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**Environmental effects on gross production and respiration in a facultative
oxidation pond**

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Abstract

Oxygen exchange by effluent samples taken at weekly intervals from a facultative oxidation pond was investigated over a 7 month period. Concentrations of ammonia, nitrate, nitrite, total and reactive phosphorus, alkalinity, total inorganic carbon, and free CO₂ were measured over 12 months. Gross daily oxygen production within the community compensation depth ranged from 8 gO₂ m⁻² in winter to 43 gO₂ m⁻² in summer. The corresponding range for dark respiration was 5-17.5 gO₂ m⁻² d⁻¹. On average, light saturated rates of net oxygen production and total net production extended to the upper 2 and 15% of the 1.3 m mean depth profile respectively. Community respiration to gross production ratios ranged from 1.58-7.14. Light saturated rates of net oxygen production and dark rates of oxygen consumption increased with seasonal rise in pond temperature as did net production per unit detectable pigment. However, the most important factor affecting the rate of oxygen production was the concentration of detectable pigment. In laboratory studies, oxygen exchange rates were optimal at pH 5-8, but rates declined rapidly as the pH was increased from 8.0-8.5. Pond pH varied between 6.7 and 7.8 throughout the year. Net CO₂ uptake under saturating irradiance (at pH 4.5) was maximal at 30 μM CO₂ and compensation was reached at about 5 μM CO₂. The minimum concentration of free CO₂ observed in the pond was 190 μM.

INTRODUCTION

Facultative oxidation ponds are large shallow basins which depend on oxygen for the successful treatment of biodegradable wastes. They are usually characterised

by the presence of high concentrations of organic and inorganic compounds; particularly ammonia, nitrate, phosphate, and carbon dioxide. These compounds are produced from the degradation of waste material by anaerobic bacteria located at the sludge/water interface (Brockett 1978). Algae in the water are able to absorb these compounds and, in the presence of light, supply oxygen to aerobic bacteria which can oxidise hydrogen sulphide and other odour producing compounds. As a result of favourable interactions between organic waste material, bacteria, and algae, oxidation pond operation is successful to the extent that there is little obnoxious odour and the oxygen demand of the waste influent is sufficiently reduced to enable its discharge into some receiving body.

Facultative ponds are highly reliant upon oxygen supply from photosynthetic algae and successful pond operation is dependent upon favourable environmental conditions (e.g., Ludwig & Oswald 1952; Bartsch & Allum 1957; Humenik & Hanna 1971). Light, temperature, and available nutrients have the greatest effect on photosynthetic oxygen production. However, the response of algae to such factors in facultative ponds has not been intensively studied. This is surprising since, in addition to producing oxygen during the light, algae impose a respiratory oxygen demand on the pond system at night and during their decomposition (King 1976). Knowledge of the manner in which the environment influences photosynthetic oxygen production is pertinent to the management of water purification systems. The present study of the seasonal changes in light, temperature, and nutrient levels in a facultative oxidation pond located in Auckland was carried out to identify the factors most limiting to photosynthetic oxygenation.

MATERIALS AND METHODS

The Manukau Purification Works is located at Mangere, Auckland, and is operated by the Auckland Regional Authority. The complex has 4 facultative ponds each of c. 120 ha with an average depth of c. 1.3 m. Primary treated effluent is received from industrial and domestic sources. The ponds operate in parallel but effluent from each mixes in a main return channel after passage through a pond, which takes from 5-7 days. Retention time within the entire pond system varies from 24-28 days depending on the flow. Mixing is achieved by water circulation, wind turbulence, and mechanical aeration. Further details of pond operation can be found in Brockett (1978).

Twenty litre samples of Pond 2 effluent were collected at weekly intervals in a black polythene bottle between 0900 and 1000 h (April 1977 to May 1978) and between 1100 and 1400 h from January-September 1978. The bottle was transported to the University laboratory within one hour of collection.

Analyses of ammonia, nitrate, nitrite, alkalinity, and reactive and total phosphorus were made on a 2 l sub-sample of the 20 l by Auckland Regional Authority staff at the Mangere laboratory. Chemical analyses were performed according to Standard Methods for the Examination of Water and Wastewater (APHA 1975). Total inorganic carbon was determined by acid release of CO₂ in Warburg flasks (Umbreit et al. 1957) or in a closed circuit infra-red gas analysis system (employing an ADC Series 225 infra-red gas analyser). Carbon species were calculated from molar proportions given in the tables of Saruhashi (1955) after measurement of pH (using a Radiometer pH M27 meter and combination pH electrode) and total inorganic carbon.

