PHOTOSYNTHESIS AND RELATED PROCESSES OF TWO MANGROVE SPECIES: *Rhizophora mucronata* AND *Ceriops tagal* AT GAZI BAY, KENYA

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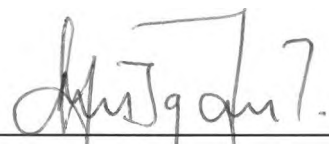
1995

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Dedicated to my wife Wangarî, daughter Warînga and the entire family of Mr. & Mrs. Paul Theuri for their love and understanding.

DECLARATION

I DECLARE THAT THIS THESIS IS MY ORIGINAL WORK AND HAS NOT BEEN

PRESENTED FOR A DEGREE IN ANY OTHER UNIVERSITY

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WE DECLARE THAT THIS THESIS HAS BEEN SUBMITTED WITH OUR APPROVAL AS

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LIST OF ABBREVIATIONS USED

Symbol	Parameter	Unit
A	CO_2 assimilation rate	$(\mu mol\ m^{-2}\ s^{-1})$
Ca	CO_2 concentration in air	(μbar)
Ci	Intercellular CO_2 concentration	(μbar)
E	Rate of transpiration	$(mmol\ m^{-2}\ s^{-1})$
g_s	Stomatal conductance	$(mol\ m^{-2}\ s^{-1})$
PFD	Photon flux density (400 - 700nm)	$(\mu mol\ m^{-2}\ s^{-1})$
T	Temperature	$(°C)$
T_l	Leaf temperature	$(°C)$
vpd	Vapour pressure deficit between the leaf and air	$(mbar)$
Ψ_l	Leaf water potential	(MPa)

ABSTRACT

Measurements were made of the gas exchange properties, water use efficiency and water relations of two mangrove species of the **Rhizophoraceae** family in the dry and wet seasons of 1992 at Gazi Bay, Kenya. The rates of photosynthesis differed significantly (P < 0.001) between the two species, with *Rhizophora mucronata* consistently having higher CO_2 assimilation rates than *Ceriops tagal*. Maximum rates of photosynthesis recorded (CO_2 uptake per unit area of one leaf) in *C. tagal* in the dry season (February-March) ranged from 0.13-5.93 μmol m^{-2} s^{-1} and from 0.13-6.12 μmol m^{-2} s^{-1} in *R. mucronata* with an average of 1.25 and 1.53 μmol m^{-2} s^{-1} respectively. During the wet season (May-August 1992) the saplings of both species had higher rates of net photosynthesis and greater stomatal conductances than their adult mangrove counterparts. Maximum rates of light saturated photosynthesis were 0.26-13.37 μmol m^{-2} s^{-1} in *R. mucronata* saplings and 0.34-8.70 μmol m^{-2} s^{-1} in *C. tagal* saplings with an average of 5.82 and 3.97 μmol m^{-2} s^{-1} respectively. By contrast, maximum rates of photosynthesis in the wet season in the adult mangrove trees ranged from 0.18 - 12.2 μmol m^{-2} s^{-1} in *R. mucronata* and from 0.15-11.5 μmol m^{-2} s^{-1} in *C. tagal* with an average of 4.04 and 3.20 μmol m^{-2} s^{-1} respectively. Similarly, maximum stomatal conductances amongst the saplings in the wet season of 1992 were about 50% greater than those of the adult trees.

The diurnal course in the rates of photosynthesis was such that CO_2 assimilation was high in the morning (between 8 and 10 hours) decreasing thereafter before rising slightly in the evening from about 15 hours. The rates of photosynthesis and stomatal conductances did not show any significant (P > 0.05) variation in relation to leaf position in the canopy. However, the bottom leaves of *Ceriops tagal* had higher CO_2 assimilation rates than the `sun' leaves located at the top of the canopy in the dry season. Proportional changes in the rates of stomatal conductances and CO_2 assimilation were closely and positively correlated in both species and were highly significant (P<0.001). As photosynthesis was measured on leaves exposed to a wide range of light conditions, it was possible to derive approximate photosynthetic light

response curves for leaves of *R. mucronata* and *C. tagal* for the uppermost level in the canopy. Photosynthesis in leaves of both species was light saturated at photon flux densities of about 800 $\mu mol\ m^{-2}\ s^{-1}$ and above. In some cases there was indication that photosynthetic rates may be depressed by photon flux densities above 1900 $\mu mol\ m^{-2}\ s^{-1}$, but the trends were not sufficiently clear to be certain.

Internal CO_2 concentration responded positively to stomatal behaviour in both species, being on average about 82 μbar in the dry season and 136 μbar in the wet season when stomatal conductances increased from about 0.030 to 0.44 $mol\ m^{-2}\ s^{-1}$ in the dry and wet season respectively.

Leaf water potential for both species ranged between -2.1 to -2.4 MPa in the morning and thereafter decreased as solar radiation increased, reaching a maximum of -4.6 MPa at about noon. There were significant differences between the water potentials of shoots at the top of the canopy and those collected from the bottom of the canopy, with water potential becoming more negative with increasing leaf height above the ground. There was a close inverse relationship between water potential and measured gas parameters such as CO_2 assimilation rate and stomatal conductance. Furthermore, there was evidence that even during the late wet season (August), the mangrove trees were operating for at least part of the day at turgor potentials that are close to zero. However, this phenomenon did not induce stomatal closure and photosynthesis continued albeit at low values.

