at the moment of the measurements probably may account for these differences and confirm that dark respiration would be a good indicator of metabolic status in these species.

Light acclimation: photosynthetic efficiency and light demands for photosyntheis

Wiencke et al. (1993) reported for the first time data on photosynthetic efficiency of several cultured Antarctic macroalgae. The a values of *A. mirabilis* [$2.4\ \mu\text{mol O}_2\ \text{g}^{-1}\ \text{DW h}^{-1}\ (\mu\text{mol photons m}^{-2}\ \text{s}^{-1})^{-1}$], *D. anceps* [$4.09\ \mu\text{mol O}_2\ \text{g}^{-1}\ \text{DW h}^{-1}\ (\mu\text{mol photons m}^{-2}\ \text{s}^{-1})^{-1}$] and *H. grandifolius* [$7.3\ \mu\text{mol O}_2\ \text{g}^{-1}\ \text{DW h}^{-1}\ (\mu\text{mol photons m}^{-2}\ \text{s}^{-1})^{-1}$] are significantly higher when compared to a values reported for *Laminaria solidungula* (between 0.25 and $0.6\ \mu\text{mol O}_2\ \text{g}^{-1}\ \text{DW h}^{-1}\ (\mu\text{mol photons m}^{-2}\ \text{s}^{-1})^{-1}$, Dunton & Jodwalis 1988). These findings served to characterize Antarctic algae as shade adapted organisms. In *A. mirabilis*, high a values close to $10\ \mu\text{mol O}_2\ \text{g}^{-1}\ \text{DW h}^{-1}\ (\mu\text{mol photons m}^{-2}\ \text{s}^{-1})^{-1}$] were found in September, but decrease strongly from October onwards to reach values close to $2\ \mu\text{mol O}_2\ \text{g}^{-1}\ \text{DW h}^{-1}\ (\mu\text{mol photons m}^{-2}\ \text{s}^{-1})^{-1}$ (Gómez et al. 1995b). A different picture is observed in *D. menziesii*: in this species a very low α was measured in October [$0.8\ \mu\ \text{mol O}_2\ \text{g}^{-1}\ \text{DW h}^{-1}\ (\mu\text{mol photons m}^{-2}\ \text{s}^{-1})^{-1}$], increasing strongly in November up to $8\ \mu\text{mol O}_2\ \text{g}^{-1}\ \text{DW h}^{-1}\ (\mu\text{mol photons m}^{-2}\ \text{s}^{-1})^{-1}$ and decreasing again towards summer (Gómez et al. 1997b). Similarly, cultured plants of this species show comparable α values, which peak in October and decrease from August-September and December to April (Gómez & Wiencke 1997a).

These clear seasonal changes in α values suggest adjustments in the light absorption efficiency in these algae. However, much of the data on α do not closely correlate on a seasonal basis, with variations in pigment content. It has been shown that the content of chlorophyll a, chlorophyll c, and fucoxanthin of cultured material of *D. menziesii* increase with thallus weight (Gómez & Wiencke 1997a). Similarly, Henley & Dunton (1995) concluded that the accumulation of pigments with size in *L. solidungula* and *L. saccharina* is better explained by developmental processes than by photoacclimation: photosynthetic efficiency in leathery and terete macroalgae is not directly correlated with the content of pigments due to their high proportion of non-photosynthetic tissues (Ramus 1978). Thus, algae show seasonal fluctuating *a* values (photoacclimation), whereas their pigment content increase almost independently from season until the final plant size is achieved (Gómez & Wiencke 1997a).

