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Photosynthesis and related physiological processes in two mangrove species, *Rhizophora mucronata* and *Ceriops tagal*, at Gazi Bay, Kenya

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Summary

Measurements were carried out of the gas exchange properties (namely, photosynthesis, stomatal conductance and transpiration rates), water use efficiency and water relations of two mangrove species, *Rhizophora mucronata* and *Ceriops tagal* at Gazi Bay, Kenya. *Rhizophora mucronata* had significantly higher photosynthetic rates than *C. tagal*. Internal CO₂ concentrations were higher during the wet season than the dry season in both species. Gas exchange properties were correlated positively with photon flux density in both species. Leaf water potentials were highest during the morning and lowest at midday and were also highest in the lower canopy leaves in both species. The two mangrove species had conservative water use. Management potential for the East African mangroves based on the results of this study is suggested.

Key words: gas exchange, irradiance, mangroves, water potential

Résumé

On a réalisé des mesures des propriétés des échanges gazeux (à savoir la photosynthèse, la conductance stomatale et le taux de transpiration), l'efficacité de l'utilisation de l'eau et des relations avec l'eau de deux espèces des mangroves, *Rhizophora mucronata* et *Ceriops tagal*, à la Baie de Gazi, au Kenya. *Rhizophora mucronata* montrait un taux de photosynthèse significativement supérieur à celui de *C. tagal*. Chez les deux espèces, les concentrations internes de CO₂ étaient plus élevées pendant la saison des pluies que pendant la saison sèche. Les propriétés des échanges gazeux ont pu être mises en corrélation positive avec la densité du flux de photons chez les deux espèces. Les potentiels hydriques des feuilles étaient maximaux le matin et les plus bas à midi; ils étaient aussi les plus élevés dans les feuilles basses de la canopée, chez les deux espèces. Les deux espèces des mangroves montraient une utilisation de l'eau conservatoire. On suggère une gestion des mangroves de l'Est africain basée sur les résultats de cette étude.

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Introduction

Taxonomically, the term 'mangrove' refers to a diverse association of woody trees and shrubs that form a dominant vegetation in tidal, saline wetlands along tropical and subtropical coasts. Mangroves occupy about 75% of the coastal fringe between 25° N and 25° S, their distribution being limited by winter frosts (Burns 1977). Geographically, mangrove vegetation may be divided into two main groups: that of the Indo-Pacific region (including Eastern Africa) and that of Western Africa and the Americas.

Kokwaro (1985) pointed out that most mangroves have adapted to their environment through development of mechanical fixation into soft or loose substrata, formation of respiratory roots and aerating devices, evolution of viviparity, use of specialized means of seed dispersal, and development of xerophytic structures in relation to soil salinity.

Anatomically, the leaves of most mangroves show many features in common with that of xerophytes. These features, which include thick cuticles and sunken stomata, have been reviewed in detail by Sidhu (1975). For most mangroves, stomata are restricted to the adaxial leaf epidermis and these epidermal characters would be expected to result in low rates of gaseous exchange. Physiological research on photosynthetic processes in mangroves is important to understand better the adaptive mechanisms that allow individual species to cope with particular environmental conditions of their habitat. East African mangrove forests are of major ecological and commercial importance, yet the future of these resources is threatened by pollution, development and over-exploitation (Kokwaro 1985; Kigomo 1991). There is an urgent need to develop sound management practices that utilize mangrove ecosystem dynamics. A better understanding of physiological processes is essential for the development of more comprehensive and predictive models of mangrove ecosystem dynamics. So far, no research on mangrove ecophysiology has been carried out along the East African coast.

The specific objective of the study was to determine the rate of CO₂ assimilation and related processes of single mangrove leaves located at different positions in the canopy for the two species.

The study site

The study site was located at Gazi Bay ≈ 50 km south of Mombasa. This mangrove area of about 615 ha is not under the direct continuous influence of freshwater (Doute *et al.*, 1981). The site was a secondary mangrove forest characterized by a young mixed stand of *Ceriops tagal* (Perr.) C.B. Robinson and *Rhizophora mucronata* Lam. and a few *Avicennia marina* (Forssk.) Vierh. and *Bruguera gymnorhiza* (L.) Lam. resting on black sandy soil. According to Gallins *et al.* (1989) four types of mangals can be individualized at the study site. The lowermost zone, closest to the sea, is formed of *Sonneratia alba* Sm. Around river-mouths *S. alba* is partly replaced by *R. mucronata*. This species becomes more important higher up and forms a distinct zone especially on silty substrate. Behind the *S. alba* is a zone characterized by a mixed vegetation consisting of *R. mucronata* closest to the channel and *C. tagal*, *B. gymnorhiza* and some *Xylocarpus granatum* Koem. occurring some 15–20 m inland.

The highest zone covered by mangroves is almost a horizontal one. It is inundated by sea water only at spring tides. The tree layer is composed solely of *A. marina*, no epiphytes, but halophytic herbs locally cover the sand. *Lumnitzera racemosa* Willd. shrubs form a narrow fringe towards the Poaceae-Cyperaceae-dominated vegetation that is never inundated by sea water. Between the *S. alba* zone and the mixed mangal zone is a dune-depression area characterized by a series of low dunes (1–2 m high) and depressions which are parallel to the tide channel. Vegetation on the dunes is composed of dense mixed shrub thickets, including *Pandanus kirkii* and *Hyphaene coriacea*.