CHAPTER ONE

1.0   INTRODUCTION AND LITERATURE REVIEW

1.1   GENERAL DISTRIBUTION OF MANGROVE ECOSYSTEMS

"Mangrove" is a botanical term referring to a taxonomically diverse association of woody trees and shrubs that form the dominant vegetation in tidal, saline wetlands along tropical and subtropical coasts. They occupy 75% of the coastal fringe between 25 °N and 25 °S, their distribution being limited by winter frosts (Burns, 1977). Odum and Heald (1975) have documented that the mangrove biome is about 43.1 million hectares worldwide. Geographically, mangrove vegetation may be divided into two main groups: that of the Indo-Pacific region and that of Western Africa and the Americas. The Indo- Pacific region is comprised of East Africa, the Red Sea, India, South-east Asia, Southern Japan, the Philippines, Australia, New Zealand, and the South-eastern Pacific archipelago as far east as Samoa. The West Africa - Americas region include the Atlantic coasts of Africa and the Americas, the Pacific coast of tropical America, and the Galapagos Islands. Distribution of several species found only in the mangrove swamps are shown in Fig. 1.

Figure 1 shows that (a) the greatest number of genera and species occur along the shores of the Indian and Western Pacific oceans, (b) there are no species common to East and West Africa, and (c) the species of the Americas and West Africa are taxonomically related. There are approximately 80 species of mangroves throughout the tropical and subtropical regions of the world. The largest number occur in South-east Asia (65 species) while a small number (11 species) occur in the New World tropics (Walsh, 1974). Macnae (1968) describes five basic requirements for extensive mangal development. These are (a) temperatures well above 20°C with a temperature range not exceeding 5°C, (b) fine-grained alluvial soils rich in organic matter necessary for growth of seedlings, (c) protected shores free of strong wave and tidal action because strong waves and tidal actions uproot seedlings and carry away soft mud,

Figure 1

Generalized distribution of mangroves.

Above: approximate limit for all species (eastern and western groups).

Below: histograms showing approximate number of mangrove species per 15° of longitude demostrating the floristic richness of the Eastern group (after Tomlinson, 1986)

Western mangroves   Eastern mangroves
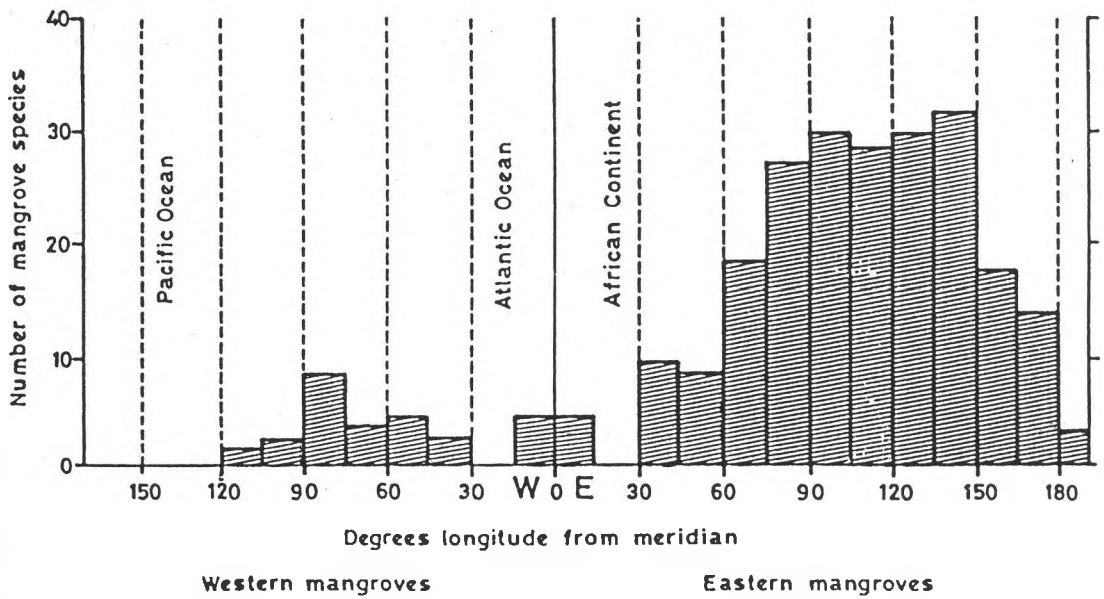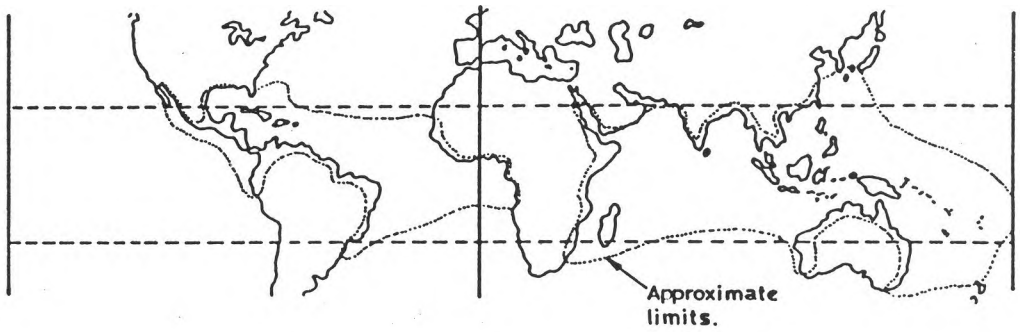
(d) salt water which exclude competition with fresh-water plants, and (e) a large horizontal tidal range on which a wide belt of alluvium will be formed and on which saline water will be distributed far inland.