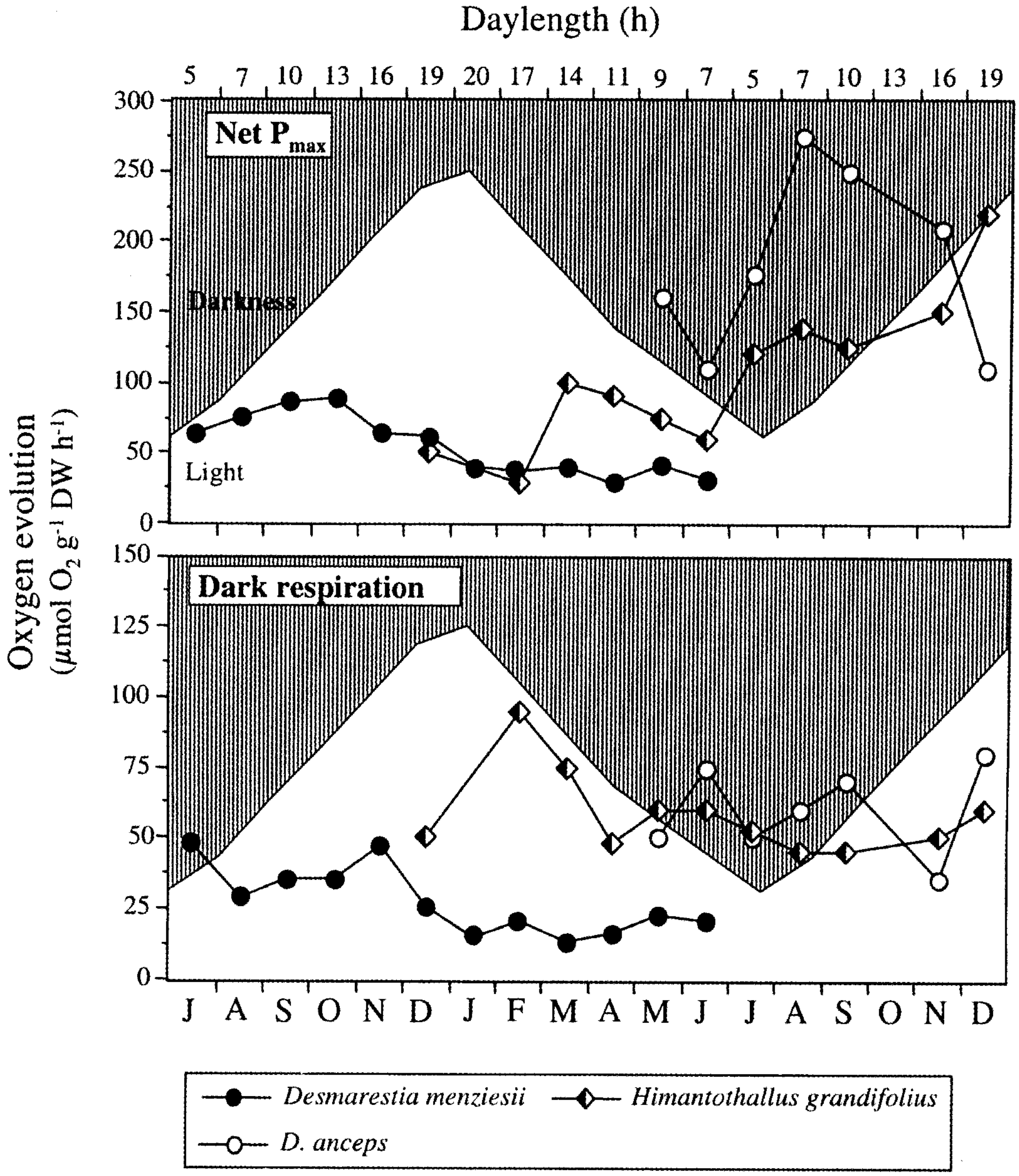

Fig. 6: Seasonal changes in photosynthetic performance (net P_{max}) and dark respiration of Antarctic macroalgae cultured under simulated Antarctic daylength conditions.

Variaciones estacionales en las tasas de fotosíntesis (P_{max} neta) y de respiración en oscuridad de macroalgas antárticas cultivadas bajo condiciones simuladas de fotoperíodo antártico.