Chlorophyll pigments were extracted from algal cells using 90% acetone and dimethyl sulphoxide (Shoaf & Lium 1976). The dimethyl sulphoxide proved necessary for maximum extraction. Three 25 ml aliquots of pond water were centrifuged (8000 g for 10 min), the supernatant decanted, and the pellet resuspended in 10 ml 50/50 (v/v) 90% acetone/dimethyl sulphoxide for 24 h in the dark at 4°C. The pigment concentration was subsequently determined spectrophotometrically (Pye Unicam SP 1800) and using the trichromatic equations of Unesco (1966). Corrections for phaeopigment were not made and therefore concentrations represent the sum of chlorophyll *a* and some phaeopigment, hereafter designated 'detectable pigment'.

Estimates of daily gross production and respiration (24 h totals) were made using hourly rates of net oxygen production and consumption (determined from the response of pond samples to darkness and increments of irradiance at each sampling date), integrated over time and depth. Gross oxygen production refers to the sum of oxygen evolved in the light and the consumption in the dark and the calculation therefore assumes that oxygen consumption by algae and other organisms in the light is equal to that in the dark.

Vertical attenuation of photosynthetically active radiation in the pond at the sampling station was measured using a LI-COR 192S submersible quantum sensor and, together with recordings of total radiation obtained from the Meteorological Office at Mangere Airport (c. 5.5 km distant), was used to construct a profile describing the proportion of the surface irradiance which was present at 2 cm depth intervals in the pond. Approximate correction for surface reflection losses was made according to Golterman (1975).

The photosynthetic response to photon flux density was determined in the laboratory from changes in dissolved oxygen concentration of pond sample (50 ml) enclosed in a perspex cuvette. Oxygen concentration was measured by a Beckman Model 777 oxygen analyser attached to an oxygen electrode (Beckman Sensor 39065) inserted into the cuvette, and rates of exchange were calculated from slopes of continuously recorded dissolved oxygen changes by a 0-100 mV recorder in the range 50-100% saturation. The electrode was recharged before each experimental run according to the manufacturers' instructions, and was calibrated before and after each run in air saturated deionised water and in nitrogen gas. Drift was always less than 3% of full scale (0-100% saturation) over the 2-3 h period of measurement. Measurement of oxygen exchange (which refers to oxygen production and consumption of all algae, zooplankton, bacteria, and chemical processes) was made initially in the dark, and subsequently at photon flux densities ranging from near dark to light saturation, imposed in a random order. Single measurements of oxygen exchange in response to a given photon flux density were made over a 20-30 min interval. The rate of exchange was constant during this period. Irradiance was provided by 40 and 150 W tungsten filament lamps and was altered by changing the lamps or varying the distance between the lamps and the cuvette. Photon flux density (400-700 nm) measurements were taken from the inside upper face of the cuvette using a LI-COR 185 meter with sensor. Temperature within the cuvette was maintained at the temperature of the pond sample during sampling by means of a thermostatted water jacket.

Since it was not possible to reliably separate algal and non-algal oxygen exchange processes the terms described as 'compensation depth' and 'compensation irradiance', are prefixed by the term 'community'. The daily community compensation

depth, the maximum depth in the pond to which net oxygen production occurred, was determined from the daily productivity-depth profiles. The community compensation irradiance was determined as the photon flux density at which net oxygen production by pond samples was zero. Gross production efficiency (on the basis of photosynthetically active radiation) was calculated using the formula of Copeland & Dorris (1964).

Oxygen exchange in relation to pH was investigated by monitoring changes in dissolved oxygen concentration of pond sample within the perspex cuvette as described above. The pH was altered by injection of 0.1 M NaOH or HCl, and a different subsample of the same algal population (with no replication) was used to determine oxygen production at a given pH. Photon flux density was saturating ($700 \mu\text{mol m}^{-2} \text{s}^{-1}$), the temperature 16°C , and the total inorganic carbon concentration 2.25 mM. Measurement of oxygen production began when the dark rate of consumption stabilised (after a few minutes). As before, rates of oxygen production were linear for 20-30 min. The long term effects of pH change on oxygen exchange were not investigated.

The response of carbon assimilation to changes in free CO_2 concentration was determined by closed circuit infra-red gas analysis using five separate algal populations collected between May and September 1978. Linear rates of CO_2 depletion were measured for up to 1 h. The pH of the pond effluent solution within the 75 ml perspex assimilation chamber was maintained between 4.0 and 4.5 by 0.1 M HCl added through an injection port, and was constantly monitored. Within this pH range, free CO_2 is the dominant carbon species. Temperature was maintained at that of the pond at time of sampling by a water jacket surrounding the chamber. The photon flux density was saturating ($700 \mu\text{mol m}^{-2} \text{s}^{-1}$).

