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Seasonal growth and productivity of *Macrocystis integrifolia* in British Columbia, Canada

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Abstract

The seasonal growth rates and nitrogen and carbon fluxes were estimated for two subtidal *Macrocystis integrifolia* Bory kelp forests in British Columbia, Canada from changes in population structure through time. Mean relative growth rates of the forests varied from a high of 4.3% d^{-1} to a low of −3.6% d^{-1}. Mean net assimilation rates of carbon (a photosynthesis analog) varied from a high of 0.66 g C m^{-2} of foliage d^{-1} to a low of −0.87 g C m^{-2} d^{-1}. The leaf area index ranged from 0.3 to 11.9. Annual carbon input on a foliage area basis was calculated at 250 g C m^{-2} yr^{-1}. Annual carbon input to the forest was estimated at 1 300 g C m^{-2} of ocean bottom yr^{-1}. The yearly nitrate nitrogen input to the forest was estimated at 60 g N m^{-2} of ocean bottom yr^{-1}. The net ecosystem production varied from −520 to +31 g C m^{-2} of ocean bottom yr^{-1}. The intra-forest, inter-forest and seasonal variabilities of these productivity parameters are discussed.

Introduction

Populations of the giant kelp *Macrocystis integrifolia* form extensive forests along the outer coast of British Columbia (B.C.) in Canada. The total standing crop of this alga has been estimated to be around 34.6 ktons covering 2.3 khectares (Coon, 1982 b). Its importance is reflected in the number of investigations into growth and translocation (Lobban, 1978 a, b), nutrient uptake kinetics and photosynthetic capacities (Smith *et al.*, 1983; Wheeler and Srivastava, 1984), distribution and cultivation (Druehl, 1978, 1979) and standing crop (Coon, 1982 b).

The genus *Macrocystis* has been extensively studied in California, where its growth, productivity, and standing crop (see North, 1971; Gerard, 1976; Kirkwood, 1977) have been measured. The primary reason for these studies has to do with the commercial exploitation of *Macrocystis* as a source of kelp meal, alginic acid and more recently, as a potentially renewable biomass source for energy production.

This study was undertaken primarily to look at the population dynamics of *Macrocystis integrifolia* in British Columbian waters over several seasons as the basis for a possible kelp harvesting industry (see Druehl and Wheeler, 1986). Using techniques developed for use on higher plant communities (see Harper, 1977), growth and productivity have been estimated from data dealing with population dynamics.

Materials and methods

Two sites in Barkley Sound, B.C., Canada were chosen for seasonal assessment of *Macrocystis integrifolia* population structure and standing crop: a semi-wave-exposed site on the SW side of Helby Island and a wave-sheltered site at the mouth of Grappler Inlet. The kelp forests at both sites were long bands running parallel to the shore. These forests were delimited on the shoreward side by the 0 tide level and the seaward side by the −4 m tide level. Both had similar slopes, the bottoms of which were rock and cobble.

About every eight weeks, from November 1979 to November 1980 for Grappler and to October 1981 for Helby, standing crop was assessed by harvesting two 2-m wide swaths through each bed perpendicular to shore. Swaths ranged in length from 11.5 to 18.2 m for the Grappler transects, and from 7 to 21 m for the Helby transects. Each harvest was made in a different location within the bed. Plants were counted and weighed (see Druehl and Wheeler, 1986).

At each harvest, one adult plant was haphazardly chosen, and two of its fronds were dried, weighed, and

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powdered. CHN analyses were performed using a Carlo Erba CHN analyser.

Higher plant growth parameters used were: the relative growth rate (RGR), net assimilation rate (NAR), the leaf area index (LAI) and the crop growth rate (CGR). They are defined below.

Relative growth rate. The relative growth rate (RGR) is defined by the formula:

$$RGR = 100\,(\ln (W_2\,W_1^{-1}))\,(t_2 - t_1)^{-1},$$

where W in this case is the mean wet weight per plant calculated from the total harvest weight divided by the total number of plants in that harvest, and t is the time of harvests (see Fig. 1 of Druehl and Wheeler, 1986). The RGR is expressed as ($\%\ d^{-1}$).