High photosynthetic efficiencies generally determine low saturation (I_k) and compensation (I_c) points of photosynthesis. As Antarctic macroalgae are exposed to very low irradiances during most part of the year, light requirements for photosynthesis are also very low. Values of I_k reported in field plants of *A. mirabilis* during September-February increased from 20 µmol photons m^{-2} s^{-1} to 50-60 µmol photons m^{-2} s^{-1}, whereas in *D. menziesii* values may vary between 25 and 100 µmol photons m^{-2} s^{-1} during the same period. These maximum saturation irradiances were substantially higher than irradiances required for saturation of growth of Antarctic macroalgae (generally 15 µmol photons m^{-2} s^{-1}; Wiencke & Fischer 1990, Wiencke 1990a, 1990b), which has been established also for temperate species (Ramus et al. 1976, Markager & Sand-Jensen 1992). Apparently, photosynthetic I_k values above the light requirements for growth results in ecological advantages to cope with strong fluctuations of the incident irradiance during the period of open-water in several Antarctic shallow waters (Klöser et al. 1993, Gómez et al. 1997a). In spring, when water transparency is high and daylength is increasing (light window, see above), macroalgae growing at depths below 20 m can still be exposed to irradiances of about 80 µmol photons m^{-2} s^{-1}. Under these conditions, net production is less constrained by high dark respiration rates, and because the number of hours to which algae are exposed to irradiances above saturation (H_{sat}) are longer, a positive net metabolic carbon balance may be expected (Gómez et al. 1997a, discussed below). On the other hand, when incident irradiance decreases, light requirements for photosynthesis by the algae may also decrease in virtue of their high α values. Interestingly, the hypothesis of a possible acclimation potential of plants at the prevailing light conditions (i.e., modifications of I_k) has been not tested. In general, culture studies reveal that such an acclimation in Antarctic macroalgae is unlikely as algae cultured under constant irradiances of 10 to 15 µmol photons m^{-2} s^{-1} cultivated during long periods show I_k always above these ranges (Table 1). When algae are cultivated under high irradiances (25-55 µmol photons m^{-2} s^{-1}), no obvious increases in I_k are observed. A clear increase of I_k with increasing culture irradiance has been demonstrated only in *A. mirabilis* (Wiencke et al. 1993). In other species such as *D. menziesii* or *H. grandifolius*, there are marked differences in I_k values between plants cultivated under similar light conditions. On the basis of these results, it may be argued that I_k is an unpredictable photosynthetic component and it may not be a good indicator of seasonal photoacclimation of sporophytes. Instead, changes in I_k seem to be useful, for example, when gametophytes and adult sporophytes are compared (Gómez & Wiencke 1996). Because of their small size, gametophytes and small sporophytes have, perhaps necessarily, developed adaptations to photosynthesize and grow under limiting condi-

TABLE 1

Light requirements for saturation of photosynthesis (I_k) of cultured Antarctic macroalgae in relation to the growth irradiance (mean ranges). Values of I_k are means and standard deviations are indicated in parenthesis

Demanda lumínica para saturación de fotosíntesis (I_k) y su relación con la radiación requerida para crecimiento de algas antárticas cultivadas en condiciones de laboratorio, expresadas como rangos de promedios. Los valores de I_k corresponden a promedios y sus desviaciones estándar se indican entre paréntesis

Species	Culture irradiance (mmol photon m^{-2} s^{-1})	I_k	Reference
Himantothallus grandifolius	25-55	18.6 (3.5)	Wiencke et al. (1993)
	7-12	15.5 (1.5)	Hanelt et al. (1997)[a]
Desmarestia anceps	25-55	32.3 (1.8)	Wiencke et al. (1993)
	7-12	49.1 (13.0)	Hanelt et al. (1997)
Desmarestia menziesii	13	21.7 (4.9)	Gómez & Wiencke (1997a)[a]
	10-13	53.6 (19.4)	Gómez & Wiencke (1996)
Ascoseira mirabilis	25-55	40.3 (5.5)	Wiencke et al. (1993)
	10-13	19.1 (3.6)	Gómez et al. (1996)
	7-12	15.6 (2.9)	Hanelt et al. (1997)
	10-13	14.0 (2.5)	Gómez et al. (1995a)

[a] Annual mean

tions of irradiance (e.g., caused by the canopy of adult sporophytes or the presence of an ice cover). In contrast, adult sporophytes are generally exposed to wide ranges of light conditions. Due to their relatively large size, these plants "escape" from some of these detrimental constraints.

In contrast to I_k, low light requirements for compensation of photosynthesis (I_c) by Antarctic macroalgae seem to be a very conservative character. In general, cultured plants from various species (Table 1) exhibit I_c values close to 10 µmol photons m^{-2} s^{-1} (Wiencke et al. 1993, Gómez et al 1995a, 1995b, 1996, Wiencke 1997a), and suggest a direct relation to the minimum light requirements for growth. In *D. menziesii*, a species with strong seasonal changes in I_k values, I_c remains constant and below culture irradiances (Gómez & Wiencke 1997a). These results suggest that saturation of photosynthesis is not necessarily a metabolic pre-requisite for growth. According to Henley (1993), net carbon assimilation still occurs below the I_k point, which is probably enough to support growth of macroalgae. This is not often taken into account by models of productivity. If light is not limiting, then high respiration rates may not affect carbon balance. Thus, the maintenance of an I_c always below the ambient irradiance would be an advantage to achieve a positive net carbon assimilation (high P/R ratios) during periods of maximum growth. This situation is supported by I_c values from field plants, which generally are higher than those of cultured plants, but lower than those prevailing among in situ measured irradiances during spring (Klöser et al. 1993, Gómez & Wiencke 1997a).