Materials and methods

Measurement of gas exchange and other variables

Sampling was done in the mixed mangal zone on two mangrove species, *R. mucronata* and *C. tagal*, during two different seasons: dry season (February and March) and wet season (May to August) 1992. CO₂ gas exchange rates of selected recently expanded leaves of the two mangrove species were measured with an ADC LCA-2 portable infra-red gas analyser (The Analytical Development Co. Ltd, Hertfordshire, U.K.) fitted with a modified broad leaf chamber (ADC PLC-2). During the measurements the gas analyser was used in a constant flow rate, variable differential mode.

Measurements were taken hourly from about 08.00 to 17.30 hours. Access to the top of the canopy was made possible by construction of a portable 4 m high tripod ladder. Measurements were made in a sequence, beginning at the bottom and working upwards through the canopy. At each leaf position one leaf was measured for each species. Four leaf positions, 1 m apart, were designated, ranging from 1 to 4 m above ground level. During the measurements, leaves were orientated to the sun's rays to ensure they received maximum incident light.

Carbon dioxide assimilation rate (A), stomatal conductance to water vapour (g_s), transpiration (E), intercellular CO₂ concentration (C_i), leaf temperature (T_l) and leaf to air vapour pressure deficit (VPD) were calculated using the equations adapted from von Caemmerer & Farquhar (1981) and as modified by Long & Hällgren (1985). Water use efficiency (WUE) (mol of carbon gained per mol of water lost) was calculated using the method developed by Farquhar *et al.* (1982). After each measurement of leaf CO₂ assimilation and water vapour exchange the leaf was cut and its water potential (MPa) determined with a portable pressure chamber.

Effects of light on photosynthesis and related variables

The effect of light on photosynthesis was investigated on clear days in August between 09.00 and 11.00 hours on the top leaves of both adult mangrove trees. An intact attached leaf was placed into the leaf chamber and gas exchange parameters recorded. White neutral filter paper was placed on the leaf chamber so that it covered the whole window area and the photosynthetically active radiation (PAR) sensor area. After CO₂ differential had stabilized, gas exchange parameters, photon flux density (PFD) and temperature were recorded and a second filter paper was placed on top of the first. This procedure was repeated until PAR recorded was almost zero.

Table 1. Physiological characteristics of two mangrove species at different levels (heights above ground) in the canopy. A=maximum rate of photosynthesis ($\mu\text{mol m}^{-2} \text{s}^{-1}$), g_s =leaf stomatal conductance to water vapour ($\text{mol m}^{-2} \text{s}^{-1}$), E=transpiration rate ($\text{mmol m}^{-2} \text{s}^{-1}$), C_i =intercellular CO_2 concentration (mbar), and WUE=water use efficiency (no units) \pm SE.

	A	g_s	E	C_i	WUE
Dry season					
<i>Rhizophora mucronata</i>					
1 m	1.792 \pm 0.238	0.0332 \pm 0.0032	0.889 \pm 0.076	104 \pm 14	0.0023 \pm 0.0003
2 m	1.341 \pm 0.131	0.0329 \pm 0.0027	0.876 \pm 0.064	77 \pm 10	0.0018 \pm 0.0002
3 m	1.508 \pm 0.211	0.0331 \pm 0.0027	0.868 \pm 0.054	79 \pm 10	0.0020 \pm 0.0002
4 m	1.474 \pm 0.196	0.0328 \pm 0.0023	0.881 \pm 0.031	80 \pm 10	0.0019 \pm 0.0003
<i>Ceriops tagal</i>					
1 m	1.703 \pm 0.276	0.0316 \pm 0.0027	0.862 \pm 0.057	102 \pm 14	0.0021 \pm 0.0005
2 m	1.241 \pm 0.141	0.0286 \pm 0.0021	0.790 \pm 0.047	79 \pm 9	0.0017 \pm 0.0004
3 m	1.119 \pm 0.101	0.0263 \pm 0.0097	0.783 \pm 0.044	73 \pm 8	0.0016 \pm 0.0003
4 m	0.963 \pm 0.101	0.0279 \pm 0.0029	0.803 \pm 0.061	65 \pm 8	0.0014 \pm 0.0003
Wet season					
<i>Rhizophora mucronata</i>					
1 m	4.150 \pm 0.310	0.0457 \pm 0.0026	0.940 \pm 0.043	128 \pm 10	0.0040 \pm 0.0008
2 m	4.148 \pm 0.333	0.0471 \pm 0.0032	0.928 \pm 0.050	148 \pm 10	0.0046 \pm 0.0011
3 m	3.985 \pm 0.287	0.0452 \pm 0.0029	0.923 \pm 0.052	148 \pm 9	0.0045 \pm 0.0007
4 m	3.867 \pm 0.334	0.0395 \pm 0.0030	0.853 \pm 0.053	159 \pm 9	0.0046 \pm 0.0006
<i>Ceriops tagal</i>					
1 m	3.396 \pm 0.303	0.0475 \pm 0.0042	0.874 \pm 0.049	126 \pm 10	0.0038 \pm 0.0003
2 m	3.247 \pm 0.295	0.0423 \pm 0.0037	0.819 \pm 0.051	136 \pm 10	0.0040 \pm 0.0003
3 m	3.089 \pm 0.243	0.0434 \pm 0.0033	0.857 \pm 0.048	124 \pm 8	0.0039 \pm 0.0003
4 m	3.064 \pm 0.262	0.0430 \pm 0.0037	0.874 \pm 0.053	119 \pm 10	0.0038 \pm 0.0003

Statistical analysis

Statistical analyses of leaf physiological variables were carried out using analysis of variance (ANOVA). The significantly different parameters at the 95% level of confidence were separated using Tukey's Multiple Range Test (Zar 1984). The effects of light on photosynthesis (A), stomatal conductance (g_s), leaf temperature (T_l), transpiration (E) and intercellular CO_2 concentration (C_i) were assessed by fitting regression lines.

