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Growth and Utilization of Internal Nitrogen Reserves by the Giant Kelp *Macrocystis pyrifera* in a Low-Nitrogen Environment

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Abstract

An adult giant kelp plant (*Macrocystis pyrifera*), moved from an inshore kelp forest to an offshore, low-nitrogen environment near Santa Catalina Island, California (USA), maintained growth for 2 wk on internal nitrogen reserves. Frond elongation rates decreased significantly during the third week, and plant growth rate (wet wt) dropped from an initial inshore rate of 3.6 to 0.9% d^{-1}. During this 3 wk period, nitrogen contents and free amino acid concentrations decreased, while mannitol and dry contents increased in frond tissues. After depletion of internal nitrogen reserves, the nitrogen content of lamina and stipe tissues averaged 1.1 and 0.7% dry wt, respectively. The experimental plant was exposed to higher ambient nitrogen concentrations during the last 2 wk. Rates of frond elongation and plant growth increased, but nitrogen content and amino acids in frond tissues remained low. Of the total nitrogen contained in frond tissue of the plant before transplantation, 58% was used to support growth in the absence of significant external nitrogen supply. Amino acids constituted a small proportion of these internal nitrogen reserves. Net movement of nitrogen occurred within large fronds, but not between different frond size classes. The nitrogen content of holdfast tissue remained relatively constant at 2.4% dry wt and accounted for 18 to 29% of the total nitrogen. Holdfast nitrogen was not used to support growth of nitrogen-depleted fronds. In comparison to *Laminaria longicruris*, which is adapted to long seasonal periods of low nitrogen availability, *M. pyrifera* has small nitrogen-storage capacity. However, internal reserves of *M. pyrifera* appear adequate to make nitrogen starvation uncommon in southern California kelp forests.

Introduction

Growth of marine macroalgae in coastal environments is sometimes limited by low nitrogen availability (Topinka and Robbins, 1976; Chapman and Craigie, 1977; Hanisak, 1979; Chapman and Lindley, 1980). Nitrogen has also been suggested as the nutrient most limiting to growth of the giant kelp *Macrocystis pyrifera* (L.) C. Agardh in southern California (Jackson, 1977; North, 1980; Wheeler and North, 1980; North *et al.*, 1981). However, the frequency and duration of N-limited growth periods and the impact of nitrogen limitation on kelp production have not been determined (North *et al.*, in press).

Certain macroalgae, including some kelps, build internal nitrogen reserves and use these to maintain growth during periods of low external supply (Chapman and Craigie, 1977; Gerard and Mann, 1979; Hanisak, 1979; Chapman and Lindley, 1980). Adult and juvenile sporophytes of *Macrocystis pyrifera* display tissue nitrogen contents up to 10 000× the maximum external nitrogen concentrations (North *et al.*, in press). Positive correlations between tissue nitrogen contents and ambient concentrations suggest that internal nitrogen is accumulated when sufficient external supplies are available (Gerard and North, 1981; North *et al.*, in press; Wheeler and North, 1981). Although growth of juvenile sporophytes increases as tissue nitrogen content increases even at relatively high internal N-levels (Wheeler and North, 1980), this apparent lack of internal N-reserves cannot be assumed for adult plants which show morphological, physiological, and ecological differences from juveniles.

Examination of nitrogen dynamics in adult *Macrocystis pyrifera* is difficult due to the complexity of the nutrient environment and of the plant itself. Ambient nitrogen concentrations vary spatially and temporally in the inshore water column (Jackson, 1977; North *et al.*, in press). Nitrogen uptake rates depend on chemical species (NO_3^- vs NH_4^+) and concentration (Haines and Wheeler, 1978), and on such environmental factors as irradiance and water movement (Wheeler, 1978). Various types of tissue (e.g. apical vs mature blades) are characterized by different nutrient uptake rates under similar conditions (Gerard, unpublished data). Growth rates, and, therefore, nitrogen

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assimilation rates vary from frond to frond (North, 1971), and nitrogen may be translocated within and between fronds (Schmitz and Srivastava, 1979). These factors all affect storage and utilization of internal nitrogen reserves.

I studied utilization of internal nitrogen reserves in *Macrocystis pyrifera* by transplanting an adult plant from a complex inshore nutrient environment to a nitrogen-poor offshore environment where nitrogen uptake and assimilation were assumed to be negligible. Santa Catalina Island, California (USA), was selected as the study site because macronutrient concentrations are known to remain low in surface water throughout the non-upwelling period. Growth rates and tissue nitrogen contents of the experimental plant were measured periodically and used to construct a nitrogen budget. The primary goals of the study were to determine (1) the magnitude of internal N-reserves in an adult giant kelp plant, (2) the period that growth could be maintained on internal reserves, (3) the net movement of N-reserves within the plant, and (4) the critical tissue nitrogen levels at which internal reserves were depleted and at which growth was N-limited in the absence of significant external supply.