By calculating RGR using plant weights, a major loss of plant tissue due to sloughing, grazing, or storms will result in a negative growth rate. These growth rates represent changes in the overall standing crop and can sometimes be independent of actual growth. In fact, the RGR will here be called the RGR' and will only correspond to the RGR (as measured only by the addition of growth increments) when there is no tissue loss. Since *Macrocystis integrifolia* is made up of ephemeral fronds (Lobban, 1978a), the "only" time the RGR and RGR' should match would be spring, when loss is minimal.

Net assimilation rate. The net assimilation rate (NAR) has been used as an analog of photosynthesis and relates growth in terms of carbon gained or lost to the foliage area. However, the same definition can also be applied to nitrogen uptake. In order to calculate NAR, a relationship between plant weight and foliage area is required. Such a relationship can be calculated from the data of Sharp (1974) and Druehl (1984a; Table 1). The weights in the NAR formula are in grams of carbon or nitrogen and are converted from measured fresh weights (fw) and dry weights (dw) using fw/dw conversion calculated for fronds from each harvest transect (Table 2). Likewise, % carbon (C) and % nitrogen (N) of sampled fronds from each harvest were determined (Table 2).

The formula for NAR is:

$$NAR = (\ln A_2 - \ln A_1)\,(A_2 - A_1)^{-1}\,(W_2 - W_1)\,(t_2 - t_1)^{-1},$$

where A is the calculated mean area per plant (from the mean weight per plant using conversion in Table 1) and W is the calculated mean g carbon or nitrogen per plant (from the mean weight per plant and conversions in Table 2).

Again, the value of the NAR, as here calculated, can be both positive and negative. The negative values, rather than representing the true net assimilation rate, reflect the loss of assimilated carbon or nitrogen from the system through tissue loss (e.g. storm damage, grazing). As such, we will refer to our numbers as NAR', and further designate them as NAR'_c or NAR'_n if referring to carbon or nitrogen assimilation.

Table 1. *Macrocystis integrifolia.* Weight to area conversions

Plant part	% of total plant weight[a]	Fresh weight cm^{-2} [b]	Fresh weight cm^{-2} of total
Scimitar and growing blades	27.4	0.023	0.0063
Mature blades	20.6	0.034	0.0070
Senescing blades	32.1	0.040	0.0131
Sporophylls	3.5	0.095	0.0033
Stipes	13.4	0.250[c]	0.0335
Holdfast	3.0	0.250[c]	0.0075
			$0.0707\ g\ cm^{-2}$
			$14.1\ cm^2\ g^{-1}$

[a] Druehl (1984a), Table 3
[b] Sharp (1974), Fig. 10
[c] Not included in ([b]), the assumption of neutral density is used

Table 2. *Macrocystis integrifolia.* Wet-to-dry weight ratios, and % C and % N of dry weight for two frond samples of *M. integrifolia* from each harvest transect

Date	Wet dry^{-1}	% C	% N
Grappler			
Nov 1979	7.89	26.1	1.98
Dec 1979	9.12	24.7	1.83
Jan 1980	9.17	23.8	2.24
Mar 1980	13.2	24.3	2.61
May 1980	14.0	25.2	1.02
July 1980	9.20	27.4	1.78
Sep 1980	8.95	26.4	1.84
Oct 1980	10.3	26.9	1.63
	$\bar{x}$ 10.2	$\bar{x}$ 25.6	$\bar{x}$ 1.87
Helby			
Nov 1979	6.02	23.5	1.42
Dec 1979	7.19	26.7	1.99
Feb 1980	10.7	25.2	1.82
Mar 1980	8.19	24.6	2.00
May 1980	10.1	25.9	1.63
Jul 1980	12.7	25.0	2.10
Sep 1980	8.52	28.1	1.90
Oct 1980	8.39	26.7	1.94
Dec 1980	7.69	24.4	1.68
Feb 1981	10.8	24.6	2.31
Jun 1981	8.83	28.4	0.88
Sep 1981	7.64	37.8	2.85
Oct 1981	8.46	27.2	2.08
	$\bar{x}$ 8.86	$\bar{x}$ 25.9	$\bar{x}$ 1.89