Results

CO_2 assimilation rate (A)

Overall, rates of photosynthesis were significantly ($P < 0.001$) higher in *R. mucronata* than in *C. tagal* during the entire study period (Table 1). In both species, photosynthesis rates were significantly ($P < 0.0001$) lower in the dry season than in the wet season.

Variations in rates of photosynthesis in relation to position of leaf in the canopy in either of the seasons were not significant ($P > 0.05$) in *R. mucronata*. There were, however, significant ($P < 0.05$) interaction differences between seasons and leaf positions in the canopy. Mean values of photosynthesis varied from 1.34 to 1.79 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in the dry season and from 3.87 to 4.15 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in the wet season, for

top and bottom leaves, respectively (Table 1). In *C. tagal*, however, the bottom leaves had significantly ($P < 0.01$) higher rates of photosynthesis than the sun' leaves located at the top of the canopy in the dry season. Photosynthetic rates varied from $0.96 \mu\text{mol m}^{-2} \text{s}^{-1}$ for the top leaves to $1.70 \mu\text{mol m}^{-2} \text{s}^{-1}$ for the bottom leaves (Table 1). However, there were significant ($P < 0.05$) differences between seasons.

Stomatal conductance (g_s)

Variations in leaf stomatal conductance between the two species were not significant ($P > 0.05$; Table 1). Comparatively, however, rates of g_s were significantly ($P < 0.001$) lower in the dry season than in the wet season. There were no significant ($P > 0.05$) differences in g_s of leaves at different levels in the canopy during the two seasons for both species (Table 1). Relatively, the topmost leaves had significantly ($P < 0.05$) lower rates of g_s than the bottom leaves (Table 1).

Transpiration rate (E)

Variations among transpiration rates and the relative position of leaf in the tree canopy and between the two species were not significant ($P > 0.05$; Table 1). Significant variations ($P < 0.01$) were, however, evident in the wet season in both species.

Water use efficiency (WUE)

Water use efficiency varied with VPD during the study period (Table 1). Comparatively, WUE in *R. mucronata* was significantly ($P < 0.05$) higher than in *C. tagal* during the wet season. Variations in WUE as related to the relative leaf position in the tree canopy were not significant ($P > 0.05$) in either the dry or wet season in both species.

Leaf water potential (ψ_l)

There were significant differences ($P < 0.001$) in leaf water potential (ψ_l) in relation to the position of the leaf in the canopy, in both species. The topmost leaves were always more water stressed than the bottom leaves: ψ_l varied from -1.6 to -2.5 MPa in *C. tagal* and from -1.7 to -2.7 MPa in *R. mucronata*, the lower values being for the top leaves (Fig. 1).

Diurnal responses of some physiological variables

Vapour pressure deficit (VPD) between the leaf and air was influenced primarily by leaf temperature, but depending on the prevailing ambient relative humidity, individual VPD values as high as 45 mbars were encountered. Diurnal trends between VPD and TI are clearly illustrated in Fig. 2. In both species, VPD and TI were positively and closely correlated. For example, the coefficient of determination (r^2) in *C. tagal* was 0.97 in the dry season but 0.57 in the wet season. In *R. mucronata*, r^2 was 0.86 in the dry season, but the relationship was less obvious during the wet season ($r^2 = 0.26$).

Leaf water potential (ψ_l) showed significant diurnal variations ($P < 0.001$) in both

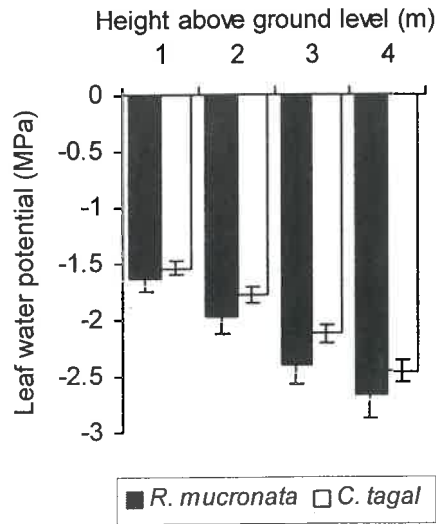


Fig. 1. Relationship between leaf position in the canopy and the corresponding mean leaf water potential (ψ_l) in *R. mucronata* and *C. tagal* under field conditions. Vertical bars are \pm SE of the means.

species. For example on 20 August 1992, ψ_l declined from a value of -2.8 and -3.1 MPa at 09.00 hours (for *C. tagal* and *R. mucronata*, respectively) to an average low value of -4.3 MPa in the early afternoon (Fig. 3). It then increased again rapidly after about 16.00 hours when solar radiation (PFD) had started to show a significant decline.