Materials and Methods

On January 9, 1981, an adult *Macrocystis pyrifera* was selected at a depth of 11 m off Laguna Beach, California (USA). Fronds with terminal blades or broken apices were removed, leaving 16 fronds at least 0.5 m long. On January 13, the experimental plant was removed intact from the substrate, placed in a covered 200 liter container supplied with flowing seawater, and was moved within 1.5 h to a mooring 1 km from Ship Rock, Santa Catalina Island, California (33°27.6′N; 118°29.6′W). The mooring was located at the 70 m depth contour, and the plant holdfast was attached to a float at 9 m depth. The plant remained at this offshore site for 5 wk.

Temperature profiles from surface to holdfast depth were measured weekly at inshore and twice weekly at offshore sites. A recording thermograph attached to the offshore float continually monitored temperature at 9 m depth. Temperature data were correlated with $NO_3^- + NO_2^-$ concentrations (determined using an autoanalyzer) in inshore water samples and with total inorganic nitrogen concentrations ($NO_3^- + NO_2^- + NH_4^+$) in water samples collected near the offshore site (R. Zimmerman, personal communication). Inshore and offshore light levels were compared by means of a Secchi disc.

Individual frond elongation rates and total frond and plant weight increases were determined for the experimental plant. Stipe length was measured weekly for each frond at least 0.5 m long. New fronds were tagged and measured when they attained 0.5 m. Frond weights were estimated using a length-weight relationship determined for 52 fronds, 0.5 to 12 m long, collected from 11 m depth near the experimental plant's original inshore location. All sampled fronds had intact apical blades and sparse epiphyte encrustation. Holdfast weight of the experimental plant was measured at the end of the experiment, after removal of dead hapteral tissue, epiphytes, and infauna. The proportion of total plant to holdfast weight was assumed to remain constant throughout the study.

Tissues of the experimental plant collected for dry content (i.e., percent of wet wt), total nitrogen, free amino acid, and mannitol analyses included mature laminae (at least 1 m from the frond apex) from fronds 0.5 to 3 m long; from basal (0 to 3 m) and apical sections of fronds 3 to 6 m long; and from basal, mid (3 to 6 m), and apical sections of fronds > 6 m long. Stipe tissues were collected from fronds in the same size categories, but initial samples were collected from adjacent plants rather than from the experimental plant. Live hapteral samples were taken from the outer 3 to 5 cm of the holdfast. Half of each tissue sample was cleaned of epiphytes, weighed, dried at 60 °C for 24 to 48 h, and reweighed to determine dry content. These subsamples were then ground, redried at 105 °C for 4 h, and analyzed for total nitrogen content by an N-analyzer and for mannitol content according to the method of Cameron *et al.* (1948). Remaining subsamples were cleaned of epiphytes and extracted with hot ethanol (Chapman and Craigie, 1977). Free amino acids were analyzed according to North (1975).

The amounts of nitrogen contained in individual fronds and the holdfast of the experimental plant were computed from weight estimates, percent dry wt and N-content data. Mean weights of basal and mid-frond sections, and percent lamina and stipe weights for each section, were determined for the 52 fronds collected at Laguna Beach and used in these calculations. For each frond, estimated total wet wt was apportioned into basal, mid, and apical sections appropriate to its length category. Lamina and stipe wet wt were estimated for each frond section. Dry wt and nitrogen contained in each tissue were calculated using appropriate percent dry wt and N-content averages determined for the experimental plant.

Results

Environmental Conditions

Temperature at inshore sites near Laguna Beach ranged from 14.7° to 15.8 °C for 1 mo prior to transplantation of the experimental specimen of *Macrocystis pyrifera*. Ambient $NO_3^- + NO_2^-$ concentrations varied from < 0.1 to 3.3 μM. NH_4^+ concentrations were assumed to remain below 1 μM (Wheeler and North, 1981).

Temperature data indicated that the experimental plant was exposed to very low nitrogen concentrations during Weeks 1–3 at Ship Rock (January 13–February 2). Temperature at 9 m depth varied from 15.5° to 16.0 °C during this period. In the San Pedro Basin (California), temperatures above 15.0 °C are correlated with ambient $NO_3^- + NO_2^-$ concentrations below 1 μM (Gerard, unpublished data). Total inorganic nitrogen concentrations

in the upper 30 m of the water column near Ship Rock were 0.2 to 0.3 μM on January 25 (R. Zimmerman, personal communication). During Weeks 4–5 (February 3–17), temperature at 9 m depth fluctuated between 14.5° and 15.0 °C. Total inorganic nitrogen concentrations in the upper 15 m of the water column during this period were as high as 4 μM (R. Zimmerman, personal communication).

