In-situ measurements of nitrogenous nutrient uptake by kelp (Ecklonia maxima) and phytoplankton in a nitrate-rich upwelling environment

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Abstract

Nitrogen uptake by the kelp Ecklonia maxima Osbeck and phytoplankton was examined under different conditions of nutrient availability in a kelp bed off the Cape of Good Hope by measuring nutrient depletion in large plastic bags by the kelp and uptake by phytoplankton. E. maxima took up nitrate and ammonia, but not urea, and showed only a weak preference for reduced nitrogen. Phytoplankton absorbed all three forms of nitrogen available, with a preference for ammonia and urea. Ambient nitrate concentration exhibited a marked and rapid decrease with northerly winds and an increase in response to offshore southerly winds. Nitrogen uptake by E. maxima was linearly related to ambient concentration and did not saturate even at nitrate concentrations > 20 μg-at N l⁻¹, resulting in a significantly higher tissue nitrogen content under upwelling conditions. Nitrate imported by upwelling was the chief source of nitrogen utilised within the kelp bed. Locally regenerated nitrogen (ammonia and urea) was calculated to contribute only ca 4% of total nitrogen uptake during upwelling and 30% during the relaxation or downwelling phase.

Introduction

The rocky infratidal zone along the west coast of southern Africa from Lüderitz to Cape Agulhas is dominated by kelp beds which, together with phytoplankton, form two of the main sources of primary productivity in the inshore region. Ecklonia maxima is the dominant kelp species in the immediate inshore depth range (0–8 m) giving way to Laminaria pallida in deeper waters (8–20 m) (Velimirov et al., 1977). Jarman and Carter (1981) estimated mean production by these two species as 1.17 kgC m⁻² yr⁻¹, while mean phytoplankton production in waters immediately adjacent to the kelp beds has been estimated as 1.13 kgC m⁻² yr⁻¹ (Carter, 1982). The entire coastline is characterised by pulsed upwelling caused by offshore south-east winds during the summer months, while the north-west winds prevalent during winter suppress upwelling (Andrews, 1974; Field et al., 1980). Phytoplankton productivity depends on the stage in the upwelling cycle, being minimal during upwelling and maximal during the relaxation or downwelling phase when warmer waters with well developed phytoplankton populations move closer inshore (Field et al., 1980; Carter, 1982). Upwelling results in an enhanced nutrient supply, which allows kelp plants to optimise their use of the favourable light conditions of summer and attain maximal growth rates during this season (Dieckman, 1980; Jarman, personal communication).

The role of kelp and phytoplankton production in overall kelp bed community energetics has been the focus of a number of studies along the west coast of the Cape of Good Hope (Newell et al., 1982; Newell and Field, 1983; Wulff and Field, 1983). This study was undertaken to investigate nitrogen utilisation by phytoplankton and by the kelp Ecklonia maxima in a typical kelp bed off the Cape Peninsula over a range of conditions in the upwelling cycle. Our approach was to examine uptake of nitrogenous nutrients by these two primary producers and to quantify the contribution of imported nitrogen (nitrate) and locally regenerated nitrogen (ammonium and urea) to primary production in the immediate inshore area.

Material and methods

Study site

Field measurements were carried out at Oudekraal on the west coast of the Cape Peninsula (Lat. 33°58'S, Long. 18°21'E). The subtidal zone here was surveyed in detail by Velimirov et al. (1977) and a centre of upwelling occurs offshore of this site (Field et al., 1980). Ambient concentra-
tions of nitrogenous nutrients in the kelp bed under different wind and upwelling conditions were measured daily over eight days during a period of mixed upwelling and downwelling. Data on wind speed and direction were obtained from the meteorological office at D. F. Malan airport, approximately 20 km from the study site. Subsequently nutrient uptake by *Ecklonia maxima* Osbeck and phytoplankton were measured *in situ* on four separate occasions under different conditions of nutrient availability.