1.2   ADAPTATIONS OF MANGROVES

While mangroves have proven ability to function in poorly oxygenated water-logged rhizosphere poor in nitrogen and phosphorous (Boto, 1982) and variable but high salinities (Bunt *et al.*, 1982), mangroves must also endure prolonged exposure to high irradiance and leaf temperatures even when stomatal conductances and photosynthetic rates are extremely low (Björkman *et al.*, 1988). Still mangrove survival and dominance are not compromised, and in the central tropical portions of their range, mangrove canopies reach heights of more than 40 m (Tomlinson, 1986).

Warming (1883) pointed out that most mangroves have adapted to their environment through (a) development of mechanical fixation into soft or loose substrata, (b) formation of respiratory roots and aerating devices, (c) evolution of viviparity, (d) use of specialized means of seed dispersal, and (e) development of xerophytic structures in relation to soil salinity.

To survive in the anaerobic, water-saturated rhizosphere, a number of adaptations in root morphology are typical of mangroves. The roots may be prop (from lower part of stem) or drop (from branches and upper part of stem) that terminate a few centimeter in the ground, for example in *R. mucronata*. In other cases horizontal roots (cable roots) grow out of the stem base and produce erect aerial roots (pneumatophores), for example in *Avicennia marina*. Mangrove roots are shallow rooted and have numerous lenticels and extensive aerenchyma which increases the availability of oxygen to roots growing in oxygen deficient sediments other than their normal function of absorption of nutrients and anchoring (Tomlinson, 1986). A common feature of mangroves is viviparity, meaning the embryo initiates germination from the seed while still on the tree. This enables the radical and hypocotyl to develop more rapidly on the loose substratum when washed ashore or when the propagule sinks directly into the mud after falling from the tree (Rabinowitz, 1978). Walter and Steiner (1936) concluded from studies in East Africa that mangrove

zonation was related to the capacity of mangroves to compete and survive in saline soils. This argument on zonation was propagated further by Rabinowitz (1978) on the dispersal properties of mangrove propagules. Species normally found at the higher elevation on the landward edge of the intertidal zone produce small propagules while those found on the seaward edge of the swamp have large heavy propagules, for example *R. mucronata*.

Anatomically the leaves of most mangroves show many features in common with that of xerophytes. These features, which include thick cuticles, wax coatings, sunken stomata and the presence of various storage tissues, have been reviewed by Macnae (1968), Walsh (1974), and in more detail by Sidhu (1975). For most mangroves, stomata are restricted to the lower leaf epidermis with the exceptions of the genera *Sonneratia* and *Osbornia* and the family Combretaceae (e.g. *Lumnitzera, Languncularia*). These stomatal and other epidermal characters would be expected to result in low rates of gaseous exchange with the leaf's environment. Indeed the reported maximum leaf conductances for water vapour exchange in mangroves are low, typically less than 0.13 mol m^{-2} s^{-1}, implying that the supply of water to the mangrove leaf is indeed limiting (Clough *et al.*, 1982). Only a few genera of mangroves (*Avicennia, Aegiceras, Aegitalis, Acanthus*) appear to posses salt-secreting glands in their leaves which function in the exudation of concentrated salt solutions from the plants (Sidhu, 1975). However all mangroves exclude salt at the roots, those possessing salt secretion glands being the least effective at root salt exclusion (Clough, 1984).

1.3   MANGROVES ZONATION - SALT TOLERANCE RELATION

The existence of often monospecific mangal zones is evident in many mangrove communities. Mangrove zonation is a regular series of vegetational bands parallel to the coastline although it is modified by local topography (Lugo and Snedaker, 1974). Zonation patterns are related to freshwater influences and to the frequency and duration of tidal inundation. These two factors combine to modify the edaphic environment by influencing the availability of nutrients, the degree of anaerobiosis of the substrate, and the salinity of the ground-water (Clough and Andrews, 1981). The position of an individual species in the

zonal sequence is presumably an expression of its physiological aptitude for the particular edaphic conditions which exist there, and to competitive interactions between species.

The productivity of mangroves is generally lower in the more elevated parts of the zonal sequence from the seaward fringe to the landward margin where tidal inundation is less frequent and of shorter duration, and where freshwater influences are mostly minimal (Clough and Andrews, 1981). This may be correlated with limited availability of nutrients and/or higher salinity because increasing salt tolerance have two major implications for the organization of mangrove forests along salinity gradients (Ball *et al.*, 1988; Ball, 1988a). First, the carbon cost of water uptake increases with increasing salinity and is greater in the more salt tolerant species. This is manifest in the field by increase in root biomass along gradients of increasing salinity. The root biomass of tropical mangrove forests is generally greater than that measured in other forests (Komiyama *et al.*, 1987). Second, water use becomes increasingly conservative with increasing salinity and with increase in the salinity tolerance of the species (Ball and Farquhar, 1984b; Ball, 1988a; Ball *et al.*, 1988). This is manifest in the field by the decreasing degree of canopy coverage along gradients of increasing salinity.