Secchi disc depth (Z_{SD}) at inshore sites ranged from 5 to 12 m for 1 mo prior to transplantation of the experimental plant. Z_{SD} at Ship Rock was 16 to 27 m during the 5 experimental weeks. The experimental plant holdfast was above an estimated photosynthetic compensation depth at both locations (Parsons *et al.*, 1977), but subsurface light levels were higher at the offshore site. Shading by adjacent plants probably further reduced inshore light levels relative to levels offshore where no shading occurred.

Growth

Fronds of the experimental plant displayed 4 distinct growth periods during the study. During each growth period, the frond elongation rate showed a significant logarithmic relationship (r, $p < 0.01$) to initial frond length (Fig. 1). Elongation rates, particularly of fronds more than 2 m in length, were highest during the inshore growth period and slightly lower during Weeks 1 and 2 at Ship Rock. Elongation rates of all fronds were lowest during Week 3. The slope (b) of the growth curve determined for Week 3 was significantly lower than the slope calculated for Weeks 1 and 2 (t-test, $p < 0.05$). Elongation rates returned toward previous high levels during Weeks 4 and 5, when ambient nitrogen concentrations increased. Fronds with terminal blades and broken apices had lower elongation rates overall, but showed a similar pattern of slow growth during Week 3 and more rapid growth during Weeks 1–2 and 4–5 (data not illustrated).

Wet weights of individual fronds of the experimental plant were estimated from length data using the length-weight relationship shown in Fig. 2. Holdfast tissue made up 11% of the total plant wet weight when the experiment was terminated. Total plant weight increased from 7.1 to 15.1 kg during the experiment (Table 1). Plant growth rate varied similarly to frond elongation rate, ranging from 3.6% d^{-1} during the inshore period to 0.9% d^{-1} during Week 3.

Tissue Analyses

The initial mean nitrogen contents of lamina tissues of the experimental plant ranged from 2.2 to 3.5% dry wt (Table 2). Sharp declines in nitrogen contents of all lamina tissues during Weeks 1 and 2 at Ship Rock indicated utilization of internal nitrogen reserves. Lamina N-contents were low at the beginning of Week 3 (January 27) and showed no further decline during the remainder of the experiment. Presumably, internal N-reserves were depleted by the beginning of Week 3. At this point, frond elongation and plant growth slowed significantly. Lamina