Nitrogen uptake measurement

**Kelp**

The method for measuring nitrogen uptake by kelp *in situ* was similar to that described by Gerard (1982). On each day of experimentation SCUBA equipment was used to enclose the fronds of three whole *Ecklonia maxima* plants in separate large plastic bags fastened round their stipes close to the junction with the fronds. Water samples were taken by means of a syringe attached to a sample tube that extended approximately 1 m into the middle of the bag. Water samples (100 ml) were collected every 20 min for 80 min to monitor the depletion of nitrate and ammonium within the bags. Previous measurements on six *E. maxima* plants revealed that urea was not taken up. Control incubations containing no kelp were performed simultaneously. Samples were filtered immediately through glass-fibre filters (Whatman GF/F) and kept in the dark on ice for later nutrient analyses. The volume of water within each bag was measured by dilution of 0.5 g of fluorescein dye injected into the bag after experimentation. The mean optical density for three samples from each bag was compared with a standard curve of optical density for known concentrations of fluorescein. Measured volumes ranged between 106 and 320 l, depending on the size of the kelp plants. Rapid dispersion of the dye when introduced into the bags indicated that mixing within them was good. Each kelp plant was then returned to the laboratory for wet weight determination. Five frond samples from each plant were oven dried to constant weight at 60°C and wet/dry weight conversions obtained separately for each plant. Uptake rates were calculated from linear regression of nutrient concentration against time and were expressed per unit oven-dried weight.

**Phytoplankton**

Phytoplankton nitrogen uptake was measured following the experimental protocol of Dugdale and Goering (1967). Sufficient amounts of either Na\(^{15}\)NO\(_3\) (99.6 at %), \(^{15}\)NH\(_4\)Cl (99.7 at %) or CO (\(^{15}\)NH\(_2\))\(_2\) (99.1 at %) were added to two litres of 212-\(\mu\)m-screened water to enrich ambient nitrogen concentrations by about 10%. Because nutrient concentrations were subject to very rapid fluctuation we had no prior knowledge of ambient concentrations on the day of experimentation and the 'ideal' enrichment was not always achieved. Enrichments ranged between 6 and 24% for nitrate, 9 and 25% for ammonium and 7 and 29% for urea. Incubations were carried out for 4 to 6 h at a depth of ca 1 m in an area unshaded by the kelp. Incubations were terminated by filtration onto glass-fibre filters (Whatman GF/F) using a hand-operated vacuum pump. A relative preference index (RPI) was calculated for both the kelp and phytoplankton according to McCarthy *et al.* (1977). For example, for ammonium:

\[
\text{RPI}_{\text{NH}_4} = \frac{V_{\text{NH}_4}}{V_{\text{NH}_4} + V_{\text{NO}_3} + V_{\text{urea}}}/\frac{[\text{NH}_4]}{[\text{NH}_4]+[\text{NO}_3]+[\text{urea}]},
\]

where \(V\) = uptake rate and \([\ ]\) = concentration.

**Analyses**

All nutrient measurements were performed on the day of collection; ammonium and urea according to Grasshoff (1976), and nitrate by the cadmium reduction procedure of Nydahl (1976). Kelp and particulate carbon and nitrogen were measured for oven-dried tissue (Heraeus CHN Rapid). Nitrogen-15 enrichments were determined by atomic emission spectroscopy following the Kjeldahl-Rittenberg oxidation procedure (Fiedler and Proksch, 1976). Phytoplankton chlorophyll \(a\) was determined according to Jeffrey and Humphrey (1975).

**Results**

Nutrient concentrations in the kelp bed over a period of eight days are shown in Fig. 1, along with predominant wind direction and maximum speed. Although the nitrate values were all relatively low due to predominantly downwelling conditions, they clearly demonstrate the rapidity with which changes in wind direction are followed by alterations in the concentration of nutrients. The decline in nitrate concentration from 2-4 August 1983 was coincident with a period of strong north-westerly (onshore) winds. On 6 August the wind veered to the west and then blew from the south for the remainder of the sampling period. An increase in nitrate concentration was clearly evident over this period. Ammonium concentrations also fluctuated rapidly, but were less obviously correlated with wind direction.

A summary of dissolved nitrogenous nutrient concentrations, particulate nitrogen and carbon, and chlorophyll \(a\) concentrations in the water column is shown in Table 1. As expected, phytoplankton biomass was lowest under conditions of active upwelling, shown here for the 8 March with an upwelling index (nitrate/total nitrogenous nutrient concentration) exceeding 90%. The highest chlorophyll \(a\) concentrations in the present study were lower than those measured by Field *et al.* (1980) and Carter (1982) during