Enhancement of the two attributes is at the expense of the growth rate, such that species tolerant of broad ranges of salinity tend to grow more slowly than less tolerant species even under optimal conditions, for example *C. tagal*. Species tolerant of lower ranges of salinity such as *R. mucronata* and *Bruguiera gymnorrhiza*, operate with lower water-use efficiency and hence can maintain larger leaves with greater projected leaf areas than those with greater tolerance. Under low salinity conditions, stands of these species have dense canopies that allow little transmission of light to the forest floor. In contrast species that are highly salt tolerant operate with very high water-use efficiency and hence maintain small leaves with a low proportion of projected leaf area. This slow growing species characteristically forms stands with open canopies, which under low salinity conditions could not exclude the rapidly growing, dense canopied species characteristic of low salinity environments. Thus, despite growing maximally under low salinity conditions, the attributes that enable species such as *C. tagal* to tolerate high saline conditions appear to exclude it from being an effective competitor under low salinity conditions. Indeed vigorous

individuals of *C. tagal* occasionally occur in low salinity environments, but the species is limited largely to high saline habitats where competition from other species is reduced or absent (Ball, 1988b).

1.4   IMPORTANCE OF MANGROVES

1.4.1   ECOLOGICAL ROLES

Functional aspects of mangrove swamps started appearing only since the early 1970s (Odum & Heald 1972; Lugo and Snedaker 1974; Teas 1976). The researchers identified four major ecological roles of the mangrove ecosystem:

(a) Mangroves aid soil formation by trapping debris. Davis (1940) demonstrated that prop roots and pneumatophores accumulate sediments in protected sites and form mangrove peats. The filamentous algae growing on the pnuematophores, rhizosphere and knee roots of mangroves also help to stabilize the fine sediments trapped by mangroves, usually forming a green-to-red felty mass over the substratum. In this way mangroves prevent excessive shifting of coastlines, buffer the destructiveness of wind and storm tides and are particularly important on coasts that are subject to major tropical storms (Tomlinson, 1986).

(b) Mangroves filter runoff as well as removing terrestrial organic matter thus ensuring that sea water contain less suspended sediments. This provides conducive conditions for inshore and offshore fish and clean beaches (for tourist attraction) (Tomlinson 1986).

(c) Mangroves serve as habitats for many species. The canopy is inhabited by floristic and faunistic elements from the tropical rain forest, including epiphytes, insects, reptiles, birds and mammals. The surface soil of swamps support animals such as crabs, amphibians, reptiles, air-breathing fishes, and mammals (Macnae, 1968). Throughout the mangal is a network of rivulets, creeks, channels, and often rivers. These contain numerous sessile forms such as algae, fungi, tunicates, sponges, and shellfish which live on mangrove prop roots and aerial roots. Mobile forms such as worms, crabs, shrimps and fish migrate within the waterways in relation to the tidal cycle. The waterways and mudflats are spawning,

nursery and feeding grounds for several species of fish, crustaceans and molluscs, the vast of which are juveniles (Odum and Heald, 1975).

(d) Mangroves are major producers of detritus that contribute to offshore productivity: mangrove litter enters into the detritus food chain as the main source of food for aquatic animal productivity, particularly, the fishes, molluscs and crustaceans (Odum, 1971). The economic utilization of mangroves depends ultimately on their biological productivity. Values for productivity in mangroves has a wide range of values (from about 4 to 9 metric tons ha^{-1} yr^{-1} (Christensen, 1978; 1983; Lugo and Snedaker, 1974; Chai, 1982). The high values may show that mangrove formations are more productive than most marine or terrestrial communities. Moreover, a substantial part of the world fish production depends on mangal ecosystems and local shrimp production is also very significant (Snedaker, 1978).

1.4.2   ECONOMIC USES

Walsh (1974) and Tomlinson (1986) provides a comprehensive review of exploitation of mangrove forests. Populations of the tropical coastal zone of the world have traditionally used mangroves for different purposes, ranging from habitation to defence against invaders. Walsh (1974) points out that in many places mangrove dwellers are totally dependent on the mangroves for fuelwood and timber, for building houses, canoes and construction of bridges between households from mangrove poles, and for rafters, masts and knees of boats. They also extract dyes and other compounds used as medicine, insecticides, antifeedants, dyes and tannin. In Kenya mangrove poles and charcoal have been exported to Iran and Middle East, particularly Saudi Arabia. Overcutting greatly depleted the availability of export grade of poles, leading to a ban on its export by the government in 1982. This was followed later by a ban on charcoal.