In studies of seasonal variation, seasons were defined by the following months; spring (September, October); summer (November-March); autumn (April, May); winter (June-August).

RESULTS

Primary productivity in the ponds

Visual inspection of Fig. 1 shows that gross production within the community compensation depth was usually highest in summer and lowest in winter. Oxygen consumption also generally followed this trend. Net oxygen production ranged from 4.6-32.2 gO₂ m⁻² d⁻¹ in the summer months, and between 2.1 and 11.6 gO₂ m⁻² d⁻¹ during the winter. Oxygen uptake within the community compensation depth (R_c) was always less than the gross oxygen production (P_g) and the R_c/P_g ratio ranged from 0.26-0.72. However, when the average depth of 1.3 m was taken into account, oxygen consumption (R) always exceeded gross production. The R/P_g ratio ranged from 1.58-7.14. Absolute values for daily pond respiration (R) ranged from 32.1-135.4 gO m⁻² d⁻¹ and respiratory measurements were highest during the summer months. Calculated gross production efficiencies ranged from 3.2-9.6% (mean: 5.6%) and did not show any seasonal dependence.

The depth profile of net oxygen exchange

Data obtained during the study for the photon flux density saturating for net oxygen production revealed no clear seasonal pattern. From January to mid February, values ranged from 1200-1700 μmol m⁻² s⁻¹). From mid February until September, values ranged from 230-600 μmol m⁻² s⁻¹) except for one sample in mid April (1700 μmol m⁻² s⁻¹). The overall range (230-1700 μmol m⁻² s⁻¹). was between 29 and 94% (mean: 51%) of the peak daily photon flux density incident on the pond surface. Light saturated rates of net oxygen production were observed to extend to a maximum depth of 10 cm, with an average depth of c. 3 cm, which is only 2.3% of the mean depth profile.

Values for the community compensation intensity revealed no definite seasonal variation, and ranged between 12 and 100 μmol m⁻² s⁻¹) or between 0.9 and 8.7% (mean: 4.8%) of the peak daily incident flux density. If a mean value of 19 cm is taken for the daily community compensation depth, from measurements made during the summer (when the community compensation depth was greatest), then net oxygen production was confined to the upper 15% of the pond.

The effects of seasonal changes in pond temperature on oxygen exchange

Seasonal increase in pond temperature was associated with change in the light saturated rate of net oxygen production (Fig. 2a), the net rate of production per unit detectable pigment (Fig. 2b), and the rate of dark oxygen consumption (Fig. 2c), but not with oxygen consumption per unit detectable pigment ($r = 0.06$, ns). The average Q_{10} values calculated from the regression lines in Fig. 2a-c are: 3.43, 1.57, and 1.60, respectively.

The light saturated rate of net oxygen production ($P_{n \max}$) was highly correlated with the detectable pigment concentration (C). The regression line relating these two variables (\pm s.e.) is:

$$P_{n \max} = 15.79 \pm 1.64 C - 4.13 \pm 2.52 \quad r^2 = 0.86, F = 76.74, P < 0.001.$$

Units for $P_{n \max}$ are $\text{gO}_2 \text{ m}^{-3} \text{ h}^{-1}$ whereas those for detectable pigment concentration are g m^{-3} . Incorporating temperature into the regression only increased the variance explained by a further 4%. Since it was found that temperature and the detectable pigment concentration were mutually correlated ($r = 0.53$, $P < 0.01$), first order partial correlation coefficients were computed. Values of the coefficients for the following correlations are: $P_{n \max}$ VS C (0.88, $P < 0.01$); $P_{n \max}$ vs temperature (0.66, $P < 0.01$); C vs temperature (-0.43, $P < 0.05$). Thus, both pigment concentration and temperature seem to strongly influence $P_{n \max}$, and the positive simple correlation between the detectable pigment concentration and temperature is spurious.

Seasonal variation in nitrogen and phosphorus compounds

Seasonal and annual means for levels of nitrogen and phosphorus compounds in the oxidation pond are shown in Table 1. When dissolved in water, ammonia exists in equilibrium with ammonium ions, and in the pH range observed in the pond (6.7-7.8) little free ammonia would be present. As results of analytical tests for ammonium ions are expressed as ammonia, all reference to ammonia strictly refers to ammonium ions (NH_4^+) in the pond. Ammonia was the dominant form of inorganic nitrogen present. Mean concentrations were observed to be higher in summer and autumn and absolute concentrations ranged from 12.1-28.5 g m^{-3} . Nitrate (Table 1) and nitrite (not shown) concentrations were comparatively low.