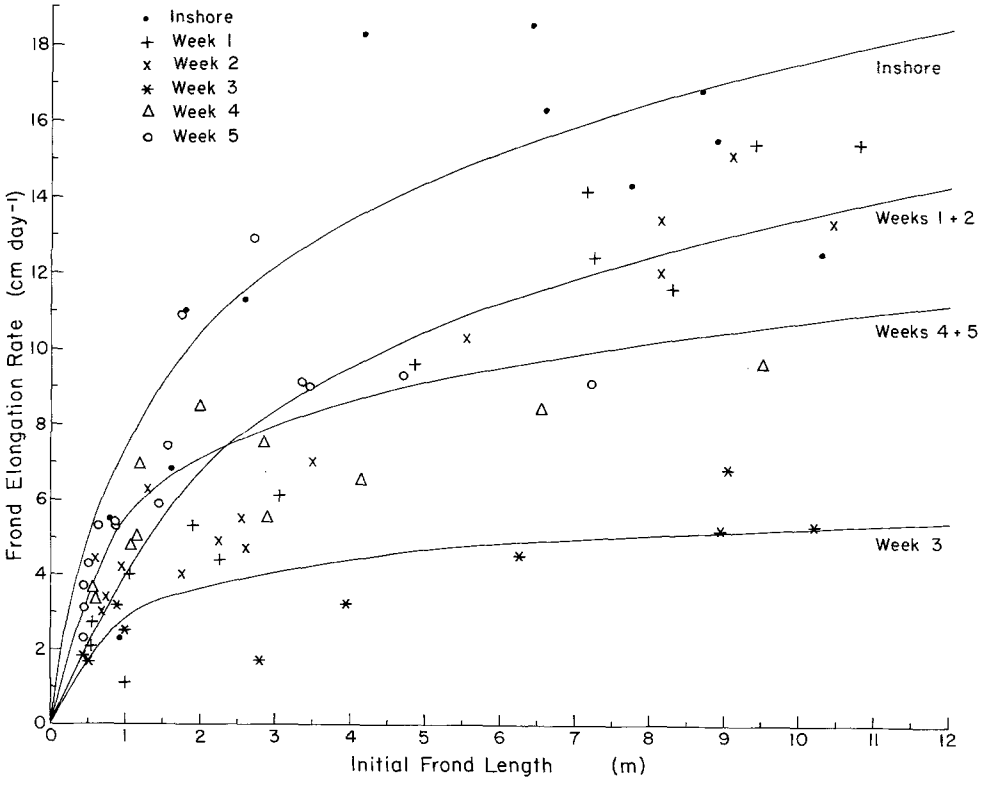

Fig. 1. *Macrocystis pyrifera.* Frond elongation rates for the experimental plant during the inshore growth period and Weeks 1–5 at Ship Rock, Santa Catalina Island, California. Data are shown only for fronds with intact apical blades. Growth curves were determined as $Y = a + b \ln X$, where Y = elongation rate (cm d^{-1}) and X = initial frond length (m). Correlation coefficients (r) for all curves were significant at $p < 0.01$

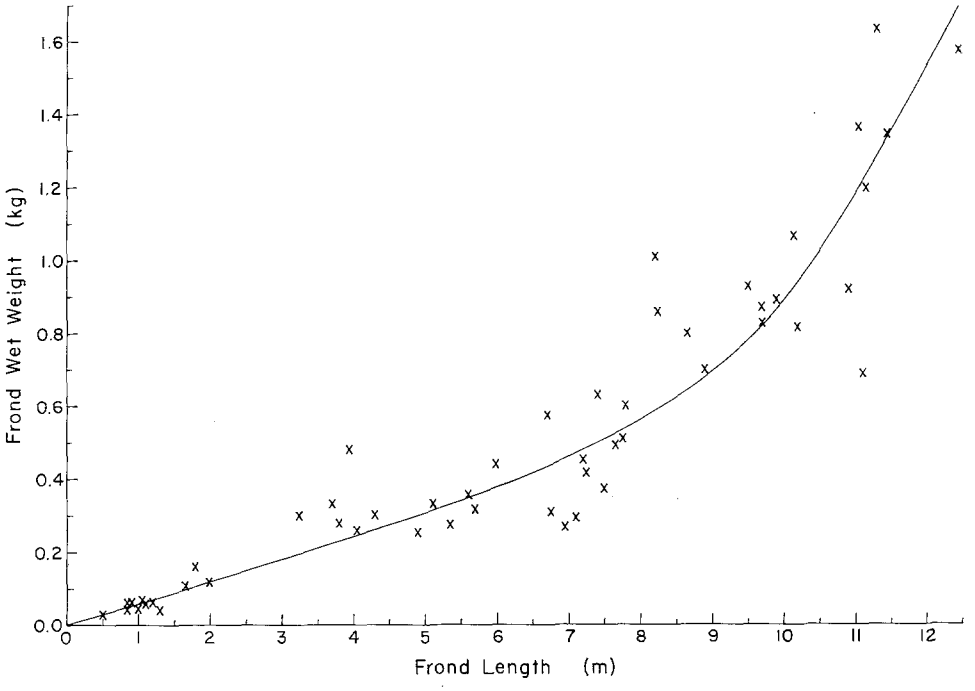

Fig. 2. *Macrocystis pyrifera.* Wet weight-length relationship for fronds from 11 m depth at Laguna Beach, California

N-contents remained low despite increased ambient nitrogen concentrations at Ship Rock during Weeks 4 and 5. No internal nitrogen reserves were accumulated during this period.

Mean stipe nitrogen content also decreased significantly during the experiment, from 1.4% dry wt on January 9 to 0.7% on February 17 ($n=12$, SD=0.2 for both means). In contrast to N-contents of frond tissues, the N-content of holdfast tissue remained relatively constant throughout the study, averaging 2.4% dry wt (Table 2).

Free amino acid concentrations (calculated as glycine equivalents) in lamina tissues of the experimental plant averaged 210 μmol g^{-1} dry wt ($n=18$, SD=115) when initially sampled on January 9. The amino acid nitrogen concentration was positively correlated ($r=0.78$) with total N-content in individual lamina samples from inshore plants (Fig. 3), and made up approximately 8% of the total nitrogen. After depletion of internal N-reserves in the experimental plant, mean amino acid concentrations were reduced to 70 μmol g^{-1} dry wt of lamina tissue ($n=35$, SD=70) and accounted for 4% of the total nitrogen. Amino acid concentrations in holdfast tissues of the experimental plant averaged 90 μmol g^{-1} dry wt throughout the study ($n=8$, SD=35), but made up only 1.5% of the total nitrogen.