Leaf water potential became low as rainfall amount decreased in the wet season. ψ_l decreased from a mean of about -1.6 MPa in all the leaf positions in both species in May to about -2.4 and -2.6 MPa in *R. mucronata* and *C. tagal*, respectively, in August 1992. Indeed, in August 1992, daily ψ_l s recorded for single leaves on clear days were as high as -4.6 MPa in *C. tagal* and -4.1 MPa in *R. mucronata*.

Response of photosynthesis, leaf temperature and intercellular CO₂ concentration (C_i) to light (PFD)

At low PFD levels, net photosynthesis increased more or less linearly with PFD, giving an incident quantum efficiency (ϕ) of about 0.017 in both species. There was little linear increase in A beyond PFD of about $800 \mu\text{mol m}^{-2} \text{s}^{-1}$. A initially increased almost linearly with C_i and with PFD, the relationship apparently becoming non-linear at values of $C_i > 130$ mbars in the wet season. Similarly, T_l , g_s and C_i increased almost linearly with increase in PFD, although that of T_l was not explicitly clear.

Diurnal trends in PFD, VPD, T_l and measured gas exchange parameters for the top, exposed leaves of *R. mucronata* and *C. tagal* are shown in Figs 4 and 5, respectively. The two figures represent the dry and wet seasons at Gazi. A notable feature of the data for all diurnal trend experiments is the close positive correlation between CO_2 assimilation rates and stomatal conductances during the wet season.

Seasonal trends in PFD, T_l , VPD and measured gas parameters are as shown in Fig. 6. They depict a close association between T_l , A, E, g_s and trends in rainfall. VPD remained relatively high in the dry season, being 30 mbars or more. In the wet

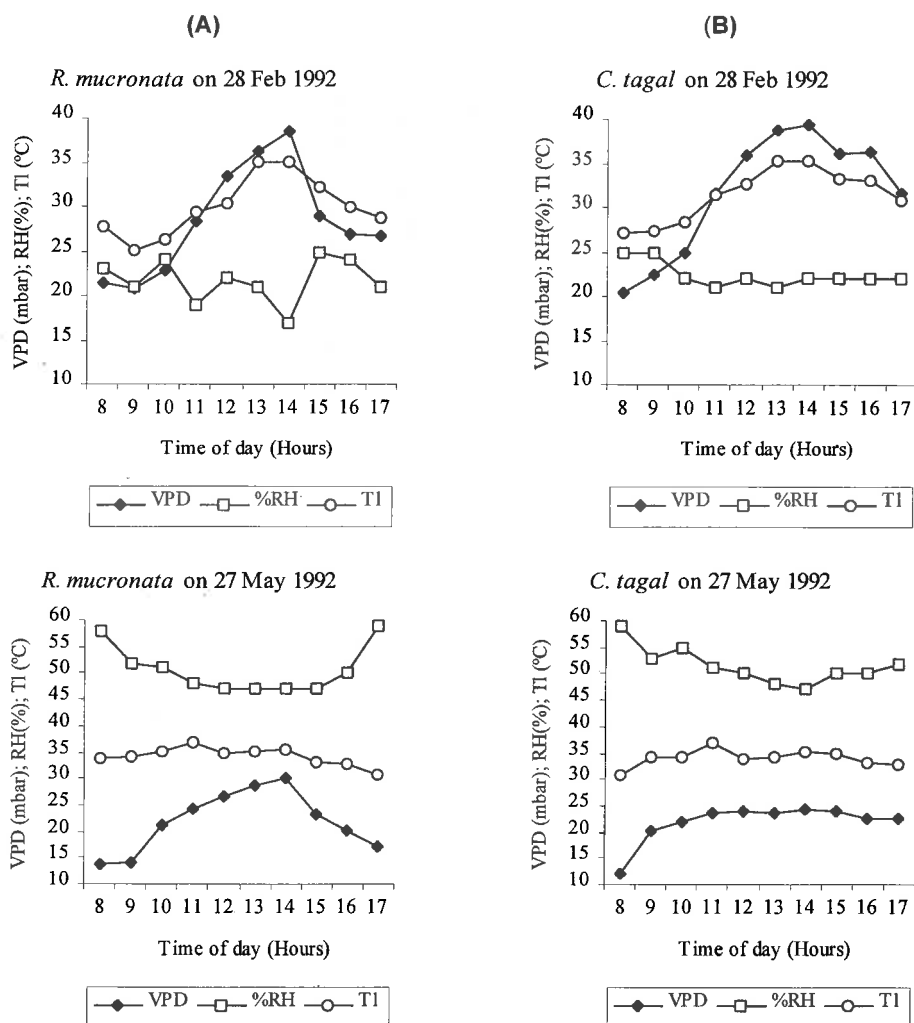


Fig. 2. Diurnal trends in vapour pressure deficit (VPD), relative humidity (% r.h.) and leaf temperature (T_l) during the dry (28 February 1992) and wet (27 May 1992) season for the topmost leaves of: (A) *R. mucronata* and (B) *C. tagal* under field conditions.

season, however, optimal VPD values of about 20 mbars and below persisted. PFD values in the dry season averaged about $1500 \mu\text{mol m}^{-2} \text{s}^{-1}$ and dropped to an average of $1100 \mu\text{mol m}^{-2} \text{s}^{-1}$ in the wet season. Clear skies characterized the dry months, whereas the wet season had varying degrees of cloud cover.