Total phosphorus, which incorporates algae, bacteria, zooplankton, and fungi in addition to inorganic phosphorus, ranged from 1.78-7.05 g m⁻³ whereas reactive phosphorus ranged from 0.22-3.31 g m⁻³. Seasonal variation for both compounds was similar and mean concentrations were observed to be highest in summer and lowest in winter.

Seasonal variation in alkalinity, pH, and inorganic carbon compounds

Alkalinity ranged from 7.5-20.7 meq l⁻¹ and a seasonal pattern was apparent, with higher mean values in summer and lower mean values in spring (Table 2). The annual range for pH was 6.7-7.8, for free carbon dioxide 8.4-85.4 g m⁻³, and for total inorganic carbon 94.2-227.0 g m⁻³. In this pH range, bicarbonate was the dominant form of dissolved inorganic carbon and carbonate was virtually absent. Seasonal variation in pH was very small but mean concentrations of free CO₂ were highest in autumn and lowest in winter. Mean concentrations of total inorganic carbon were higher in autumn and summer than in winter.

During a 24 h survey in February 1978 (mid-summer) pH was determined hourly in water samples taken from the surface and at a depth of 80 cm. Throughout that period, the pH varied from 7.2-7.4, and there was no measurable difference in pH between the surface and 80 cm depth samples. This result suggests that variations in pH during the day are also small.

A correlation analysis revealed no significant correlations between total cell numbers or cell numbers of individual species or total detectable pigment concentration, and concentrations of any of the nutrients monitored.

Oxygen exchange in relation to pH and carbon dioxide concentration

At pH 6.0, the rate of net oxygen production achieved a maximum, but the rate was still 90% of the maximum in the pH range 5.0-8.0 (Fig. 3a). The rate declined rapidly as the pH increased from 8.0-8.5. This decline was most likely because of a reduction in free CO₂ since this component formed less than 20 μM of the total inorganic carbon pool at pH 8.5. Thus, the annual pH range noted above for the ponds, is within the limits for optimal oxygen production.

Carbon dioxide uptake in response to changing free CO₂ concentration in the medium is shown in Fig. 3b. Since the data were obtained over a four month period where variations occurred in algal cell numbers and probably also bacteria and zooplankton numbers, the results are expressed on a relative basis. The data show that CO₂ uptake was saturated at 30 μM and that compensation was reached at about 5 μM. The saturation figure (30 μM) was well below the lowest free CO₂ concentration recorded in the ponds during the study (190 μM).

DISCUSSION

The oxygen balance of facultative ponds is affected by the population size and composition of both algal and non-photosynthetic oxygen consuming organisms. These latter organisms are obviously prolific and have a considerable effect on pond operation and performance (Brockett 1971). However, in the present study their effects on pond oxygen balance could not be determined in isolation from those of the algae.

In so far as photosynthetic oxygen production is concerned, light, temperature, and nutrients have greatest effect. The data show that net oxygen production by pond samples is saturated only by photon flux densities characteristic of those in the upper 2% of the water column. This suggests that net oxygen production in the remaining 98% of the water column is light limited. However, there was still a positive net production of oxygen in the upper 15% of the column and thus the lower 85% only was responsible for net oxygen consumption on average. Of course, gross oxygen production would continue to greater depth than net production, but this would depend on the extent of dark oxygen consumption by the pond community.

Since the presence of non-photosynthetic organisms in pond samples undoubtedly affected net production in these laboratory studies, it is not possible to state categorically that the photosynthetic oxygen production profile is the same as determined for the community. Pragmatically, the data produced are of value because they give an indication of oxygen production which is in excess of immediate requirements and which is thus available to the pond community at

large. This oxygen can be distributed to the lower layers of the pond by wind induced turbulence, mechanical mixing, and molecular diffusion.

Although levels of net productivity were comparable to those reported by Robb (1974) for oxidation ponds ($2.7-11.8 \text{ gO}_2 \text{ m}^{-2} \text{ d}^{-1}$) and by Day et al. (1970) for estuarine oxidation ponds ($0.5-5.0 \text{ gO}_2 \text{ m}^{-2} \text{ d}^{-1}$), community respiration was high and a negative oxygen balance ($R/P_g > 1$) existed in this pond throughout the study. Measurements of redox potential (Brockett 1971) and dissolved oxygen (Irving 1979) revealed that this pond was typically anaerobic throughout the depth profile from early evening until the following morning.

The mutual correlation of temperature with both the net oxygen production and the detectable pigment concentration suggests that seasonal temperature changes can affect oxygen production through changes in detectable pigment, i.e., algal population size and composition. This conclusion is consistent with results of Rowe's (1975) statistical analysis of algal cell counts taken over a ten year period. He showed that cell counts of algal species were positively correlated with temperature changes.