Abundant food can be obtained as honey, fish, crustaceans, molluscs and alcohol (from Nypa trees). Human populations living at the fringe of the mangroves regularly visit them to collect food for themselves and fodder for their cattle. The high productivity of mangrove waters, estuarines and tropical lagoons, specially those bordered by mangroves has caused them to be the stage of seasonal migration of

fishermen. Large mammals are hunted for meat, for example dugong and deer. Agricultural use of mangal is directed mostly to its conversion from the forest form and in many places salt-resistant rice varieties have been successfully cultivated, for example, in Sierra Leone (Walsh, 1977). However conversion of the mangal environment to agricultural activities is usually difficult because the previously anaerobic soils, when oxygenated, become highly acidic. More successful conversion for mariculture and aquaculture has been achieved in Philippines and Indochina yielding fish, shrimp and shellfish (Tomlinson, 1986).

At the Kenya coast, breeding ponds as part of the mariculture programme has been set up at Ngomeni for breeding of prawns. However, solar salt production compete with shrimp pond construction for the mangrove areas. Of the 8 existing solar salt farms (salinas), occupying a total area of 9 922 ha. of tidal swamps between Ngomeni and Karawa, 50% of the ponds are located in mangrove zones. Salt production from mangrove swamps, however, has been harmful to the mangrove trees near the salt works. These mangrove trees are subsequently dying off due to underground seepage of highly saline water from the saline pans to the mangrove areas. Further, the diversion of freshwater runoff due to the construction of the salt pans also contribute to the progressive salinization and decay of the mangrove forest. Destruction of mangrove forest for salt production has not only caused the depletion of mangrove trees, but has been attributed to the declining trend in marine fish production owing to the destruction of fish breeding grounds. This has particularly been so in the north coast of Kenya while overcutting has been the major cause in the south coast of Kenya (Kigomo, 1991). Yap and Landoy (1986) found that brine shrimp farming in Kenya could be equal or more productive than salt pond operations and be more advantageous as it does not cause destruction of the mangrove forests. Oysters have been successfully cultivated with little or no mangrove conversion using artificial support for the crop in many parts of the world and in Kenya experimental trials are at an advanced stage at Gazi. This is an activity which could be well combined with mangrove management and conservation.

1.5   PHYSIOLOGY OF MANGROVES

Most of the productivity studies in mangroves are based on litterfall studies, but litterfall is only an indirect measure of the rate of primary productivity and it is not clear if the ratio of litterfall to primary production is fixed for all mangrove forests. Thus, the observed wide range of variations in litterfall rates of different types of mangroves may not necessarily reflect a difference in the rate of primary productivity. Physiological research on photosynthetic processes in mangroves is of fundamental importance to the understanding of adaptive mechanisms which allow individual species to cope with the particular environmental conditions of their habitat and are among the most sensitive indicators of environmental stresses. Golley *et al.,* (1962) found that the bulk of CO_2 assimilation by mangroves was carried out by shade leaves of the tree canopy, a finding that was confirmed by Miller (1972), and that light saturation occurred at 1020 μmol m^{-2} s^{-1} , which is about 50% of incident light in the tropics. Lewis and Naidoo (1970) studied transpiration rates of *A. marina* and found that they were high at mid-morning and low in the afternoon. They attributed the low rates to incipient wilting resulting from excessive transpiration. Joshi *et al.,* (1984) reported that maximum stomatal opening for several species of mangroves were at 10 hours, *C. tagal* and *Lumnitzera racemosa* at 11 hours when most photosynthesis took place. Moore *et al.,* (1973) studied net photosynthesis, dark respiration and transpiration of three mangrove species and found that there were seasonal variations and that highest values occurred in summer.

The photosynthetic characteristics of mangroves are consistent with those of C_3 plants' photosynthetic biochemistry.   Mangrove photosynthesis typically is saturated at moderate light intensities with photosynthetic rates maximal at leaf temperatures less than 35 °C (Moore *et al.*, 1972; 1973; Atiwill and Clough, 1980; Andrews *et al.,* 1984; Ball *et al.,* 1988). High salinities of intertidal mangrove habitats impose high leaf water deficits and low stomatal conductances and hence low photosynthetic rates in mangroves leaves (Björkman *et al.*, 1988). The high leaf water deficit (low water potential) is a direct consequence of the high soil salinity. Low stomatal conductance is a requisite for a low ratio of

transpiration to carbon fixation (high water use efficiency) which is necessary for maintenance of a physiologically acceptable salt-carbon balance within the leaves (Andrews and Muller, 1985; Ball, 1986). Because of high water use efficiency, mangroves are unusually conservative for C_3 species. They become increasingly conservative in water use with increase in the salinity tolerance of both the salt-secreting and the non- secreting species (Ball *et al.,* 1988). Clough and Sim (1989) found that water use efficiency of mangroves increases with increasing environmental stress thereby maximizing photosynthetic carbon fixation while minimizing water loss. Mangroves generally exhibit maximum growth under relatively low salinity conditions, ranging from 5-50% sea water (25 to 250 mM) but differ in the range of salinities over which high growth rates are sustained. The salt concentration of sea water is approximately 35g/l, which in solution includes 483 mM Na^+ and 558 mM Cl^-. Many mangrove species grow best at salinities of 100 to 500 mM which is 8 to 35 parts per thousand (‰) (Clough and Andrews, 1981). According to Clough (1986) the maximum rates of light saturated photosynthesis appear to be little affected by such salinity levels, falling within the range of 9-15 μmol m^{-2} s^{-1} (Atiwill and Clough, 1980; Ball and Chritcheley, 1982; Andrews *et al.,* 1984; Andrews and Muller, 1985) while the Florida mangroves species appear to have lower rate of stomatal conductance and assimilation rates (Moore *et al.,* 1972; 1973). These studies showed that mangrove photosynthesis in the field might be more affected by temperature, irradiance, humidity and partial pressure of CO_2.