Changes in mannitol content in lamina tissues of the experimental plant were inversely related to changes in nitrogen content. Mannitol contents were initially low, and rose during the first 2 wk at Ship Rock, indicating accumulation of photosynthetic products in response to high light levels at the offshore site (Table 3). Mannitol contents in fronds < 3 m long increased during Week 3 when

Table 1. *Macrocystis pyrifera.* Estimated wet weights of fronds and holdfast for the experimental plant on each measurement day, and specific growth rate (μ) during each interval, calculated as $\mu = 100 \times 1/t \times \ln(W_t/W_0)$, where t is growth interval (days), W_0 is initial plant wt, and W_t is final plant wt for that interval

	Growth periods and dates						
	Inshore	Week 1		Week 2	Week 3	Week 4	Week 5
	Jan. 9	Jan. 13	Jan. 20	Jan. 27	Feb. 2	Feb. 10	Feb. 17
Frond wt (kg)	6.3	7.3	8.7	10.2	10.8	12.2	13.4
Holdfast wt (kg)	0.8	0.9	1.1	1.3	1.4	1.5	1.7
Plant wt (kg)	7.1	8.2	9.8	11.5	12.2	13.7	15.1
μ (% d^{-1})		3.6	2.5	2.3	0.9	1.5	1.4

Table 2. *Macrocystis pyrifera.* Nitrogen content of lamina and holdfast tissues of the experimental plant ($\bar{x} \pm 1$ SD, $n = 3$). nd: no data

Total frond length (m)	Frond section (m from basal end)	N-content (% of dry wt)					
		Inshore + Week 1	Week 2	Week 3	Week 4	Week 5	
		Jan. 9	Jan. 20	Jan. 27	Feb. 2	Feb. 10	Feb. 17
0.5 – 3	Entire	2.6 ± 0.6	1.7 ± 0.7	1.1 ± 0.1	1.0 ± 0.1	0.9 ± 0.1	1.0 ± 0.1
3 – 6	0 – 3	3.5 ± 1.2	2.1 ± 0.1	1.3 ± 0.3	1.1 ± 0.03	1.2 ± 0.2	1.2 ± 0.2
3 – 6	3-apex	2.9 ± 0.3	1.6 ± 0.2	1.1 ± 0.1	0.8 ± 0.1	0.9 ± 0.1	1.0 ± 0.1
> 6	0 – 3	2.2 ± 0.7	1.4 ± 0.3	1.0 ± 0.3	1.1 ± 0.2	1.3 ± 0.05	0.9 ± 0.1
> 6	3 – 6	2.6 ± 0.6	1.8 ± 0.3	1.3 ± 0.3	1.3 ± 0.1	1.1 ± 0.2	1.2 ± 0.2
> 6	6-apex	3.0 ± 0.2	2.0 ± 0.01	1.3 ± 0.1	1.2 ± 0.2	1.1 ± 0.3	1.0 ± 0.1
Holdfast		2.5 ± 0.1	nd	2.4 ± 0.5	2.3 ± 0.2	2.4 ± 0.1	2.4 ± 0.1

growth was severely N-limited, then declined during Weeks 4 and 5 when growth rates increased. Mannitol contents in larger fronds showed no significant changes after Week 2. Mannitol apparently reached a maximum concentration at this time, and some other carbohydrate, such as laminaran, may have been accumulated during Week 3.

The dry content (% of wet wt) of both lamina and stipe tissues increased significantly during the study (t-test, $p < 0.01$). Dry content of lamina samples collected during the inshore period and Weeks 1–2 at Ship Rock averaged 11.5% wet wt ($n = 44$, SD = 1.9). Samples collected during Weeks 4–5 at Ship Rock averaged 14.1% ($n = 47$, SD = 2.5). The mean dry content of stipes increased from 9.4% ($n = 12$, SD = 0.8) on January 9 to 13.3% ($n = 12$, SD = 2.1) on February 17 (for N-budget calculations, this increase was assumed to occur during Week 3). The dry content of holdfast tissue remained relatively constant throughout the study, averaging 17.7% wet wt ($n = 12$, SD = 2.5).