Leaf area index. A measure of the total foliage cover in a plant stand is the Leaf Area Index (LAI). This measures the foliage area over a given area of bottom, or the degree of layering of foliage that occurs. These numbers are calculated using wet weight to area conversions (Table 1) and the standing crop data presented in Fig. 8 of Druehl and Wheeler (1986).

Table 3. *Macrocystis integrifolia.* LAI and CGR' using carbon and nitrogen as the basis for productivity calculations for two wild populations of *M. integrifolia.* Net productivity values are calculated from the means of duplicate transects

Harvest interval	T days	LAI $m^2\,m^{-2}$ (1)	(2)	CGR' $g\,C\,m^{-2}\,d^{-1}$ (1)	(2)	Net prod. $g\,C\,m^{-2}\,T^{-1}$	CGR' $g\,N\,m^{-2}\,d^{-1}$ (1)	(2)	Net prod. $g\,N\,m^{-2}\,T^{-1}$
Grappler									
Oct–Dec	49	1.3	1.8	−0.39	−0.45	− 20	− 30.6	− 34.7	− 1.6
Dec–Jan	50	0.8	1.4	−0.12	−0.55	− 17	− 4.1	− 34.6	− 1.0
Jan–Mar	55	0.6	0.5	−0.15	+0.03	− 7	+ 17.5	+05.4	+ 0.6
Mar–May	49	1.3	0.7	+0.08	+0.37	+ 10	− 19.4	+ 11.2	− 0.2
May–Jul	63	3.5	7.0	+2.30	+1.55	+121	+155	+131	+ 9.0
Jul–Sep	57	7.6	9.7	−3.27	−0.99	−127	−206	− 52.4	− 7.3
Sep–Oct	40	5.2	5.1	+0.24	−0.86	− 13	− 9.4	− 79.1	− 1.8
						− 52			− 2.3
Helby									
Oct–Dec	45	2.6	1.4	−2.64	−0.14	− 63	−150	+ 2.2	− 3.4
Dec–Feb	55	0.3	2.3	−0.04	−0.04	− 12	− 3.5	− 31.3	− 1.0
Feb–Mar	50	0.8	1.7	+0.51	+0.26	+ 19	+ 42.5	+ 26.2	+ 1.7
Mar–May	48	3.0	1.4	−0.00	+0.61	+ 14	− 23.1	+ 32.5	+ 0.2
May–Jul	65	9.3	10.4	+1.37	−3.05	− 55	+151	−161	− 0.3
Jul–Sep	55	11.3	5.4	+1.04	+3.56	+127	+ 17.0	+231	+ 6.8
Sep–Oct	44	7.5	8.6	+1.75	−1.69	+ 1	+142	− 97.2	+ 1.0
						+ 31			+ 5.0
Oct–Dec	55	10.7	5.4	−6.32	−2.61	−245	−465	−193	−18.1
Dec–Feb	46	2.0	–	−0.45	–	− 21	− 14.8	–	− 0.7
Feb–Jun	120	2.1	–	+0.57	–	+ 69	+ 8.8	–	+ 1.1
Jun–Aug	82	9.7	–	+1.89	–	+155	+255	–	+20.9
Aug–Oct	61	8.3	11.9	−5.37	−10.3	−478	−402	−772	−35.8
						−520			−32.6

Crop growth rate. By multiplying the NAR by the LAI, the crop growth rate (CGR) can be calculated. This number represents the net change in carbon or nitrogen per area of bottom per unit of time, and is equivalent to productivity measures. As with previous measures, the negative numbers give a different picture, and as such, we will refer to a CGR'. CGR' can be calculated for both nitrogen and carbon, and therefore will be designated CGR'_c and CGR'_n.