It is possible for the pigment dependence on temperature to be attributable to a correlation between solar radiation and temperature, and that pigment concentration is in fact dependent on solar radiation. It is difficult to prove this in practice, however, because integral solar radiation over a period of days may influence subsequent population growth and thus pigment synthesis and degradation. Furthermore, individual cells probably receive solar radiation which is both intermittent (during the night, and when retained below the euphotic zone during the day) and non-uniform (when mixing with the bulk liquid). For these reasons, a causal relationship between solar radiation and pigment concentration should not be expected necessarily. Nevertheless, the significant negative partial correlation between temperature and pigment concentration together with observations such as the occasional low rate of net production at high temperature (Fig. 2a, b) suggest that high temperature and high pigment concentration stimulated oxygen production independently, rather than in concert. This may have arisen because as temperatures increased during the late summer there was a decline in oxygen production (Fig. 1, March) which was associated with the disappearance of algae, particularly larger euglenoid species.

The ponds often become unstable at this time of year (Brockett 1978) and may become anaerobic for 2-3 weeks. Although the reasons for the instability are unknown, it is not because of the inability of algae to grow in aerated pond liquor (Brockett 1978).

The slightly higher mean values for ammonia, nitrate, total phosphorus, and reactive phosphorus during the summer (Table 1) might suggest that organic loading to the pond was higher at this time of year than at other times. The effect could be to both increase the oxygen demand of the pond community and to reduce light penetration. Such events could have led to the death of algal species which could not tolerate prolonged anaerobiosis. When the algae began to proliferate again, which seemed to be promoted by reduction in organic loading and increased artificial mixing, the brown coloration was replaced by green. Thus, in early autumn, as temperatures began to decline, algal oxygen production began to improve. These events could explain the negative partial correlation between temperature and the detectable pigment concentration.

Light penetration in this pond (data not shown) was lower than in other similar environments such as sewage ponds (Bartsch & Allum 1957), oil refinery effluent holding ponds (Minter 1964) and oxidation ponds (Robb 1974). Furthermore, although chlorophyll a often contributes to the attenuation of photosynthetically active radiation (Ganf 1974), in the present study detectable pigment concentration only accounted for a small amount of the variation in the calculated attenuation coefficient ($r = 0.43$, $P < 0.05$). It was also found that respiration per unit detectable pigment was temperature independent, which may have arisen in part because detectable pigment rather than only chlorophyll a was determined, although as previously noted net production per unit detectable pigment (a measure of the oxygen producing ability of the algae) was temperature dependent. Collectively these observations suggest that non-photosynthetic organisms such as bacteria and zooplankton and other suspended solids were responsible for the high light attenuation and the high community oxygen demand. Further investigation of the factors responsible for light attenuation in the pond was not attempted because of the time constraint. However, dissolved material was found to have a strong

selective influence on light attenuation in the Bromley ponds (Robb 1974) and study of this material in the Auckland pond could be enlightening.

Since photosynthesis is light limited in all but the upper few centimetres, temperature may have little effect on photosynthetic oxygen production by the algae in the lower depth profile of the pond. However, in so far as the community is concerned, temperature has the effect of stimulating oxygen uptake (Fig. 2c) and thus contributing to overall pond oxygen consumption.

There were no significant correlations between cell counts of individual species or total cells or of detectable pigment, and concentrations of ammonia, nitrate, nitrite, total and reactive phosphorus, free CO₂, and total inorganic carbon. This result is interpreted to mean that these nutrients were not limiting to algal growth. It is interesting to note that in his earlier study of the Mangere oxidation ponds, Rowe (1975) found that cell counts of *Euglena acus* were quite closely related to ammonia concentration over the 10 year period from 1963 to 1972. Ammonia concentrations then ranged from 0-20 (mean: 10 g m⁻³) compared to the range of 12.2-28.5 (mean: 19.6 g m⁻³) found in the present study. These data support the view that sufficient ammonia is now (1978) present for the growth of these cells.

Pond pH was very stable (Table 2) because of the strong buffering capacity of the inorganic carbon, nitrogen, and phosphorus components. The observed range in variation ensured that more than sufficient free CO₂ was available for photosynthetic carbon assimilation at all times. Although there was little evidence that levels of free CO₂ as high as 2.2 mM considerably inhibited carbon assimilation in the short term (Fig. 3a) the possibility of long term effects, such as the acidification of cell contents and the inactivation of pH sensitive enzymes (Coleman & Colman 1981), cannot be ruled out.