Nitrogen Budget

The amounts of nitrogen contained in individual fronds and the holdfast of the experimental plant were computed from weight estimates, morphometric parameters deter-

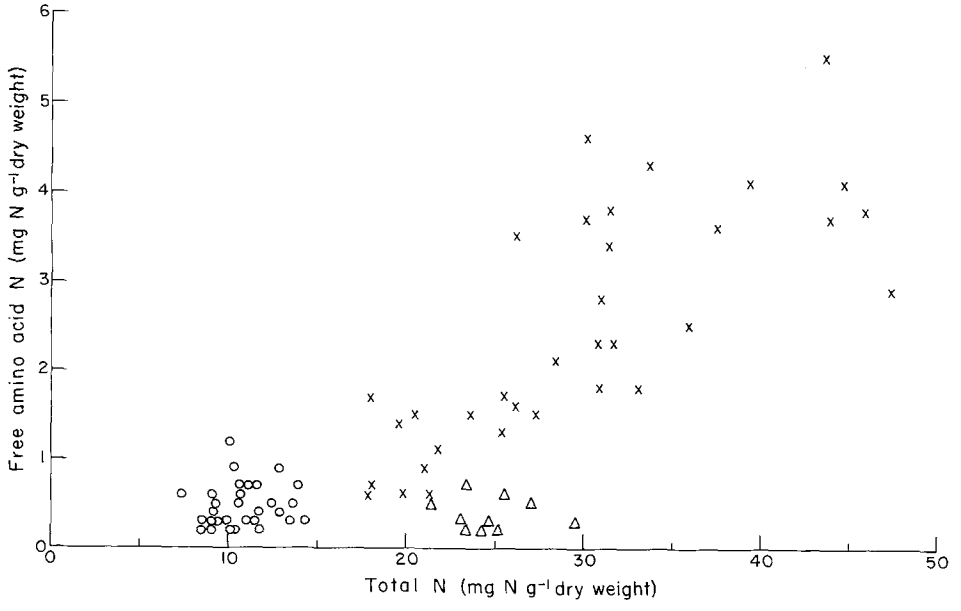

Fig. 3. *Macrocystis pyrifera.* Free amino acid nitrogen and total nitrogen in tissues. x: lamina samples from an inshore plant collected on January 9 or February 5; ○: lamina samples from the N-starved experimental plant collected on February 2 or February 17; △: holdfast samples from the experimental plant collected January 9, February 2, or February 17

Table 3. *Macrocystis pyrifera.* Mannitol contents in lamina tissues of the experimental plant ($\bar{x} \pm 1$ SD, $n = 2$–3 for all values, except where NR indicates no replicate samples)

Total frond length (m)	Frond section (m from basal end)	Mannitol (% of dry wt)				
		Week 1	Week 2	Week 3	Weeks 4+5	
		Jan. 13	Jan. 20	Jan. 27	Feb. 2	Feb. 17
0.5 – 3	Entire	6 NR	13 ±3	20 ±7	33 ±5	23 ±4
3 – 6	0 – 3	10 ±1	15 ±0.3	24 ±6	21 ±10	19 ±5
3 – 6	3-apex	6 ±0.4	19 ±3	22 ±4	29 ±11	24 ±4
> 6	0 – 3	5 ±1	11 ±2	16 ±5	14 ±8	7 NR
> 6	3 – 6	5 ±1	9 ±0.1	14 ±3	16 ±5	14 ±0.4
> 6	6-apex	7 ±0.2	8 ±1	17 ±5	20 ±5	24 ±7

Table 4. *Macrocystis pyrifera.* Nitrogen (g) contained in fronds and holdfast of the experimental plant. Lamina values include nitrogen removed by tissue sampling

	Growth periods and dates						
	Inshore	Week 1	Week 2	Week 3	Week 4	Week 5	
	Jan. 9	Jan. 13	Jan. 20	Jan. 27	Feb. 2	Feb. 10	Feb. 17
Laminae	11.4	13.6	11.4	9.4	11.6	12.6	13.1
Stipes	3.3	3.8	4.4	5.0	3.7	4.1	4.4
Frond total	14.7	17.4	15.8	14.4	15.3	16.7	17.5
Holdfast	3.3	3.8	4.6	5.4	5.7	6.4	7.1
Plant total	18.0	21.2	20.4	19.8	21.0	23.1	24.6

mined for inshore fronds (data not shown), dry content and N-content data. Total plant nitrogen increased from 18.0 to 24.6 g during the study (Table 4). At any time, frond tissues accounted for 71 to 82% of total plant nitrogen. Estimates of total plant nitrogen during Weeks 1–3 at Ship Rock ranged from 19.8 to 21.2 g. During this period, ambient nitrogen concentrations were low, and N-assimilation by the plant was assumed to be negligible. For example, N-uptake by the experimental plant was estimated to be less than 0.1 g d^{-1} when ambient inorganic-N concentration was 0.3 μM, based on NO_3^- uptake rates measured *in situ* (Gerard, unpublished data) and NH_4^+ uptake rates measured in the laboratory (Haines and Wheeler, 1978; Wheeler, 1978). Total plant nitrogen values for Weeks 1–3 represent an increase of 2 to 3 g over the initial 18.0 g total, indicating that the plant assimilated 0.65 g N d^{-1} during the inshore growth period. During Weeks 4 and 5, when ambient nitrogen concentrations were as high as 4 μM at Ship Rock, total nitrogen for the plant increased by 0.2 to 0.3 g d^{-1}.