Results

Values for RGR', NAR', LAI and CGR' showed considerable variation between duplicates, populations and observation periods (Table 3; Figs. 1, 2). Generally, RGR' and $NAR'_{c\text{ and }n}$ values were positive in Grappler from February through July 1980, and for Helby in February–October 1980 and February–July 1981. The maximum RGR' was 4.3% d^{-1} for Helby during April–May 1980, and the minimum was −3.6% d^{-1} for Helby during October–November 1979 (Fig. 2). Values of NAR'_c ranged from 0.66 (May–July 1980, Grappler; July–September 1980, Helby) to −0.87 $g\,C\,m^{-2}$ of foliage area d^{-1} (August–October 1981, Helby; Figs. 1, 2); and NAR'_n ranged from 53 (February–March 1980, Helby) to −65 $mg\,N\,m^{-2}$ of foliage area d^{-1} (August–October 1981, Helby; Figs. 1, 2).

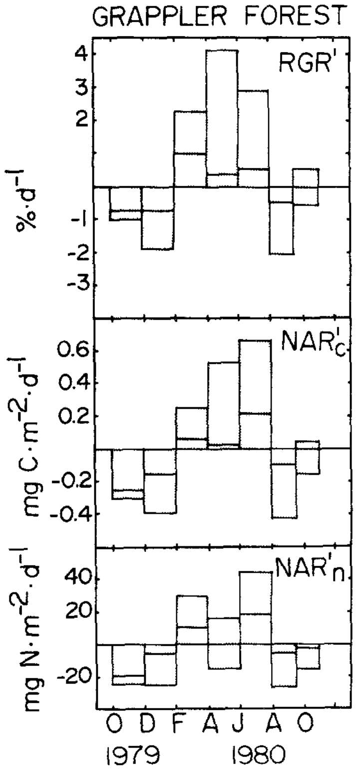

Fig. 1. *Macrocystis integrifolia.* Mean relative growth rates and mean net assimilation rates for both carbon and nitrogen were estimated for two duplicate, 2-m wide transects through the kelp forest near Grappler Inlet. Data from both transects are shown

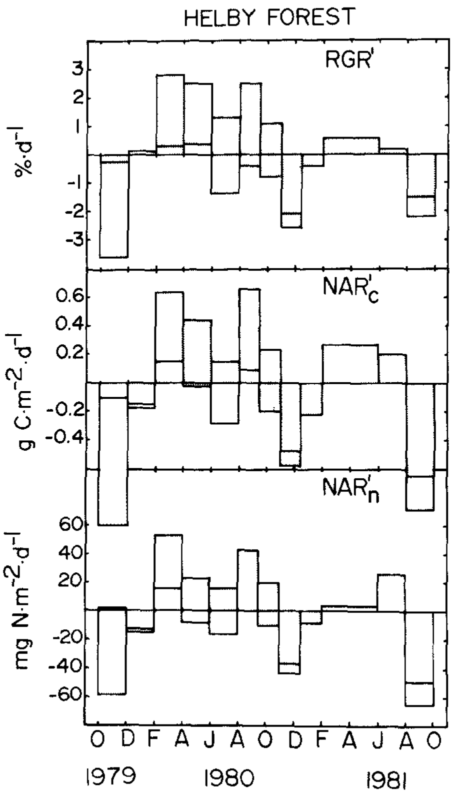

Fig. 2. *Macrocystis integrifolia.* Mean relative growth rates and mean net assimilation rates for both carbon and nitrogen were estimated for two duplicate, 2-m wide transects through a kelp forest off Helby Island. Data from both transects are shown

The LAIs ranged from a winter low of 0.3 to a summer high of 11.9 m^2 of surface area per square meter of bottom (Table 3). This indicates that there can be an equivalent of almost twelve layers of *Macrocystis integrifolia* blades in the kelp canopy.

The CGR's for Grappler and Helby have been tabulated in Table 3. Using this measure, it is easy to locate the periods of most dynamic change. For Grappler, these periods are March to May for carbon gain and July to September for carbon loss. Nitrogen gain was greatest in May–July. Nitrogen loss followed carbon loss with the loss of plant tissue in the fall.