A possible indirect mechanism of pH inhibition of CO₂ assimilation in waste water treatment ponds is through increase in free ammonia concentration with pH rise. Abeliovich & Azov (1976) found that at pH > 7.9 and ammonia concentration of 2 mM, photosynthesis was severely inhibited, although respiration was unaffected. In the present study, pH never exceeded 7.9 and, although the maximum observed

ammonia concentration was 1.7 mM, the pH at that time was 7.2 and thus most of the ammonia would have been in the ionised (NH_4^+) form. It is possible that the rapid decline in relative photosynthesis (Fig. 3a) as the pH increased above 8.0 was because of uncoupling of photophosphorylation by ammonia. Nevertheless the data in Fig. 3b still support the conclusion that the supply of inorganic carbon was the major limitation to photosynthesis at the higher pH in Fig. 3a. Ammonia inhibition of photosynthesis would be an important factor to consider in future should changes in pond buffering capacity change.

We conclude that photosynthetic oxygenation is limited by light distribution through the pond depth profile, that both detectable pigment concentration and temperature strongly influence the light saturated rate of net oxygen production by pond samples, and that photosynthetic oxygenation is not limited by inorganic nitrogen, phosphorus, or carbon availability. Increases in detectable pigment (chlorophyll *a*) concentration and reduction in the level of particulate organic matter entering the pond are achievable objectives which would lead to greater photosynthetic oxygenation and improvement in pond oxygen relations.

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Table 1 Seasonal and annual mean (\pm standard deviation) concentrations of ammonia, nitrate, and total and reactive phosphorus.

	NH ₃	NO ₃ ⁻	Total P	Reactive P
Season	(g m ⁻³)	(g m ⁻³)	(g m ⁻³)	(g m ⁻³)
Autumn	23.0 \pm 2.0	0.039 \pm 0.019	4.59 \pm 0.77	1.88 \pm 0.57
Winter	17.2 \pm 4.7	0.031 \pm 0.034	3.28 \pm 0.95	0.91 \pm 0.32
Spring	16.4 \pm 2.9	0.024 \pm 0.014	4.75 \pm 0.88	1.49 \pm 0.30
Summer	21.8 \pm 4.1	0.053 \pm 0.048	5.11 \pm 0.99	1.90 \pm 0.63
Annual	19.6 \pm 4.6	0.040 \pm 0.038	4.38 \pm 1.19	1.57 \pm 0.62

Table 2 Seasonal and annual mean concentrations (\pm standard deviation) of alkalinity, pH, free CO₂ and total inorganic carbon (TIC).

	Alkalinity		Free CO ₂	TIC
Season	(meq l ⁻¹)	pH	(g m ⁻³)	(g m ⁻³)
Autumn	10.4 \pm 1.9	7.3 \pm 0.5	34.8 \pm 30.3	166.6 \pm 11.6
Winter	10.1 \pm 1.2	7.1 \pm 0.1	19.4 \pm 2.5	122.9 \pm 13.7
Spring	9.6 \pm 1.7	7.1 \pm 0.1	22.1 \pm 7.5	116.7 \pm 11.4
Summer	12.2 \pm 2.6	7.2 \pm 0.2	24.5 \pm 17.5	166.9 \pm 21.0
Annual	10.9 \pm 2.3	7.2 \pm 0.2	24.2 \pm 16.5	139.8 \pm 30.6