Discussion

The results indicated that gas exchange characteristics of Rhizophoraceae mangroves exhibited diurnal and seasonal shifts in metabolic patterns of photosynthesis, with highest values in the morning. Seasonally, the highest values occurred in the wet season. *Rhizophora mucronata* showed less resistance to CO_2 exchange than *C. tagal*

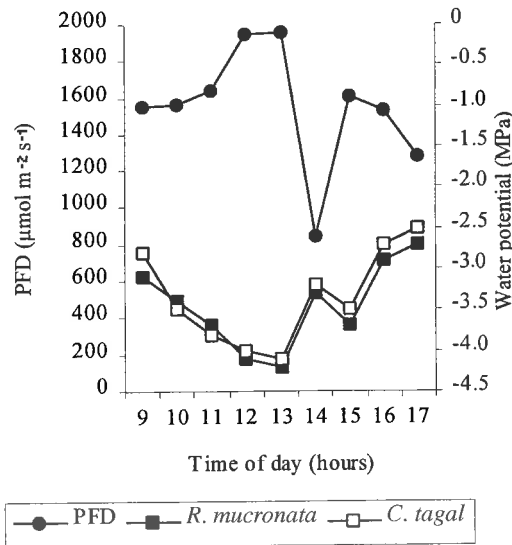


Fig. 3. Changes in photon flux density (PFD) and leaf water potential (ψ_l) in exposed top leaves of: (A) *R. mucronata* and (B) *C. tagal* on 20 August 1992.

due to its relatively higher rates of stomatal conductance. As a result, *R. mucronata* had consistently higher rates of photosynthesis than *C. tagal*. Stomates were widest open to allow CO_2 influx in the morning up to about 10.00 hours and were partially open in the afternoon and to some extent in the evening as evidenced by g_s rates. From the individual plant curves it appeared that much of the variability in A arose from stomatal behaviour, which could occur if leaf water deficits were at a level where stomata are sensitive to changes in water deficit. During the course of the day, values of ψ_l were low in the afternoon, primarily due to higher PFD and higher T_l that caused significant stress in the plants.

Maximum rates of photosynthesis observed in this study were moderately low, rarely rising above $5.0 \mu\text{mol m}^{-2} \text{s}^{-1}$ in the wet season and remaining well below $2.0 \mu\text{mol m}^{-2} \text{s}^{-1}$ in the dry season. Rates well above $25 \mu\text{mol m}^{-2} \text{s}^{-1}$ have been reported for field situations in the luxuriant mangrove forests of the Asia-Pacific Region (Moore *et al.*, 1973). More commonly, rates of net photosynthesis in the field lie in the range of $5\text{--}20 \mu\text{mol m}^{-2} \text{s}^{-1}$. The calculated quantum efficiency (ϕ) for both species was 0.017. Aksornkoae *et al.* (1991) found a ϕ -value of 0.019 for both *Bruguiera parviflora* and *Rhizophora apiculata* in Thailand. Normally, for *Rhizophora* species, values of 0.03 or higher would be expected (Tsilemanis, 1988). Presently, there are no data available on photosynthetic gas exchange characteristics of mangroves in East Africa that can be used for direct comparison with those obtained in this study. However, our data seem realistic by comparison with data from Florida mangrove species (Clough & Sim, 1989).

Anatomically, the stomata of mangroves are adapted so that gaseous exchange between the air space inside the leaf and external air is restricted considerably to prevent excessive water losses (Ball, 1988). This means that at the level of intact leaves, photosynthetic rates are a function of the ease with which stomata allow CO_2 to enter the leaf, and the biochemical capacity of the leaves to fix CO_2 . At the

