

## Respiration and net photosynthesis of cotyledons during establishment and early growth of propagules of the mangrove, *Avicennia marina*, at three temperatures

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Respiration and net photosynthesis of discs excised from cotyledons of *Avicennia marina* (Forssk.) Vierh. were measured at temperatures of 17, 21 and 25°C in a Gilson Respirometer. Cotyledonary material was also analysed for TNC (total non-structural carbohydrates). Rates of respiration and net photosynthesis were significantly different at the three temperatures, with the lowest rates recorded in each case at 17°C and the highest at 25°C. TNC values revealed an initial decrease, followed by a small increase, and thereafter a drop to fairly constant low levels. While seedlings at 25°C grew well, very little growth was recorded at 17°C. Growth at the different temperatures was related to the relative excess of photosynthesis over respiration. The ecological implications of these results are discussed.

Respirasie en netto fotosintese van snitte van die saadlobbe van *Avicennia marina* (Forssk.) Vierh. is by temperature van 17, 21 en 25°C in 'n Gilson Respirometer gemeet. Saadlobmateriaal is ook vir TNC (totale nie-gestruktureerde koolhidrate) ontleed. Die tempo's van respirasie en netto fotosintese het betekenisvol by die drie temperature verskil, met die laagste tempo's in elke geval by 17°C en die hoogste by 25°C. TNC-waardes het 'n aanvanklike afname getoon, gevolg deur 'n klein toename, en daarna 'n daling na redelik konstante lae vlakke. By 25°C het saailinge goed gegroei, terwyl baie min groei by 17°C aangeteken is. Dit blyk dat groei by die verskillende temperature verband hou met die mate waarin fotosintese respirasie oorskry. Die ekologiese implikasies van hierdie resultate word bespreek.

**Keywords:** Assimilation, establishment, mangrove, total non-structural carbohydrates

### Introduction

Mangroves are tropical species which also extend into subtropical and temperate regions. Temperature has been suggested as the most important factor limiting the distribution of mangroves away from the tropics into cooler areas (Chapman 1976; Oliver 1982). In South Africa the natural distribution of *Avicennia marina* (Forssk.) Vierh. extends almost to East London (Steinke 1986a) where significantly lower temperatures are experienced (Schulze 1980) than in Durban with its subtropical climate (Trewartha 1968). Investigations under laboratory and field conditions (Steinke & Charles 1987) indicated that at low temperatures (17°C) early growth of *A. marina* seedlings was slow in comparison with that at higher temperatures which are experienced under subtropical or tropical conditions. However, this work also suggested a need for closer examination of the responses of seedlings to different temperatures. In order to obtain more information on these responses, an experiment was conducted in growth cabinets to determine respiration and net photosynthesis at three temperatures.

### Methods

Approximately 600 mature propagules, whose abscission was judged to be imminent, were picked in the Beachwood Mangrove Reserve (Mgeni Estuary) in the early morning. They were immediately transported to the laboratory where they were placed in large tanks of seawater to cast off their pericarps. In the late afternoon the propagules which had shed their pericarps were divided randomly into three

groups and placed on river sand in asbestos-cement trays. These were watered initially with 50% seawater and thereafter with tapwater to which nutrients had been added. Each group was allocated randomly to a growth cabinet at 17, 21 or 25°C. The photoperiod in the three cabinets was set on a 12-h light/dark cycle with a light intensity of 140  $\mu\text{mol m}^{-2} \text{s}^{-1}$  at plant height.

A batch of 10 propagules was also used as a zero time sample (day 0). The material was dried in a forced-draught oven at 80°C for one week and weighed. Sampling thereafter was carried out on days 1, 3, 4, 7, 9, 11, 13, 15, 21, 28 and 35. On each sampling day, 10 propagules (seedlings) were removed at random from each temperature treatment. Using a cork-borer, a disc of 8 mm diameter (50  $\text{mm}^2$ ) was removed from the middle of the upper half of the outer cotyledon of each propagule (Steinke 1986b). These discs were used for the determination of respiration on each of the above days, and on days 1, 7, 13, 21, 28 and 35 the rate of net photosynthesis was also determined with the same material. Samples of tissue in the form of discs have frequently been used in similar studies (Tamas & Bidwell 1970; Atkins & Canvin 1971; Zurzycki & Starzecki 1971; Kumarasinghe *et al.* 1977; Delieu & Walker 1981; Harris *et al.* 1983). These measurements were carried out at the respective treatment temperatures with a Gilson Differential Respirometer.

Ten 15-ml reaction flasks were used per treatment and each contained one sample disc with a 1-ml film of water at the bottom of the flask. All manometric determinations were

carried out in a run of 60 min, following a 30-min equilibration period. For respiration measurements 0.4 ml of 20% potassium hydroxide was added to the centre well of each reaction flask together with a fluted filter paper to absorb the  $\text{CO}_2$  produced during the observations (Umbreit *et al.* 1964; Mathieson & Dawes 1974; Dawes *et al.* 1978). For photosynthesis measurements a 0.25%  $\text{CO}_2$  atmosphere was maintained in the reaction flasks using the Pardee method (Umbreit *et al.* 1964). Although this is a saturating  $\text{CO}_2$  condition, field observations have indicated that  $\text{CO}_2$  levels are not usually limiting (Steinke, unpublished). Respiration determinations were conducted in complete darkness achieved by wrapping the reaction flasks in heavy-duty black plastic, whereas photosynthesis was measured under a constant light intensity of  $225 \mu\text{mol m}^{-2} \text{s}^{-1}$  (measured on a Licor Quantum Meter using a 192 S sensor).