At Helby, where the forest was monitored for two years, the first year mean maximum carbon gain occurred during the period from July to September and mean maximum loss of carbon occurred during the period from October to December. As with the Grappler forest, the mean maximum nitrogen input in the Helby forest occurred during the period from May through July and greatest losses occurred soon after with tissue losses.

During the second year at Helby, mean maximum carbon gain occurred during June to August and mean maximum loss of carbon occurred during August to October. Nitrogen showed large losses in the second year from October to December and at the end of the next season from August to October. Almost all of the nitrogen assimilation occurred between June and August.

Annual net productivity was estimated by multiplying CGR'_n and CGR'_c by the interharvest time in days (Table 3). During 1980 there was a net C and N loss at Grappler and a net C and N gain at Helby. Helby demonstrated a net C and N loss in 1981.

Discussion

The use of growth analysis formulae has been restricted mostly to vascular plant populations. Their use with *Macrocystis integrifolia* is made, however, with a couple of reservations. The first caveat is that the concepts of mean relative growth rate, mean net assimilation rate and mean crop growth rate are only valid if there are no abrupt discontinuities in the plant parameters being studied (Radford, 1967). These abrupt discontinuities occur in fall and winter, with sudden loss of plants and frond tissue. Secondly, the data of Coon (1981) show that the ratio of surface area to fresh weight changed from 14.6 to 17.9 cm^2 g^{-1} in *M. pyrifera* in only four months during summer. Whereas this difference is not too severe, the ratio probably changes more dramatically during the winter months, which may overestimate the winter losses reported here.

Relative growth rates of *Macrocystis integrifolia* populations were as high as 4.3% d^{-1}. Coon (1981) showed that mature plants of *M. pyrifera* can sustain growth rates of 6.4% d^{-1} (fw) for short periods, but for the whole 6-week experimental period, the mean maximum growth rate was closer to 2.0% d^{-1}. Young *M. pyrifera* plants had an average RGR of 2.8% d^{-1} when grown with nitrate enrichment (Druehl, 1984b).

The net assimilation rate of carbon has the units of photosynthesis, and comparisons can be made between it and measured photosynthetic rates. Peak values of the NAR'_c give between 0.6 and 0.7 g C m^{-2} d^{-1}, which are well within the range of the photosynthetic maxima generated by Smith *et al.* (1983) for *Macrocystis integrifolia* from Grappler Inlet.

We have extrapolated the data of Smith *et al.* (1983) to give a photosynthetic production estimate to compare with the CGR_c. Their data on photosynthesis of three age classes of blades of *Macrocystis integrifolia* growing near the present study site, but during different years, varied over 18 months. By subtracting a constant respiration factor for each age tissue, and multiplying by a constant biomass distribution factor (see Druehl, 1984a for respiration and distributions, and the legend to Table 4 for calculations), the calculated net carbon assimilation ranged from 0.20 to 1.30 g C m^{-2} d^{-1}, assuming photosynthetic saturation for the entire daylength (Table 4). By multiplying these daily production numbers by the respective number of days between each harvest period and summing these for the year, a yearly carbon input rate can be extrapolated. The number arrived at here is 250 g C m^{-2} of blade surface yr^{-1}. This number compares favorably with other numbers produced for *Laminaria* spp. For example, Drew (1983) estimated that *Laminaria digitata* and *L. saccharina*

Table 4. *Macrocystis integrifolia.* Photosynthetic productivity extrapolations for *M. integrifolia* for Grappler kelp forest. Photosynthesis is expressed on unit plant area, productivity on a per unit bottom area