In order to maintain a positive water balance mangroves must have tissue water potentials which are lower than the osmotic potential of the substrate. Scholander (1968) measured the hydrostatic pressure potential in the xylem of a number of mangrove species and found values ranging from -2.7 to -5.7 MPa, the higher values of the range being recorded at night. Atiwill and Clough (1980) also obtained similar results. The hydrostatic pressure potential in the xylem ranged from -2.5 to -2.9 MPa at night and averaged -3.5 MPa during the day-time. Generally the highest water potential in mangrove leaves is dictated by the prevailing osmotic potential of the substrate and lies in the range -2.5 to -4.0 MPa. Sea water has an osmotic potential of -2.5 MPa. Aksornkoae *et al.,* (1991) showed that shoot water

potentials of -4.5 to -5.0 MPa were close to the point of zero turgor, but this did not induce stomatal closure or cessation of photosynthesis and net photosynthesis remained positive at all levels in the canopy.

1.6   FUTURE OF MANGROVES

Mangrove forests are of major ecological and commercial importance, yet the future of these resources is threatened by pollution, development and over-exploitation. There is an urgent need to develop sound management practices based on a functional understanding of the physical and biological processes underlying mangrove ecosystem dynamics. Such biological processes include dispersal (Rabinowitz, 1978), herbivory (Smith, 1987) and the physiological bases of species interactions and responses to environmental variables. Understanding these processes is essential for the development of more comprehensive and predictive modelling of mangrove ecosystem dynamics than has been previously possible. Apart from this, very limited research has been done along the East African coast on these lines. This lack of knowledge not only reflects on the local management but also has more general implications on the coastal water resources.

1.7   OBJECTIVES OF THE STUDY

The specific objectives of the study were:

a) to determine the rate of CO_2 assimilation by single leaves located at different positions in the canopy under natural conditions;

b) to determine the rates of CO_2 assimilation of mangrove saplings;

c) to quantify diurnal and seasonal patterns of mangrove photosynthesis and related processes; and

d) to assess the major environmental and physiological factors affecting photosynthesis.

CHAPTER TWO

2.0   THE STUDY AREA

2.1   THE KENYAN MANGROVE ECOSYSTEM

2.1.1   GEOGRAPHICAL DISTRIBUTION

The Kenya coastline extends from 1° 40' S to 4° 41' S. The coastline is approximately 574 km long and runs in the NE-SW direction from Kiunga in the north to Vanga in the south and lies between longitudes 39° 12' E and 41° 20' E. It is relatively little indented, but where there are inlets, they are in the nature of bays (for example Ungwana, Maftaha i.e. Gazi Bay, Funzi) and creeks (for example Dandori, Mongoni, Mida, Kilifi, Mtwapa, Tudor). The continental shelf is relatively narrow along the East African coast, the 100 fathom line being generally 3 to 10 km offshore, except in Lamu where it extends some 45 to 60 km long.

According to Gregory (1896), the physiography of the Kenya coastal region is divisible into 4 main units, namely; Coastal Plain, Foot Plateau (in the south), Coastal Range and Nyika Plateau, occurring in that order from the Indian Ocean westwards. The Coastal Plain, on which the mangroves are found, rises gently from sea level to about 30 meters above mean sea level (a.m.s.l.) and has a width which varies from 4 Km to 10 Km. The Foot Plateau borders on the Coastal Plain and rises westwards initially in a form of broad terraces and then steadily to an elevation of 135m a.m.s.l. The Coastal range rises abruptly west of the Foot plateau to an altitude which varies between 150m and 420m a.m.s.l. The elevation of the Coastal Range drops westwards to about 200m a.m.s.l. where it merges with the Nyika plateau. The Coastal Range is non-existent south of Shimba Hills and Foot Plateau merges directly with Nyika Plateau. Nyika Plateau rises gradually to 900 m. Some exceptions to this are the Shimba Hills and Taita Hills, which rise to over 2000m in places.

2.1.2   CLIMATE

The climate is hot and humid all year round except where altitude gives a cooler local climate. According to Moorjani (1977) the monthly mean air temperature (at Mombasa) is lowest in July-September (24 °C) and highest in March (28.5 °C) and in between there is a gradient of decreasing temperatures. Average monthly temperatures of surface waters along the Kenyan coast range from 24.8 °C (in March-April) to 29.1 °C (in October).

The Kenya coast receives rainfall ranging between 760 mm-1500 mm per annum. The area is characterized by two monsoon seasons; the dry North-east monsoon (November-March) and the wet South-east monsoon (April-October) which is characterized by high cloud, rain, wind energy and decreasing temperature and light. During the North-east monsoons, the situation is reversed. Rainfall decreases from South to North and its reliability increases southwards. Average rainfall from Shimoni to just north of Mombasa is 1270 mm, Kilifi to Malindi 1010 mm and Mambrui to Kiunga 760 mm per annum. North of Mombasa there is a bimodal distribution of rainfall (April-August and October-November) while south of Mombasa the long rain season persist longer and the short rain season begins earlier. In some years there is scarcely a break in the cloudy rain season in the south coast.