At the end of the measurements for each sampling day, the discs and the remaining cotyledonary material from the propagules were oven-dried as described above and weighed. Oven-dried material was ground in a Cassella mill to pass a 1-mm mesh sieve and, as it had been shown (Steinke & Charles 1987) that carbohydrates were the most important

reserve material in *A. marina* cotyledons, it was analysed for total non-structural carbohydrates (TNC) (Marais 1965).

## Results

Although it was intended that morphometric data should be recorded for each temperature treatment, this was not possible due to the poor growth at the low temperature over the experimental period (Figure 1). The differences due to temperature were marked. While seedlings at  $25^\circ\text{C}$  had produced two pairs of leaves by the end of the experiment, those at  $21^\circ\text{C}$  had produced only one pair of leaves, which were still expanding. There was also a correspondingly greater growth of roots at  $25^\circ\text{C}$ . The seedlings at  $17^\circ\text{C}$  showed little growth of tops or roots during the experimental period.

The cotyledons decreased in mass during the experimental period. The linear equation,  $y = a + bx$ , was fitted to the cotyledon data and examination of the various regression coefficients,  $b$ , in the above equation provided a basis of comparison of mean relative rates of decrease (Snedecor 1957). Heterogeneity regression analysis (Table 1) revealed that there was a significantly faster decrease in mass with each increase in temperature.

In general, fairly constant levels of oxygen were utilized during respiration and evolved during photosynthesis for the duration of each measurement period, as revealed by the time-course data. The rates of respiration were significantly different at the three temperatures (Figure 2). In each treatment there was an initial high rate of respiration which decreased to a fairly constant level thereafter. The respiration readings on day 15 had to be discarded owing to a malfunction in the apparatus. There was no significant

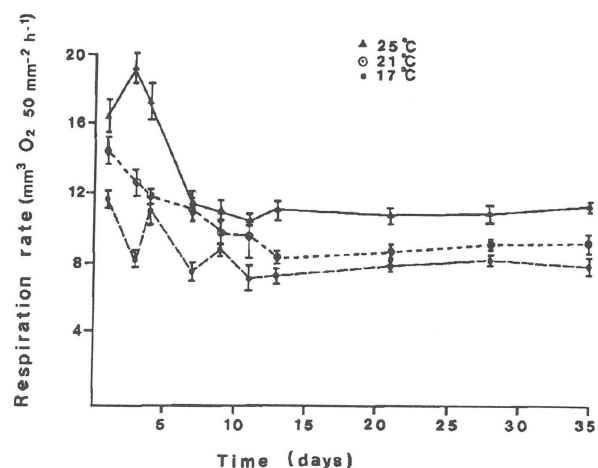
**Table 1** Heterogeneity regression analysis of the cotyledon data for three temperatures

Source	D.F.	S.S.	M.S.	F
Mean regression	1	8.208		
Heterogeneity regression	2	0.738	0.3690	8.56 <sup>a</sup>
Total regression	3	8.946		
Error	270	11.633	0.0431	

<sup>a</sup>  $P < 0.01$ .



**Figure 1** Seedlings of *A. marina* after growth for 35 days. From left to right: seedlings at 17, 21 and  $25^\circ\text{C}$ . Note at  $17^\circ\text{C}$  the appearance of the first true leaves at the edge of the cotyledon.



**Figure 2** Mean rates of respiration of *A. marina* at three temperatures. Vertical bars represent standard errors.

difference in the rates of net photosynthesis at the three temperatures on day 1, but thereafter significant differences occurred in the different treatments (Figure 3). With both respiration and photosynthesis the rates were lowest at 17°C and highest at 25°C. There were, however, greater differences in photosynthesis than in respiration at the different temperatures. A comparison of the mean rates of net photosynthesis and respiration is provided for the period of the experiment (Table 2). At 25°C photosynthesis exceeded respiration even when the initial high rate of respiration was included. At 21°C, however, photosynthesis exceeded respiration only after the respiration rate had fallen from its high initial values, i.e. from day 9 or day 11 onwards. This lag was prolonged in the case of seedlings at 17°C where the mean rates of respiration and net photosynthesis were not very different, even after the decrease to the constant low level from day 11 onwards.

The results of the carbohydrate analyses (Figure 4) should be considered as tentative. The samples had to be combined to provide sufficient material for analysis, consequently the absence of replications ruled out statistical tests. The results revealed a sharp decrease in carbohydrate levels after the pericarps had been shed, followed by a small increase which by day 15 had once again decreased to a fairly constant low level.