Harvest interval T	Pmax[a] nmol C cm^{-2} h^{-1} y	m	o	Day-length h	Net PS[b] g C m^{-2} d^{-1}	Net productivity[c] g C m^{-2} T^{-1}
Oct–Dec	0.50	0.50	0.30	9.0	0.20	39
Dec–Jan	0.94	0.86	0.64	8.9	0.37	20
Jan–Mar	0.90	1.30	0.60	9.0	0.41	13
Mar–May	0.30	0.40	0.30	12.5	0.32	15
May–Jul	0.70	1.20	0.70	16.0	1.21	400
Jul–Sep	1.40	1.40	0.60	14.5	1.30	640
Sep–Oct	1.50	1.30	0.70	11.5	0.90	190
						1 300

[a] Assumes Pmax for one side of blade disk only. Data from Smith *et al.* 1983. y: young tissue; m: mature tissue; o: old tissue

[b] Uses formula: $P_n=[(B_y * P_y) * (D\text{-}(24 * R_y))]+[B_m * P_m) * (D\text{-}(24 * R_m))]+[(B_o * P_o) * (D\text{-}(24 * R_o))]$. B is the percentage of biomass in each category (see Druehl, 1984a); P is the photosynthetic rate in nmol C m^{-2} h^{-1} of the given age-class blade; R is the respiration rate as percentage of gross photosynthesis; D is daylength

[c] Calculated by multiplying Pmax column first by the LAIs presented in Table 3 and then by the number of days between each harvest also from Table 3

Table 5. *Macrocystis integrifolia.* Nitrate uptake extrapolations for *M. integrifolia* for the Grappler kelp forest

Harvest interval T	Uptake rates[a] y	m	o	Availability ratio[b]	Uptake rate mg N m^{-2} d^{-1}	Net N productivity[c] g N m^{-2} T^{-1}
Oct–Dec	56	24	22	0.5	56	4.3
Dec–Jan	40	30	20	0.5	50	2.8
Jan–Mar	34	30	20	0.6	54	1.7
Mar–May	100	60	64	0.2	50	2.5
May–Jul	140	110	90	0.05	19	6.3
Jul–Sep	130	90	70	0.2	64	31
Sep–Oct	96	30	30	0.5	86	18
						67

[a] Assumes uptake through one side of blade disk. Uptake rate is calculated using the formula: $v=(B_y * U_y * 24)+(B_m * U_m * 24)+(B_o * U_o * 24)$. B is the ratio of aged tissue to total blade tissue see Table 5; U is uptake rate in columns 1–3 and uptake rates are assumed constant for entire 24-h day. y is young, apical tissue, m is mature tissue and o is older, senescing tissue. Data from Wheeler and Srivastava (1984)

[b] Assumes a linear relationship between uptake rate and seawater nitrate from 0 to 20 μmol l^{-1}. See Wheeler and Srivastava (1984) for ambient seasonal seawater nitrate

[c] As in Table 4, the net N productivity is calculated by multiplying the daily uptake rate per unit of foliage area by the LAI and the number of days between harvests. Two LAI values are chosen for each calculation and represent the LAI of a given transect through the forest

from Scotland produce 405 and 135 g C m^{-2} of blade surface yr^{-1}, respectively. Johnston *et al.* (1977) calculated the annual production of *L. saccharina* to be 120 g C m^{-2} of blade surface yr^{-1}.

Multiplying the net photosynthetic rate by the LAI for the corresponding time of year (Table 3) gives an estimate of the photosynthetic productivity (the equivalent of CGR) for each harvest period and can be further summed for the entire year. The value of the net annual photosynthetic productivity, 1 300 g C m^{-2} of ocean bottom yr^{-1}, is 6 to 10× the summation of the positive CGR' intervals. This estimate compares favorably with *in-situ* production rates of whole *Macrocystis integrifolia* plants studied by Tuominen (1980), also in Grappler Inlet. The large difference between the photosynthetic projections and the CGR' is probably due to carbon loss through the removal of plant tissue. Since our value of CGR' is based on the net biomass existing at each harvest time, the value is more aligned with the net ecosystem production, which is the difference between the primary productivity value and any community carbon loss (usually just respiration). In mature terrestrial ecosystems, this value is near zero.