Photosynthetic characteristics in relation to depth zonation

Antarctic macroalgae are mostly subtidal organisms. Despite this well known fact, few efforts have been made to explain zonation patterns in terms of physiological characteristics. Despite the action of different environmental factors that limit light penetration during a great part of the year (e.g., ice-cover, phytoplankton blooms) algae are able to grow down to considerable depths (Zielinski 1990, Klöser et al. 1993, 1994). Much of the available data characterize Antarctic shallow waters as being extremely transparent (Bienati & Comes 1971, Priddle et al. 1986), particularly during late-winter spring. Under such conditions, macroalgae can potentially occur at depths close to 40 m as inferred from I_c and I_k for photosynthesis of cultured material (Wiencke et al. 1993, Gómez et al. 1995a, 1995b, 1996, Gómez & Wiencke 1996).

The hypothesis that light requirements for photosynthesis of Antarctic macroalgae may be related to their actual zonation patterns has primarily been tested using a large spectrum of species collected from different depths at King George Island. Figure 7 summarizes the photosynthetic performance and light requirements for saturation of photosynthesis in 36 species belonging to the green, red and brown algae (Weykam et al. 1996). Although algae from shallow waters or intertidal locations (green and some brown algae) show higher net P_{max} and I_k than species from deeper habitats, no evidence for a marked adaptation of algae to depth can be demonstrated. In general, net P_{max} (Fig. 7A) is similar (< 25 µmol O_2 g^{-1} FW h^{-1}) and not depth-related in most red and brown algae. However, species such as *Desmarestia antarctica* Moe et Silva, *Geminocarpus geminatus* (Hook. et. Harv.) Skotts. and *Phaeurus antarcticus* from depths between 1 and 3 m have very high P_{max} values (75 to 125 µmol O_2 g^{-1} FW h^{-1}) only comparable to values measured in the intertidal green alga *Urospora penicilliformis* Gain, and the Chrysophyte *Antarctosaccion applanatu* (Gain) Délepine. In contrast, the photosynthetic efficiency (α, Fig. 7B) shows no obvious differences at all among species groups, with values ranging between 0.25 for *Cystosphaera jacquinotii* (Montt.) Skotts. and 4.3 µmol O_2 g^{-1} FW h^{-1} (µmol photon m^{-2} s^{-1})$^{-1}$ for *A. applanatum*, and 80 % of the species exhibiting values close to 2 µmol O_2 g^{-1} FW h^{-1} (µmol photon m^{-2} s^{-1})$^{-1}$. Red algae (generally understory species) exhibit the highest a values at depths between 12 and 20 m.

Similar to net P_{max}, only I_k values of some species collected between 0 and 3 m depth are high (Fig. 7C), agreeing with previous data on cultured plants (Wiencke et al. 1993). Interestingly, the highest I_k values were determined in the shallow water brown algae *P. antarcticus* and *A. utricularis* (125 and 81 µmol photon m^{-2} s^{-1}, respectively), whereas the lowest ones (between 14 and 50 µmol photon m^{-2} s^{-1}) were found in the red algae collected over a long vertical range. These ranges are in agreement with incident irradiances measured in situ at King George Island (Klöser et al. 1993, Gómez et al. 1997a). Regarding physiological zonation, these data suggest a preliminary pattern. In general, macroalgae growing at large depths exhibit, irrespective of the algal division, low I_k values. Photosynthesis of species from shallow waters can also be saturated at similarly low irradiances. On the other hand, the highest I_k values might be expected in macroalgae