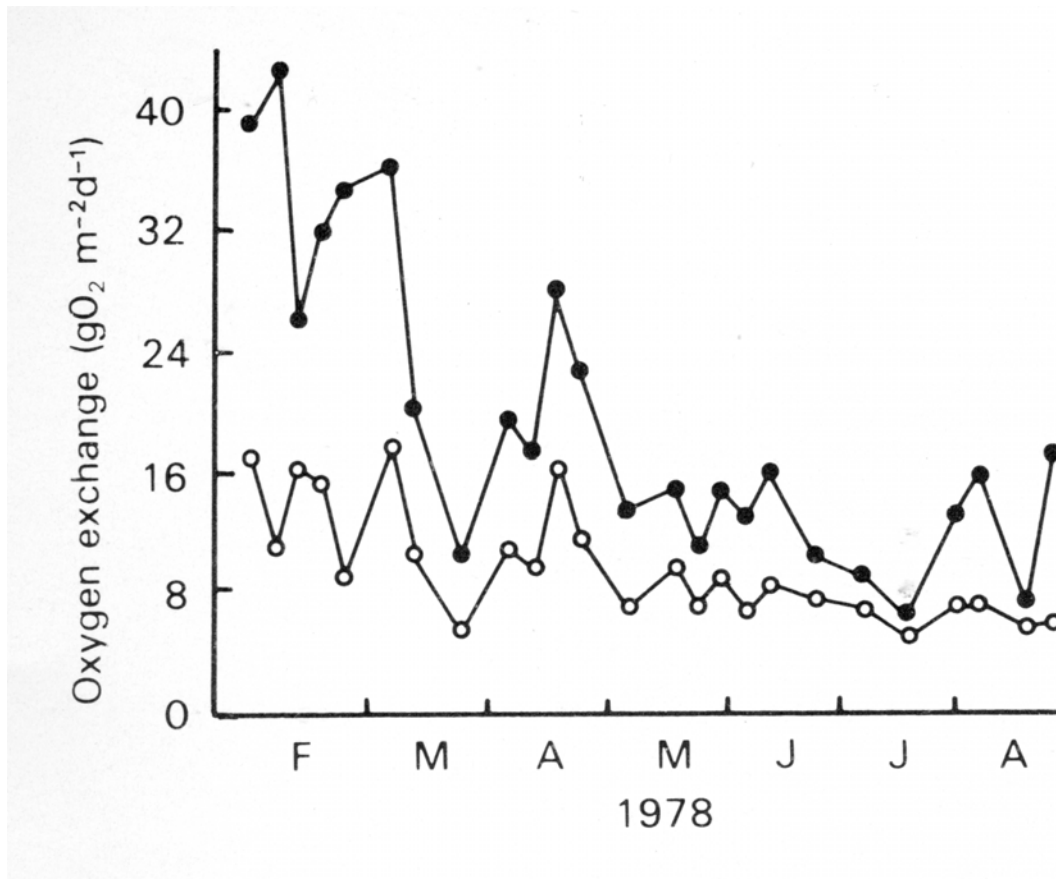


Fig. 1 Seasonal variation in gross production (●) and respiration (○) calculated for the daily compensation depth. Values are daily integrated rates of oxygen exchange.