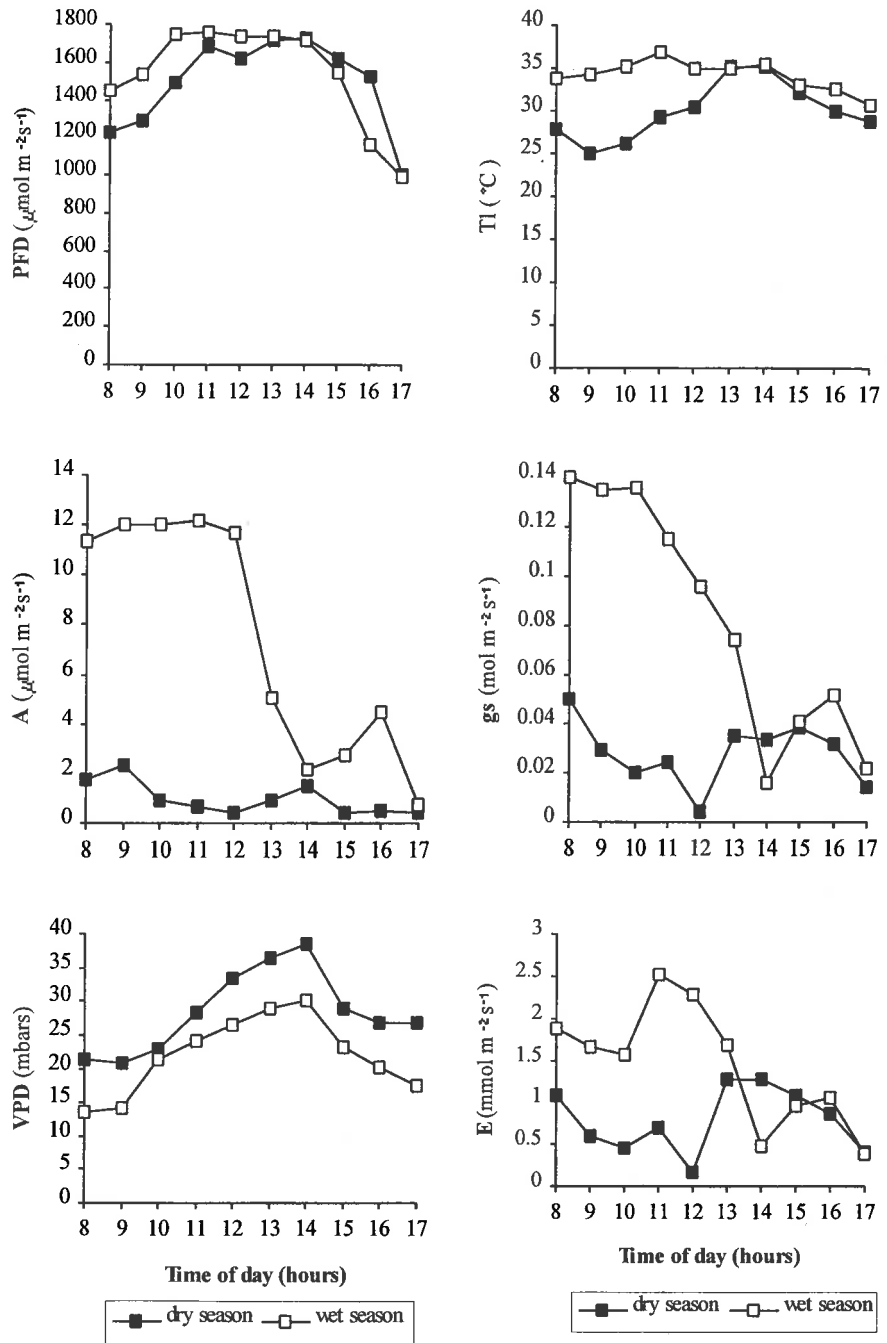


Fig. 4. Changes in photon flux density (PFD), vapour pressure deficit (VPD) and measured gas exchange parameters: CO₂ assimilation rate (A), stomatal conductance (g_s), and transpiration (E) in exposed top leaves of *R. mucronata* in the dry (28 February 1992) and wet (27 May 1992) seasons.