Along the coast the relative humidity is high, ranging from 65 to 80% most of the year with a mean diurnal range of 26 - 31%. Relative humidity is usually higher in the mornings than in the afternoons. May, June and July are very humid months whereas, January, February and March are less humid. The mean annual potential evaporation varies between 2000 mm and 2200 mm per annum (Narok Groundwater consultants, 1984). From April to July the hours of bright sunshine per day are shorter than the rest of the year.

2.1.3   SOILS

Geologically the area is diverse with tremendous variations in soil types and fertility. Most soils are derived from sand deposits, limestone or shales. The resulting soils are therefore light and well drained.

Nearer the coast they are sand, but further inland they are a mixture of sands, clays and loams, distributed sporadically. According to Caswell (1953) the rock types show a geological succession from the seaward side to the west. They range from the Quaternary rocks (lagoon sand and coral reef), Tertiary rocks (for example Magarini sands) the Jurassic shales, and Triassic sandstones (for example Maji-ya Chumvi Beds, Mazeras sandstones, Mariakani Sandstones).

2.1.4   SALINITY AND TIDAL CYCLES

The minimum and maximum surface water salinity along the Kenya coast vary little and ranges from 35 to 36‰ (about 500 mM) (Tiensongrusmee, 1991), while the average varies from 34.8‰ in May (end of dry season) to 35.4‰ in December (end of wet season). The North-east monsoon winds brings sea water with a lower salinity from the Malayan archipelago (along the South Equatorial Current and the East African Coastal current). The South Equatorial Current brings sea water with a higher salinity from the North Australian coast because of a northwardly displaced South Equatorial current (Moorjani, 1977; Onyango, 1989). This variation is insignificant as far as the plants of the intertidal and shallow waters are concerned. During ebb tide, water salinities at various seepage points in the mangrove swamps range from 16 to 20‰. (ca. 230 - 285 mM) (Ruwa and Polk, 1986) signifying presence of submarine groundwater discharge. Surface sea layer oxygen content throughout the year is almost at saturation but begins to decrease before the thermocline is reached. On the Kenya coast there are two tidal cycles for every period of somewhat over 24 hours. The levels reached by each tide differ appreciably from the corresponding tide before and after the tide following. The maximum tidal range does not usually exceed 3.8 m but may sometimes be over 4 m.

2.15   MANGROVE VEGETATION

The Kenya coast mangrove forests extend from Vanga in the south to Kiunga in the north (Fig 2). Estimate of total cover of mangrove forest in Kenya vary from different sources, for example, ForestDepartment (1983) 64,436.9 hectares; Doute *et al.,* (1981) 52,980 ha.; Yap and Landoy (1986) 50,000 ha.; World Bank (1990) 61,3985 ha. About 75% of the mangrove forest occurs in the north,

Figure 2

Extent of mangroves along the Kenya Coast (source: Kokwaro, J. O. 1985)
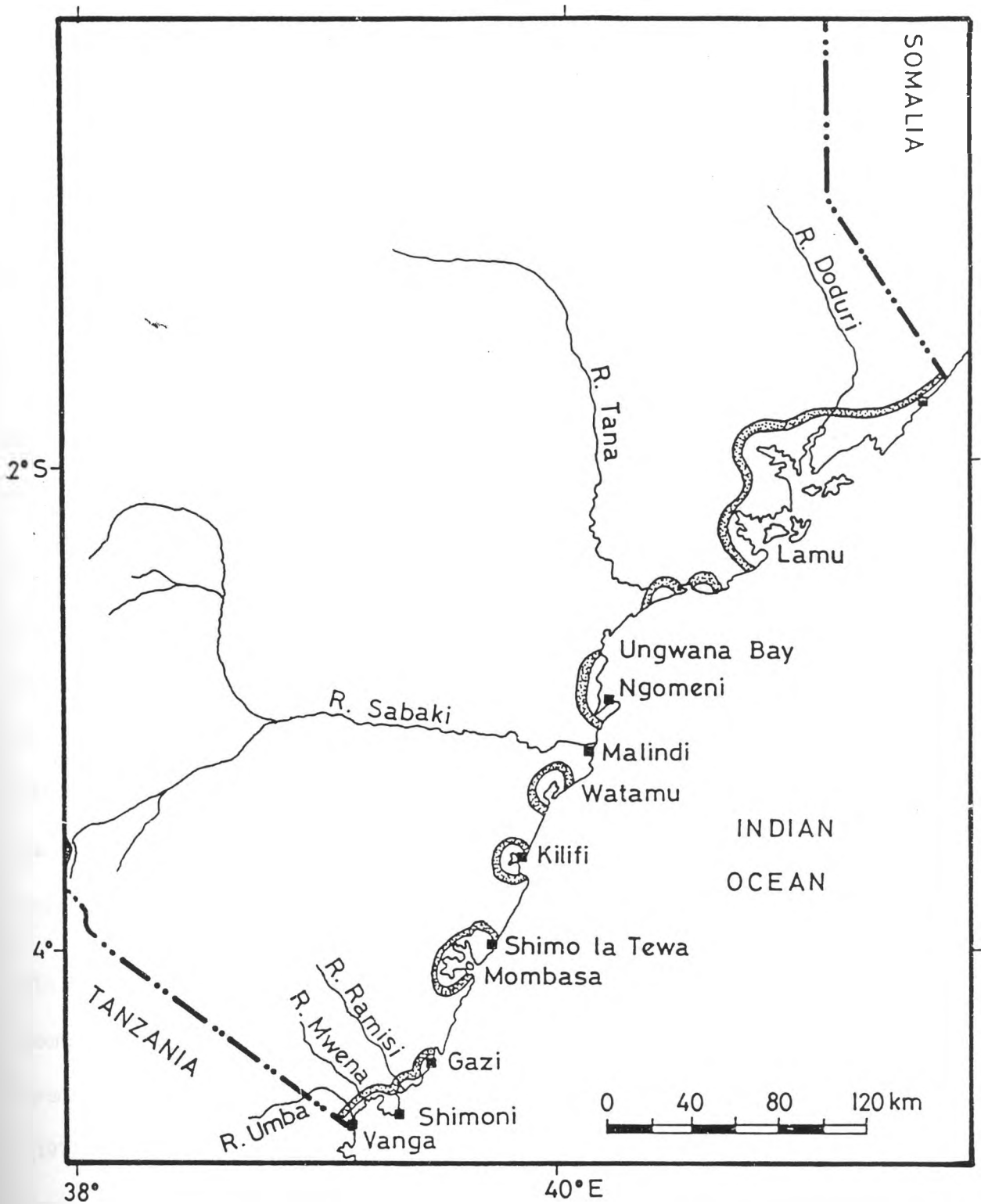
within Lamu area where 46,230 ha. are found (Forest Department, 1983). In the central coast, mangrove swamps occur around Mombasa area, especially Tudor Creek, Port Reitz, Kilifi and Mida Creek. In the southern coast, growth of mangrove forests is found at Vanga, Shirazi and Gazi (Maftaha Bay).