Table 5. *Macrocystis pyrifera.* Proportion of nitrogen estimated for each section of fronds > 6 m total length. N-values are percents of subtotals for fronds > 6 m

Frond section (m from basal end)	Growth periods and dates			
	Week 1	Week 2	Week 3	
	Jan. 13	Jan. 20	Jan. 27	Feb. 2
0 – 3	12	11	10	12
3 – 6	24	20	18	18
6-apex	64	69	72	70

To determine whether any net movement of nitrogen occurred within the experimental plant, nitrogen contained in different sections of each frond size-class was

estimated for Weeks 1–3, when N-assimilation was assumed negligible. Mid-sections of fronds >6 m long showed a decrease in proportion of total nitrogen for these fronds (Table 5). The proportion of nitrogen in apical sections increased by the same amount, indicating upward net movement of internal N-reserves. The proportion of total frond nitrogen in fronds >6 m long remained at 84 to 86% during this period, showing neither a net loss to nor gain from smaller fronds.

Discussion

In the absence of significant external nitrogen supply at Ship Rock, the experimental specimen of *Macrocystis pyrifera* maintained high growth rates for 2 wk. Rapid reduction in tissue nitrogen contents (Table 2) indicated that internal N-reserves were utilized during this period, and increasing mannitol levels (Table 3) indicated that light was not a growth-limiting factor. Accumulation of carbohydrate reserves in other kelp species coincides with N-limitation of growth (Chapman and Craigie, 1978; Chapman and Lindley, 1980). Thus, growth of the experimental plant appeared to be nutrient-limited before internal N-reserves were depleted. The slight drop in growth rates immediately after transfer to Ship Rock may have been caused by brief exposure and handling during transplantation (Gerard and Mann, 1979), but more probably reflected the change in external N-supply. Both external and internal N-sources were available to the inshore plant, whereas N-supply was primarily internal at Ship Rock.

The pronounced decrease in growth rates of the experimental plant during the third week at Ship Rock (Fig. 1, Table 1) probably resulted from nitrogen starvation. Tissue nitrogen contents reached minimum levels, averaging 1.1 and 0.7% of lamina and stipe dry wt, respectively. These nitrogen contents indicated critical levels at which internal N-reserves were depleted. Nitrogen contents above these levels represented N-reserves. Therefore, 58% of frond nitrogen calculated for the experimental plant before transplantation to Ship Rock was used to support production of new tissue in the absence of significant external N-supply. Most of this nitrogen (83%) was contained in lamina tissue.

Free amino acid nitrogen in lamina tissues of the experimental plant made up only 8% of the total nitrogen before transplantation to Ship Rock. Most of the internal N-reserves must, therefore, have been contained in other nitrogenous compounds. *Macrocystis pyrifera* does not build large internal pools of NO_3^- as do some *Laminaria* spp. (Chapman and Craigie, 1977; Gerard and Mann, 1979; Chapman and Lindley, 1980). NO_3^- and NH_4^+ concentrations in lamina tissues of juvenile and adult *M. pyrifera* are typically low (Wheeler and North, 1980, 1981). Mature laminae of *M. pyrifera* collected off Corona del Mar, California, during the upwelling season, had high total nitrogen contents and maximum internal NO_3^- concentrations of less than 15 μmol g^{-1} wet wt (Gerard, unpublished data), an order of magnitude lower than maximum levels in *L. longicruris* (Chapman and Craigie, 1977). Nonstructural proteins could have constituted a large part of the internal N-reserves in my experimental specimen of *M. pyrifera*. Free amino acids might then have composed a small pool of readily available nitrogen.

Free amino acids account for 10 to 13% of the dry weight in sieve tube exudate of *Macrocystis pyrifera*, and probably function in N-transport within the plant (Parker, 1966; Schmitz and Srivastava, 1979). Net movement of nitrogen within the experimental plant involved only 3 to 7% of total frond nitrogen, and was directed upward from senescent-mature to mature-apical sections of large fronds (Table 5). This translocation pathway was previously demonstrated for *M. pyrifera* using ^{14}C (Parker, 1965; Lobban, 1978). Most net movement of nitrogen occurred during the first week at Ship Rock, when tissue nitrogen contents and amino acid concentrations were high. No net transport of nitrogen was observed between different frond size-classes.