## Discussion

Although the decrease in mass of cotyledons confirmed previous work (Steinke & Charles 1987), there appears to be no detailed information on changes in TNC composition of these organs during establishment and early growth. The sharp decrease after the shedding of the pericarps has been interpreted as being a response to a high demand for these compounds with active growth initiation. This was confirmed by the high initial rates of respiration that were recorded. The subsequent increase in TNC content suggested that photosynthesis exceeded the demand for carbohydrates at a time of apparently slow growth, resulting in a small build-up of storage compounds again. The constant low levels recorded after approximately day 15 indicated that the cotyledonary reserves had been utilized and that photosynthates were being used directly to support growth. As might have been expected from the growth of the seedlings, there appeared to be a delayed response at the lowest temperature.

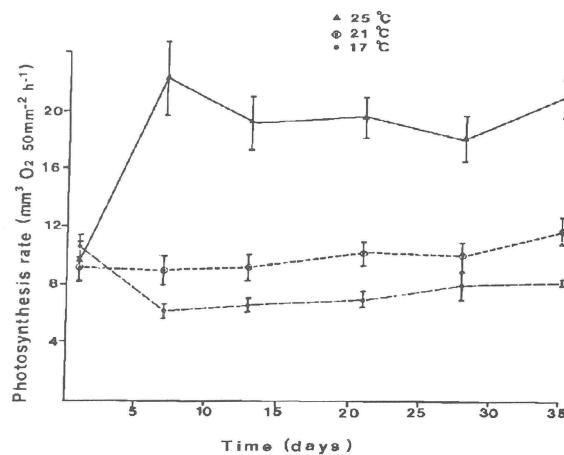
Although there have been several studies of the effects of very low temperatures on mangrove survival and distribution (McMillan 1975; Markley *et al.* 1982; McMillan & Sherrod 1986; Provancha *et al.* 1986), the significance of

**Table 2** A comparison of mean rates ( $\text{mm}^3 \text{O}_2 50 \text{mm}^{-2} \text{h}^{-1}$ ) of net photosynthesis and respiration in cotyledons of *A. marina* during the period of the experiment

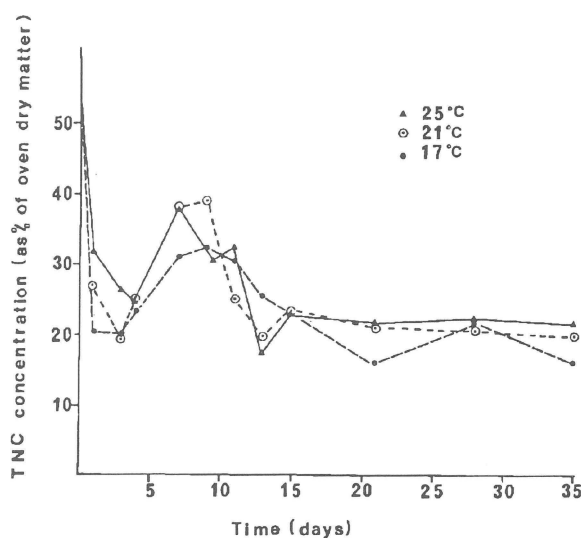
Temperature (°C)	Mean rate of net photosynthesis (entire period)	Mean rate of respiration (entire period)	Mean rate of respiration		
			Day 7	Day 9	Day 11
25	18.31	12.95	10.95	—	—
21	9.96	10.50	—	9.15	9.03
17	7.80	8.60	—	7.93	7.74

different temperatures for photosynthesis in mangroves does not appear to have received much attention. The relative rates of respiration and photosynthesis suggest an explanation for the differences in growth of the seedlings at the three temperatures (Table 2). Although the excision of the discs could have had the effect of increasing respiration at the expense of net photosynthesis, this technique has proved useful especially in providing an indication of relative results of respiration and photosynthesis (Zurzycki & Starzecki 1971). The results suggest that the greater growth of the seedlings at 25°C was due to the large excess of photosynthesis over respiration, whereas the poorer growth at the cooler temperatures was in proportion to the lower relative values of photosynthesis and respiration.

The ecological implications of these results are interesting. They suggest that the respiratory mechanisms of this tropical species are less sensitive to low temperatures than are the photosynthetic mechanisms. Poor growth at low temperatures appears to be due not so much to an effect on respiration but rather to a curtailment of photosynthesis. Under these conditions the poor growth would mean re-



**Figure 3** Mean rates of net photosynthesis of *A. marina* at three temperatures. Vertical bars represent standard errors.



**Figure 4** Mean total non-structural carbohydrate levels of cotyledons at three temperatures.

duced competitive ability and in this way limit the potential of these plants to migrate into cooler regions. McMillan (1975) has shown that populations of both *A. marina* and *A. germinans* from higher latitudes show adaptation to chilling conditions which permits survival in habitats with recurrent low winter temperatures. It would be interesting to repeat this experiment with propagules from the southern limit of mangroves along our coastline to determine if these plants have acquired a greater tolerance of low temperatures than that possessed by the more northerly communities.

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