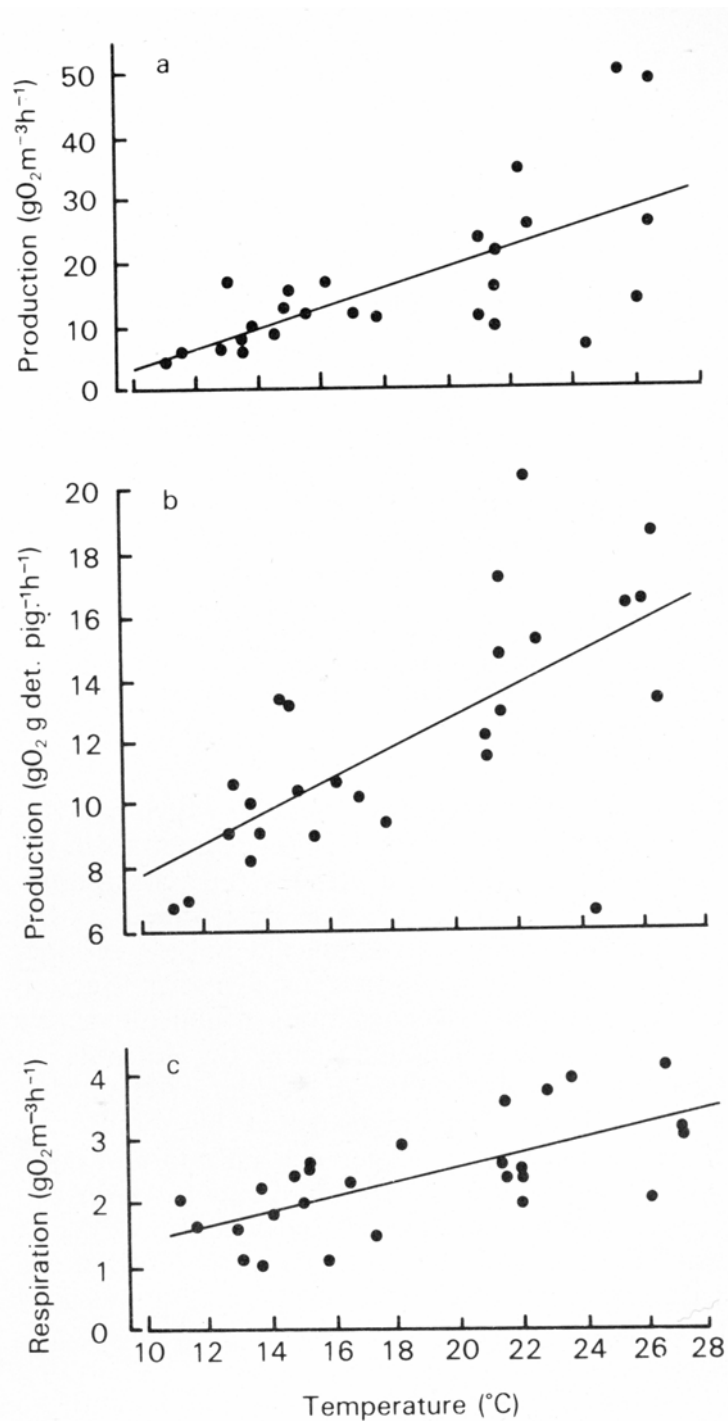


Fig. 2 Variation in (a), light saturated rate of net oxygen production, $Y = 1.60 \pm 0.38 X - 12.63 \pm 7.24$, $F = 17.02$, $r = 0.67$, $P < 0.01$; (b) net production per unit detectable pigment, $Y = 0.50 + 0.14 X + 2.77 \pm 2.17$, $F = 20.42$, $r = 0.68$, $P < 0.01$; and (c) dark respiration, $Y = 0.12 \pm 0.03 X + 0.19 \pm 0.22$, $F = 13.58$, $r = 0.69$, $P < 0.01$, with seasonal change in pond temperature.

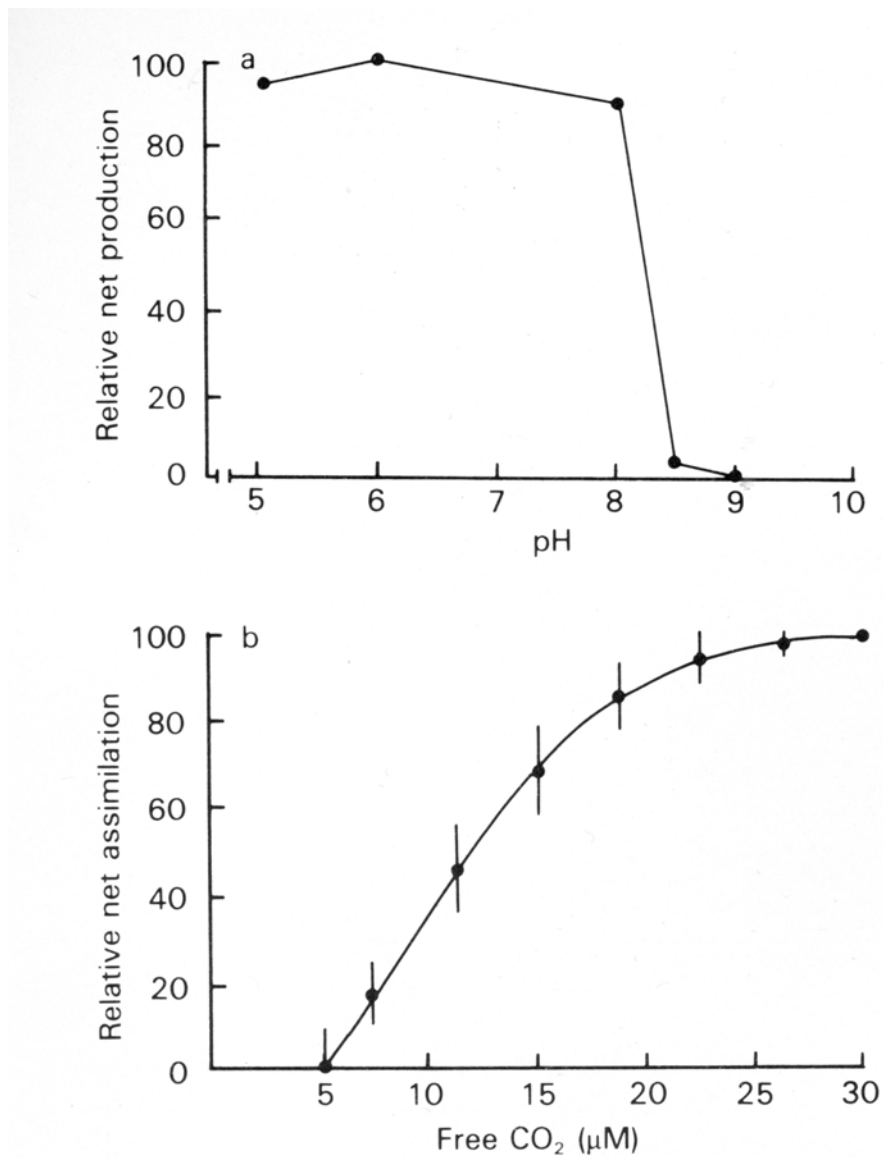


Fig. 3 The response of oxygen production to pH of the medium (a) and the response of CO₂ assimilation to free CO₂ concentration in the medium (b). Bars represent standard deviations.