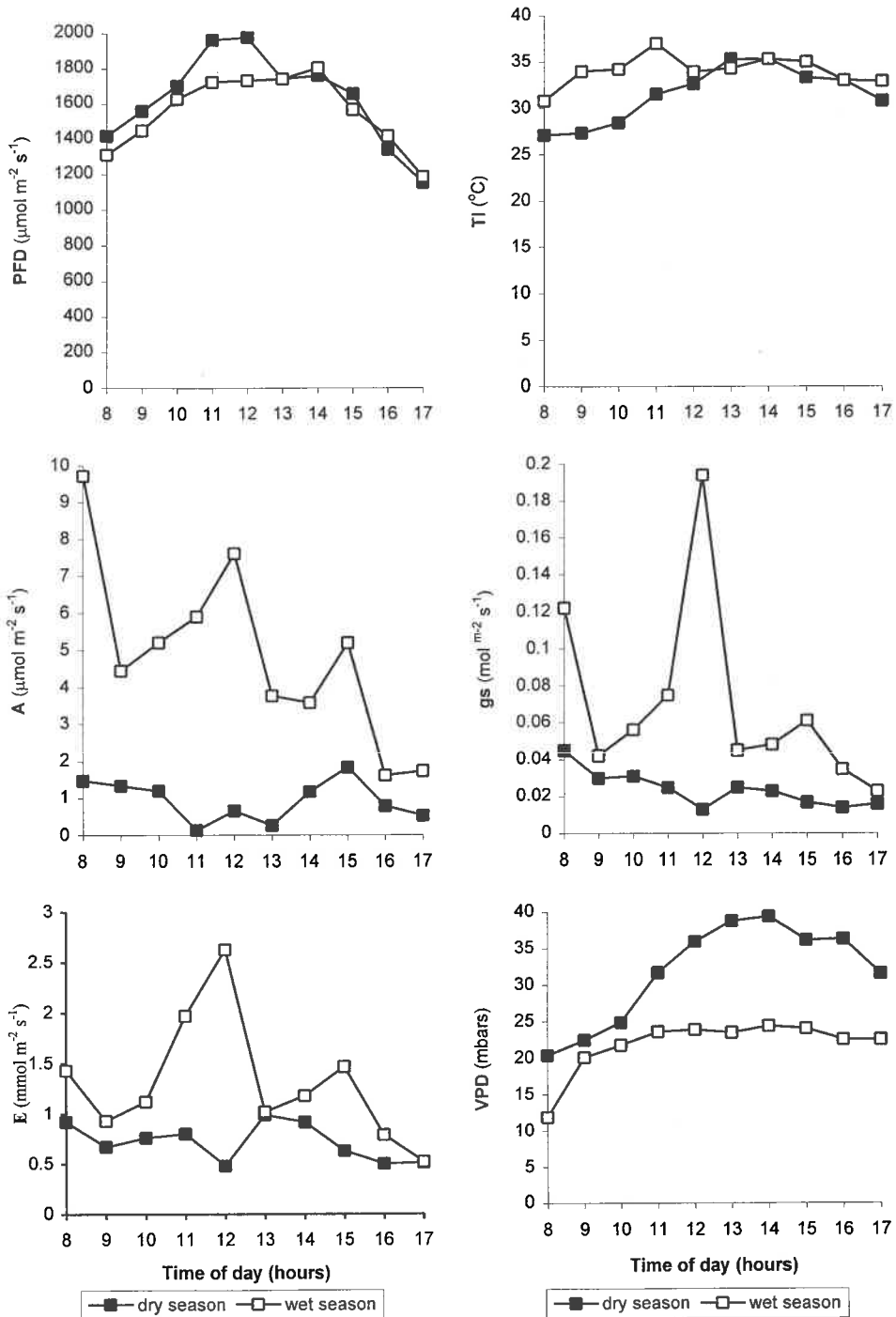


Fig. 5. Changes in photon flux density (PFD), vapour pressure deficit (VPD) and measured gas exchange parameters: CO_2 assimilation rate (A), stomatal conductance (g_s), and transpiration (E) in exposed top leaves of *C. tagal* in the dry (28 February 1992) and wet (27 May 1992) seasons.

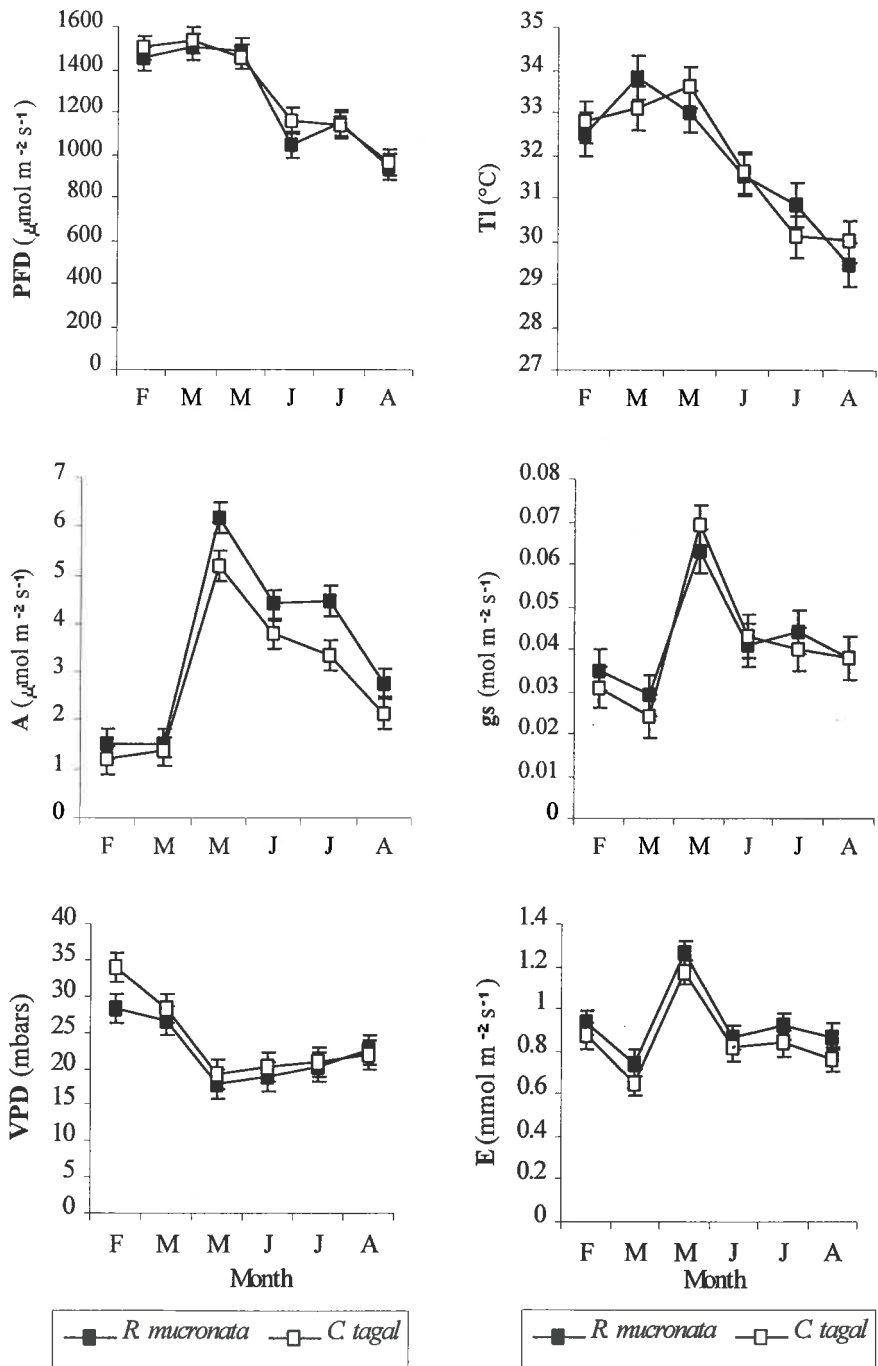


Fig. 6. Monthly changes in photon flux density (PFD), leaf temperature (TI), vapour pressure deficit (VPD), and measured gas exchange parameters: CO₂ assimilation rates (A), stomatal conductance (g_s), and transpiration rates (E) in leaves of *R. mucronata* and *C. tagal* under field conditions.

biochemical level the amount and properties of CO₂ carboxylation enzyme ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCO) may strongly influence gas exchange characteristics in mangroves. Essentially, the control of stomatal behaviour in mangroves remains coupled with metabolism when challenged by changes in the environment, except under extreme environmental conditions, for example, high insolation, high temperature and water stress, when such control may be lost (Ball, 1986).