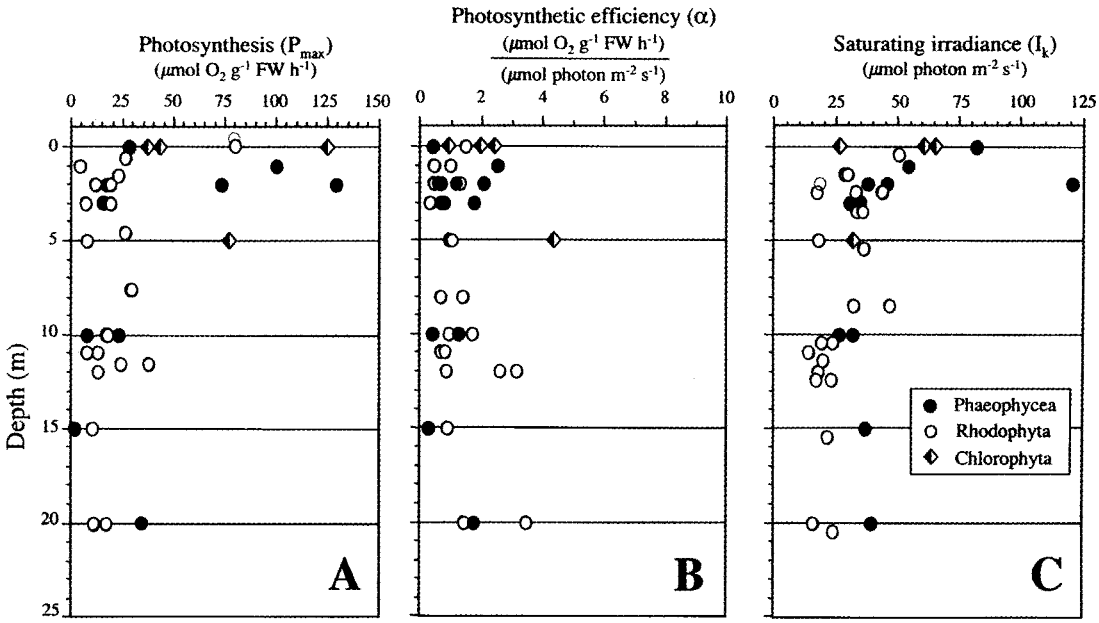

Fig. 7: Influence of depth on changes in photosynthetic parameters; (A) net P_{max}, (B) photosynthetic efficiency (α), and (C) saturation point of photosynthesis (I_k) of red, green and red algae collected at Potter Cove, King George Island during spring-summer 1993-1994.

Cambios en parámetros fotosintéticos en función de la profundidad; (A) P_{max} neta, (B) eficiencia fotosintética (α) y (C) radiación de saturación de fotosíntesis (I_k), medidas en diferentes especies de algas rojas, verdes y pardas recolectadas en la Isla Rey Jorge durante la primavera-verano 1993/1994.

growing in shallow waters. Low light requirements for saturation of photosynthesis of species living at supralittoral and upper sublittoral levels are also reported for other macroalgal assemblages of temperate regions, and may be primarily related to low light requirements for growth (Orfanidis 1992, Leukart & Lüning 1994).

In contrast to algal zonation patterns from other geographical regions where dominant species generally form narrow belts (see Lüning 1990), vertical distribution of dominant Antarctic macroalgae, *Desmarestia* or *Himantothallus*, can become very extended (Klöser et al. 1996). Intuitively, such patterns firstly suggest that these species have high acclimation potential for photosynthesis to the various light climates over the depth gradient. However, a relationship between the photosynthetic capacity and depth has only been partially demonstrated (Gómez et al. 1997a). Using O_2-based photosynthetic measurements, erratic changes in net P_{max} were found in the brown algae *D. menziesii* and *H. grandifolius* and in the red algae *K. antarctica* Hariot, *G. skottsbergii* and *Palmaria decipiens* with increasing depth. Similarly, α values reveal no evidence for an enhanced light use of plants collected at 30 m depth as compared with plants from 10 and 20 m. Only *H. grandifolius* shows increasing α values with increasing depth. Overall, these findings indicate no photoacclimation of macroalgae in terms of photosynthetic O_2 production both at saturating and subsaturating irradiances. These results can be interpreted in several ways. Firstly, the high light penetration during spring-summer does not limit irradiance for photosynthesis (see discussion below). Secondly, the absence of depth-dependent variation in α values may be related to the thick (leathery and terete) thallus structure of the studied species leading to negligible variations in thallus-specific pigment content (Markager 1993). Because no evidence shows that thallus morphology varies with depth within species, one can argue that the relation between surface area/volume and the content of chlorophyll a remains constant (Gómez et al. 1997a), and sets the optimum light utilization in these plants over a broad range of vertical zonation. Finally, slight decreases in chlorophyll a of *K. antarctica*, *P. decipiens* and *G. skottsbergii* collected at 30 m depth could be linked to increased levels of accessory pigments such as phycobilins (Gómez et al. 1997a). Therefore, the proportion of chlorophyll a to the total capacity of light absorption of plants at low light decreases such that higher α values on a chlorophyll a basis may be expected (Kirk 1994).