Despite its high nitrogen content, the holdfast of the experimental plant did not contain significant internal N-reserves. There was never evidence of nitrogen movement out of the holdfast to support frond growth, nor was N-content reduced by hapteral growth. Holdfast tissue appeared to act as a nitrogen sink. The proportion of total plant nitrogen in holdfast tissue increased, while N-reserves in frond tissues were used to support both frond and hapteral growth. I may have overestimated N-accumulation in the holdfast by assuming that holdfast growth was proportional to frond growth. Holdfast growth during the 5 experimental weeks did, however, cover much of the netting holding it to the float at Ship Rock.

Ambient nitrogen concentrations increased during the last 2 wk at Ship Rock. The experimental plant showed an immediate growth response; however, N-contents of lamina tissues did not increase. Chapman and Craigie (1977) similarly found that accumulation of internal N-reserves was delayed a month or more in *Laminaria longicruris* after increased nitrogen availability enhanced growth. Apparently, higher ambient nitrogen concentrations and/or longer exposure times of the experimental specimen of *Macrocystis pyrifera* were necessary to support growth and build measurable N-reserves. *L. saccharina* sporophytes, for example, required constant exposure at 10 μM NO_3^- to maintain maximum growth and build internal N-reserves simultaneously (Chapman *et al.*, 1978).

How great is the maximum nitrogen storage capacity of adult *Macrocystis pyrifera?* Nitrogen contents of lamina tissues from large fronds typically range from 1 to 4% dry wt for populations of *M. pyrifera* along the southern California coast (North *et al.*, in press). Nitrogen contents of the experimental plant were near the high end of this range when initially sampled inshore. If the experimental plant had started with maximum N-contents found in coastal populations (4% of dry lamina tissue >6 m above basal stipe ends, 3% in deeper laminae), growth could have been maintained on internal N-reserves for approximately 3 wk.

Even this hypothetical maximum period is short compared to 21 wk of rapid growth by *Laminaria longicruris* at low ambient nitrogen concentrations, 16 wk after internal NO_3^- pools were depleted (Gerard and Mann, 1979). These plants may have had greater organic N-reserves or proportionately slower growth than my experimental specimen of *Macrocystis pyrifera.* Alternatively, these specimens of *L. longicruris* may have been exposed to external N-sources characteristic of the inshore environment. Adults of *M. pyrifera* in an inshore forest at Santa Catalina Island maintained relatively high frond growth rates during January and February, 1981, even though ambient N-concentrations were similar to those at Ship Rock, 2 km from the inshore site (R. Zimmerman, personal communication). The inshore environment apparently provides nitrogen supplies, possibly through faunal or microbial regeneration, which are absent in the offshore environment. Thus, the N-storage capacity determined previously for *L. longicruris* may have been overestimated relative to that shown herein for *M. pyrifera.*

Starting with high internal nitrogen reserves, *Macrocystis pyrifera* can sustain relatively rapid growth for at least 2 to 3 wk in the absence of a significant external N-supply. Is this nitrogen storage capacity adequate to prevent N-starvation from being a common or even regular occurrence in southern California kelp forests? The nutrient environment along the southern California coast is spatially and temporally complex. The largest nitrogen supplies come from upwelling of nutrient-rich water, typically a bottom phenomenon, and runoff of terrestrial origin, a surface source. *M. pyrifera* utilizes both these nutrient sources (North *et al.,* in press). Upwelling occurs primarily from March through July, and runoff during the rainy season from November through March. August through October is the longest seasonal period of predictably low external N-supply, and N-starvation would be most likely to occur in early autumn after internal N-reserves are depleted. No evidence of seasonally reduced growth has been found for inshore populations (North, 1971), but occasional canopy die-offs during autumn have been attributed to sustained low ambient nitrogen concentrations (Jackson, 1977; North *et al.,* in press). During a 20 mo study of four southern California kelp forests, tissue N-contents approached critical low levels, as determined herein, only once (North *et al.,* in press). An upwelling event at this time correlated with a significant increase in frond elongation rates. Nitrogen starvation does occur, but not regularly, in southern California kelp forests.

Overall, the nitrogen storage capacity of *Macrocystis pyrifera* appears suitable to the southern California nutrient environment. Inshore populations usually display tissue nitrogen contents below maximum capacity, but rarely deplete internal N-reserves.

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