The rate of transpiration throughout the day was related directly to levels of g_s and VPD (Figs 4 and 5). Substantial regulation of E by sensitive stomatal responses has been observed with several conifers and some herbaceous angiosperms (Jarvis, 1980). Stomatal responses to humidity may reflect a mechanism that prevents extreme water loss and extreme water deficits when plants are subjected to extreme evaporative demands. According to Lange *et al.* (1971), stomatal response to humidity is mediated by cuticular transpiration of the outer epidermis.

Photosynthetic capacity was correlated closely and positively with maximum g_s in both species in the wet season (*R. mucronata*, $r^2=0.91$; *C. tagal*, $r^2=0.64$). The way in which A and g_s are correlated appears to have great ecological significance. Schulze & Hall (1982) documented that if during variations of environment or plant internal conditions, A and g_s change proportionally in a straight line relationship which passes through the origin, intercellular CO₂ concentration, C_i , remains constant. Furthermore, if leaf temperature and atmospheric vapour pressure do not vary, WUE also remains almost constant. In our study, the linear relations did not pass through the origin, which suggests that either stomatal conductance or CO₂ assimilation responded strongly to changes in environment or plant internal conditions. As such, C_i and WUE are not maintained constant; C_i decreases whenever g_s is more affected by changes of environment or plant internal conditions than A.

Water use efficiency is one outstanding feature of the gas exchange characteristics in mangroves and when compared with that of other C₃ plants growing under similar conditions it is unusually high (Ball, 1986). Although mangroves grow in an abundance of water, conservative water use in mangroves is an important adaptation in coping with the saline environments, in which the ability to grow depends to a large extent on the maintenance of salt concentrations within the leaves at physiologically acceptable levels. According to Ball (1988), the high WUE in mangroves is a consequence of the high energy costs incurred in salt exclusion during water uptake and, as a result, mangroves cannot afford to lose extra water like other C₃ non-halophytes.

Restriction of water efflux from the leaves, and hence high water use efficiency, also restricted the rates of CO₂ influx into the leaves, causing the leaves to operate at low C_i . Indeed, C_i levels in the dry season were almost half those encountered in the wet season in the mangrove trees. Thus, conservative water use within the constraints of C₃ photosynthetic metabolism is at the expense of the assimilation rate and hence also the growth rate in mangroves.

In the analysis of light response curve, photosynthesis was apparently saturated at PFD of about 800 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at leaf temperature of about 33–34°C. Although these results were similar in both species, light response characteristics varied slightly from leaf to leaf. Generally, mangroves become light saturated at moderate light intensities, 30 to 50% of incident light in the tropics (600–1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$; Atwill & Clough, 1980). Because of the low stomatal conductances and associated low

light-saturated CO₂ uptake rates, it is clear that the adaptation relates to the need to maintain a high water use efficiency. Low light-saturated rates of photosynthesis imply that mangroves are able to use only a small fraction of solar radiation incident on fully exposed leaves during days of predominantly clear skies. In our study, therefore, the leaves received an abundance of excess excitation energy. This large excess energy may cause excessive excitation of the photochemical apparatus, leading to photodamage. However, most of the excess radiation energy in mangroves is dissipated in the antenna chlorophyll of mangrove leaves rather than from the photochemical centres, thereby protecting the photosystems from damage (Björkman, Demmig & Andrews, 1988) and enabling photosynthesis to continue, but at low values, during the photoperiod.

Water potentials and their diurnal variations were similar to those previously reported for mangroves in the intertidal zone (Scholander *et al.*, 1966). Values at the higher end of the range were recorded in the morning and the lower values during midday and afternoon, when transpirational loss from leaves generally exceeds water intake by the roots. The significant differences in ψ_1 of leaves at the top of the canopy from those at the bottom of the canopy could be attributed to hydrostatic pressure gradients along the xylem.

In the foregoing discussion, it is evidently clear that photosynthesis and hence net primary production and growth rate of mangrove forests is influenced greatly by environmental conditions. Mangroves growing in arid climates are subject to high solar radiation, high leaf temperatures and low ambient relative humidities. Consequently, these trees have high rates of water loss, partial stomatal closure and very conservative water use. High salinities simply worsen the situation. In seasonally monsoon climates, as that occurs along the East African coast, mangrove forests experience arid conditions in the dry season. The Kenyan mangrove ecosystem responds strongly to environmental conditions of the monsoon climate.

Notwithstanding the restriction of growth and primary productivity in mangroves by high light intensity, ψ_1 and VPD, there can still be improvement in the productivity of mangrove forest by more effective management. The present management strategy of East African mangrove forests is to allow natural regeneration of clear-felled areas. This strategy does not result in extensive, closed canopy, and even-aged stands of mangrove forest. Work in Malaysia and Australia (Aksornkoae *et al.*, 1991) suggests that closed canopy, even-aged stands have higher primary productivity and faster growth rates than stands with open canopies.

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