As it has been outlined previously, Antarctic macroalgae are shade-adapted organisms, a characteristic that evolved probably in response to seasonal fluctuations in light availability. Thus, low light requirements for photosynthesis may provide plants with additional advantages to penetrate to deeper, less well illuminated habitats. Under optimum conditions in the Antarctic spring-summer, water transparency allows average irradiances close to 20 µmol photons m^{-2} s^{-1}at 30 m, with 1 % surface irradiance at depths larger than 40 m (Gómez et al. 1997a). Although these levels are clearly lower than average midday irradiances (30 to 325 µmol photon m^{-2} s^{-1}) measured at 30 m in some clear temperate coasts and tropical waters (Peckol & Ramus 1988), they exceed reported saturation and compensation points of photosynthesis in most Antarctic macroalgae studied so far (Table 2). Despite discrepancies in I_c values between different studies of the same species, I_c values of plants from 30 m may be regarded as the minimum light requirement for photosynthesis in these species. In the particular case of *H. grandifolius* and the red algae *P. decipiens* and *G.*

TABLE 2

Light requirements for saturation (I_k) and compensation (I_c) of photosynthesis of Antarctic macroalgae collected at different depths. Sites are (1) Signy Island, South Orkneys, and (2) King George Island, South Shetlands. In situ depth irradiances for King George Island taken from Gómez et al. (1997a). In situ irradiance, I_k and I_c values are means and mean ranges. Standard deviations are indicated in parenthesis

Demanda lumínica para saturación (I_k) y compensación (I_c) de fotosíntesis de varias macroalgas antárticas recolectadas a diferentes profundidades. Los sitios corresponden a (1) Signy Island, South Orkneys y (2) King George Island, South Shetlands. Datos de radiación in situ para la Isla Rey Jorge fueron tomados de Gómez et al. (1997a). Los valores de irradiación in situ, I_k e I_c representan promedios y rangos de promedios. Las desviaciones estándar se indican entre paréntesis

Species	Site	Depth	In situ irradiance	I_k	I_c	Reference
		(m)	(µmol photon $m^{-2}s^{-1}$)			
Brown algae						
Himantothallus grandifolius	1	5-10	75-17		30	Drew (1977)
	2	10	264	26.5 (3.3)	8.1 (0.8)	Weykam et al. (1996)
	2	10	264	29.3 (2.9)	9.8 (1.2)	Gómez et al. (1997a)
	2	20	85	25.7 (5.9)	5.9 (0.6)	Gómez et al. (1997a)
	2	30	21	22.4 (2.2)	6.4 (0.5)	Gómez et al. (1997a)
Ascoseira mirabilis	2	3	700	35.6 (6.2)	13.3 (2.0)	Weykam et al. (1996)
Desmarestia anceps	1	1-10	200-17		15	Drew (1977)
	2	10	264	32.1 (3.1)	15.5 (1.1)	Weykam et al. (1996)
	2	10	264	58.0 (8.2)	26.6 (1.4)	Gómez et al. (1997a)
	2	20	85	31.7 (4.3)	7.9 (0.4)	Gómez et al. (1997a)
	2	30	21	44.3 (5.7)	20.6 (0.5)	Gómez et al. (1997a)
	1	5-22	n.d	14.6 (1.9)	1.04	Brouwer (1997)
Desmarestia antarctica	1	1 - 10	700-17		20	Drew (1977)
	2	2	780	38.0 (13.3)	11.0 (5.3)	Weykam et al. (1996)
Red algae						
Palmaria decipiens	1	1-10	200-17		15	Drew (1977)
	2	8	346	48.6 (5.7)	5.7 (0.8)	Weykam et al. (1996)
	2	10	264	36.8 (8.8)	10.4 (2.3)	Gómez et al. (1997a)
	2	20	85	41.5 (6.1)	6.7 (0.5)	Gómez et al. (1997a)
	2	30	21	18.6 (5.6)	5.8 (2.4)	Gómez et al. (1997a)
Gigartina spp.	1	1-10	200-17		15	Drew (1977)
Gigartina skottbergii	2	10	264	31.4 (3.9)	3.9 (1.7)	Gómez et al. 1997a
	2	20	85	14.4 (4.1)	1.0 (0.4)	Gómez et al. 1997a
	2	30	21	15.5 (2.2)	1.6 (1.2)	Gómez et al. 1997a

skottbergii from King George Island, respiration is compensated by photosynthesis at irradiances between 1.6 and 6.4 µmol photon m^{-2} s^{-1}, corresponding to 8 and 30 % of the average irradiance at this depth (Gómez et al. 1997a). In general, these values are comparable to I_c values (between 3 and 9 µmol photon m^{-2} s^{-1}) reported in several *Laminaria* species, including the Arctic *L. solidungula* (Dunton & Jodwalis 1988). Although Drew (1977) reported higher I_c values for *P. decipiens*, *Gigartina* spp., and *D. menziesii* closely matching minimum ambient irradiances at only 10 m depth (17 µmol photon m^{-2} s^{-1}), these values are significantly lower than compensating irradiances of 18 subtidal Mediterranean macroalgae (mean 57.9 µmol photon m^{-2} s^{-1}, Enríquez et al. 1995).