Net assimilation rates based on nitrogen can also be extrapolated. Peak values of from 29 to 44 mg N m^{-2} of blade tissue d^{-1} were found to occur in early spring and midsummer in the Grappler forest, and from 19 to 53 mg N m^{-2} d^{-1} in the Helby forest for basically the same time periods. Seasonal, laboratory-derived maximum uptake rates of nitrate were measured for *Macrocystis integrifolia* by Wheeler and Srivastava (1984) and they indicate that maximum uptake velocities occur during midsummer months when nitrate is mostly absent from the surface waters of Barkley Sound (Fig. 1 of Wheeler and Srivastava, 1984). Extrapolating their data, an estimate can be made for whole plant N absorption, based on the plants' ability to take up nitrate and the availability of nitrate to the kelp forest. These data were generated from the same plants and tissues discussed above for the photosynthetic predictions, and thus, the same general biomass distributions apply. The only difference is that nitrate uptake does not appear to be significantly light dependent. The formula used for the calculations is presented in the legend to Table 5, where the calculations are made. From Tables 3 and 5, the data indicate that *M. integrifolia* forests should be able to accumulate N at the rate of 55 to 65 g N m^{-2} of ocean bottom yr^{-1}. These estimates are only 5× the (+) CGR'$_n$ values, which occur for only a few months, and thus are probably conservative. As a comparison, some terrestrial, deciduous forest ecosystems can accumulate N at a rate of 0.3 to 12.9 g m^{-2} yr^{-1} (Cole, 1981).

Using the data in Table 1, we can back calculate the annual net carbon productivity estimate to 52 kg wet weight m^{-2} yr^{-1}. This number is lower than the estimates based on similar physiological projections for *Macrocystis pyrifera* forests in California (see Coon, 1982a). For those forests, Coon presents estimates which range from 75 to 152 wet kg m^{-2} yr^{-1}. The shortened growing season and lower temperatures in B.C. could account for these differences. The high productivity values shown for these ecosystems are probably due to the high LAI values, and not to an inherent high photosynthetic rate, since photosynthetic rates of *M. integrifolia* have been shown to correspond at most to shade tolerant C_3 species (Smith *et al.*, 1983).

Larcher (1975) lists LAI values for a number of terrestrial communities. These vary from 0.5 for alpine communities, to 11.6 for meadows and 11.4 for tropical rain forests. These LAIs include multiple species layering and therefore, the LAI for any one species in these systems is correspondingly lower. Yet, *Macrocystis integrifolia* alone in our kelp forests can account for LAIs as high as 11.9. There are probably at least three other layers due to a *Laminaria* spp., foliose red, and crustose red algal understory. Lüning (1969) reported LAI's as high as 5.7 for a *Fucus serratus* community, and 5.3 for *Laminaria* spp. forests of Helgoland in the North Sea, and Adams and Austin (1978) reported LAIs as high as 6.5 for *Iridaea cordata* communities on Vancouver Island, B.C. Many of these plants can occur within the more intertidal forests of *M. integrifolia.*

What we have tried to do here, is to give a very rough carbon and nitrogen budget for an entire *Macrocystis integrifolia* forest using indirect techniques. Our estimate for the yearly fixation of carbon is not unusual as far as aquatic systems are concerned (see Littler and Murray, 1974), but it ranks quite high in relation to terrestrial communities (Larcher, 1975). Productivity estimates using N give comparably high results (see Cole, 1981). If the photosynthetic rates are not unusual (Smith *et al.*, 1983), the question then appears to be: how can these subtidal communities sustain such high LAI values?

Kelp forests in B.C. seem to be dynamic ecosystems, where net carbon and nitrogen flux can be either negative or positive for the year and different in different parts of the same forest or in differently wave-exposed forests, depending on the severity of the physical stresses. Yet, even with the stresses involved, the community appears to be able to capture carbon and nitrogen in large quantities. The nutrient acquisition strategies involved in marine ecosystems appear, then, to be different than for terrestrial systems. This may be due to the open nature of coastal systems, the efficient uptake capabilities of the plants and the energy bonus added by water motion.

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