The use of minimum light requirements for photosynthesis (I_c) to predict maximum depth penetration of macroalgae has been recently challenged as I_c values for photosynthesis and for growth are related, but do not have identical physiological properties (Markager & Sand-Jensen 1992). Such a discrepancy is explained by a close relationship between dark respiration and growth rate. The rate of dark respiration rate increases with growth, which also causes the I_c for photosynthesis to increase. In contrast, the more active the growing activity, the lower the I_c for growth. Therefore, I_c values for photosynthesis are always higher than I_c values for growth. For example, *Laminaria solidungula* exhibits an I_c for growth close to 0.6 µmol photon m^{-2} s^{-1} (Chapman & Lindley 1980), whereas its I_c for photosynthesis reaches to 3 µmol photon m^{-2} s^{-1} (Dunton & Jodwalis 1988). Similarly, Orfanidis (1992) reported that I_c for growth of Mediterranean macroalgae ranges between 0.5 and 1 µmol photon m^{-2} s^{-1}, which contrasts with the I_c for photosynthesis reported above (Enríquez et al. 1995). No estimation of growth-I_c are available for other Antarctic macroalgae. However, minimum requirements for growth extrapolated from irradiance-growth curves reported by Wiencke (1990a) and Wiencke & Fischer (1990) indicate that macro- and microthalli of several brown algae can grow at irradiances lower than 1 µmol photon m^{-2} s^{-1}.

Light availability and carbon balance

Growth of macroalgae at deep habitats is achieved by an efficient use of low irradiances for photosynthesis by means of an optimal conversion of light energy to assimilated carbon, and through reducing carbon losses during respiration (Markager 1993). Studies conducted in seagrasses show that variations in the photosynthesis/respiration ratio on a daily basis (daily carbon balance) can be considered as a physiological indicator of depth suitability (Dennison & Alberte 1982, 1985). This model compares the relative effects of intensity of quantum irradiance and duration of daily exposure to these irradiances on photosynthesis. Key elements defining this type of productivity model include the daily light course of irradiance, and the saturation point for photosynthesis (I_k), which determine the daily period to which plants are exposed to irradiances near the I_k, denominated H_{sat}. Polar macroalgae exposed to marked seasonal changes in daylength generally exhibit $H_{sat} > 0$ h only during the short open water season. *Laminaria solidungula* in the Alaskan High Arctic, which exhibits a mean I_k of 38 µmol photon m^{-2} s^{-1}, was exposed from August to September 1986 to total H_{sat} periods of up to 148 h (Dunton & Jodwalis 1988). This value corresponds to an extrapolated daily H_{sat} of 3 h. However, depending on the year, H_{sat} may become as low as 39 h during these months, an extrapolated daily $H_{sat} < 0.5$ h, which was correlated to low carbon allocation (Dunton 1990). For Antarctic macroalgae, H_{sat} measured during optimum light conditions in spring to five brown and red algae generally decreases with depth from values close to 14 h at 10 m to values between 7 and 12 h at 30 m depth (Gómez et al. 1997a). These values are comparable to ranges of H_{sat} between 7.2 and 13.3 h measured in subtidal (3 m) populations of the temperate *Colpomenia peregrina* Sauv. (Matta & Chapman 1991). Such similarities reflect the ability of Antarctic macroalgae to efficiently use low light as *C. peregrina* plants are exposed to midday irradiances close to 400 and 800 µmol photon m^{-2} s^{-1} in winter and summer, respectively, with I_k values mostly > 100 µmol photon m^{-2} s^{-1}. In Antarctic macroalgae, photosynthesis of plants growing between 10 and 30 m depth is saturated at significantly lower irradiances (Table 2). Species such as the red algae *P. decipiens* and *G. skottbergii* have low I_k-values, ranging between 18 and 15 µmol photon m^{-2} s^{-1}, somewhat lower than in situ irradiances measured at 30 m depth (close to 20 µmol photon m^{-2} s^{-1}, Gómez et al. 1997a). For the brown algae *H. grandifolius* and *D. menziesii* collected at 30 m, these authors reported I_k values of 22 and 44 µmol photon m^{-2} s^{-1}, respectively. Interestingly, I_k values of these species do not increase markedly with increasing depth: I_k values of 26 and 32 µmol photon m^{-2} s^{-1} measured at 10 m clearly are below the irradiances measured at this depth (> 200 µmol photon m^{-2} s^{-1}). The reason why algae growing under non limiting ambient irradiance in spring maintain low I_k and I_c values seems related to the fluctuating irradiance input that characterizes the Antarctic. Firstly, most of the Antarctic brown algae are perennial organisms with a high longevity, thus constant low light requirements would ensure the survival and formation of biomass under a wide variety of light conditions. Secondly, low light requirements for photosynthesis may be favorable at shallow sites when extra and/or intra specific canopy effects limit incident irradiance. This is especially evident in red algae, which generally attain a smaller size than brown algae and show understory characteristics.

Sublittoral macroalgae have developed metabolic strategies to maximize carbon fixation while avoiding excessive carbon losses due to respiration. Because I_c for photosynthesis exceed I_c-values for growth at great depths, and available irradiances are normally below the levels required for saturation of photosynthesis, carbon assimilation may be just compensating dark respiration. In the studied Antarctic brown algae, dark respiration has a strong seasonal component and during the growth period, respiratory activity may account for a considerable proportion of the gross photosynthesis (Gómez et al. 1995b, 1997a, 1997b). As dark respiration is assumed to occur over the 24 h period and light carbon fixation only during the H_{sat} period, a positive daily carbon balance indicates the light conditions at which growth may be possible. In this sense, productivity of Antarctic macroalgae appears to be constrained at depths > 30 m (Gómez et al. 1997a). For the red algae *P. decipiens*, *K. antarctica* and *G. skottsbergii* metabolic carbon balance between 0.6 and 0.8 mg C g^{-1} FW d^{-1} at 30 m sets the limits for growth. At upper subtidal levels, carbon balance increases significantly (values up to 3.5 mg C g^{-1} FW d^{-1}). The brown alga *H. grandifolius* dominates depths below 15 m, and its daily carbon balance was low but relatively similar over a range between 10 and 30 m, which may be related to the massive morphology of this species. *Desmarestia anceps* growing at 20 m shows a high productivity comparable to red algae, but growth of this species at 30 m is clearly limited due to its negative carbon balance (-1.9 mg C g^{-1} FW d^{-1}, Gómez et al. 1997a). On the basis of these results, it may be argued that *D. anceps* is not well suited to grow at large depths and therefore other factors, such as the use of storage carbohydrates or a high rate of light-independent carbon fixation, partially support its metabolic activity. Conversely, red algae are metabolically able to grow at large depths, but they would be out competed by the large canopy brown alga *Himantothallus* and, eventually, *Desmarestia* species (Klöser et al. 1996). At any case, daily carbon balance may be considered a good indicator of the potential capacity of macroalgae to grow (under spring conditions) over a broad vertical gradient in the Antarctic. It is, however, not clear whether macroalgae persist at these depths during winter, when light dramatically decreases, or penetration at large depths is only a spring-summer phenomenon. Further studies are required to clarify more accurately the effects of other physical and biological factors on the zonation of these plants.

CONCLUSIONS

The use of seasonally fluctuating daylengths demonstrated that not only growth but also changes in photosynthetic metabolism can be simulated in the laboratory. Daylength can thus be regarded as the major environmental factor governing the seasonal physiological performance of Antarctic brown algae. It was also demonstrated that the "season anticipator" strategy of *Ascoseira mirabilis* and *Desmarestia menziesii* relies on the ability of their photosynthetic apparatus to make use of the available irradiance at increasing daylengths in late winter-spring.

The seasonal activity of the basally located meristem in *Ascoseira mirabilis* confers to this species its perennial characteristics and governs the allocation of biomass along the blade. Therefore, intra-thallus differentiation in O_2-based photosynthesis and C-fixation represents a morpho-functional adaptation that optimizes conversion of radiant energy into primary productivity.

Heteromorphic generations in *Desmarestia menziesii* show different photosynthetic characteristics. Small gametophytes and early stages of sporophytes have by virtue of their fine morphology, high content of pigments per weight unit, high photosynthetic efficiency, and very low light requirements for photosynthesis, better suited to dim light conditions than adults sporophytes. This strategy ensures the completion of the life-cycle under seasonal changing light conditions.

Low light requirements for growth and photosynthesis evolved to cope with Antarctic seasonality and in parallel confer advantages to expand depth zonation of macroalgae. No differences in net P_{max} and photosynthetic efficiency (a) between algae growing at depths between 10 and 30 m, underlie the absence of photoacclimation. This enables algae to grow over a broad range of prevailing light climates. However, a shortening in the daily period to which plants are exposed to saturation irradiances for photosynthesis (H_{sat}), and a low carbon balance (daily P/R ratios) at depths > 30 m negatively affect primary productivity.

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