The duration of exposure to sea-water tides influences the distribution of mangrove trees between the low and high water levels within a swamp. This results in variation in nutrient distribution and hence richness. In deeper mangrove swamps, the environment is rich, green in colour indicating high productivity. Soil pH in mangrove swamps is generally at or above the neutral point. However mangrove soils are not suitable for agriculture due to problems of flooding, salinity and the formation of acid sulphate soils when dried (District Environment Assessment Report, 1985).

Results of a survey on horizontal distribution of mangrove trees (Gallins *et al.*, 1989; Speybroeck, 1992) at Gazi indicated that there exists a species zonation from the sea to the shore in regard to differing duration of sea water flooding and corresponds to Walter and Steiner's (1936) description of northern Tanzanian mangroves. Generally the lowermost zone, closest to the sea, is formed by *Sonneratia alba* which is probably the most important pioneer along open coasts. This is followed by a zone of *R. mucronata, Bruguiera gymnorrhiza, C. tagal, A. marina, Lumnitzera racemosa, Xylocarpus granatum* and *Heritiera littoralis* farthest from the sea.

The mangrove ecosystem of the Kenya coast comprises of eight species. The commonest and the most economically important species are *R. mucronata, C. tagal, B. gymnorrhiza, A. marina, S. alba* and *X. granatum* in that order while *L. racemosa* and *H. littoralis* are rare mangrove species. Based on Moorjani (1977) identification key, *R. mucronata* leaves are elliptical and strongly mucronate, with large wide-angled stiltroots. It develops embryos 40-60 cm in length which fall in large scale during June-July period. It attains heights of 20m and diameters up to 40cm. *C. tagal* has simple obovate leathery leaves, slender ribbed embryos, and knee root type of pneumatophores. It may reach the same size as *R. mucronata* in some areas. Unlike *Rhizophora*, leaves of *B. gymnorrhiza* are not mucronate. They are succulent and both sides green. Stilt-roots are small and appressed against the base of the trunk. *X.*

granatum has compound upper leaves consisting of 2-8 leaflets. *A. marina* trees are recognized easily by presence of non-succulent leaves, greyish under-side of leaves and thin, flexible pneumatophores. *L. racemosa* leaf apex is emarginate with an alternate phyllotaxis. Leaves of *S. alba* are orbicular or oval, often fleshy and with thick, tough pneumatophores. *H. littoralis* usually grows along the water margins of swamps and can reach as high as 25 m. The bottom of the tree often has long buttresses and dark or gray fissured bark.

2.2   DESCRIPTION OF THE STUDY SITE

The study site was located at Gazi Bay approximately 50 km south of Mombasa (Fig. 3). This mangrove area of about 615 hectares (Doute *et al.,* 1981) is not continuously under direct influence of freshwater. Both small rivers (Kidogoweni in the north and Mkurumuji in the south) are seasonal and temporal, depending on rainfall more inland. River Mkurumuji is the bigger of the two with a catchment of 175 km inland. It has a maximum flow rate of 5.90 m^3/s and a minimum flow rate of 0.02 m^3/s (Mailu and Muturi 1988). Seepage is restricted to a few points. Average precipitation in this area is 1270 mm/year, spread over approximately 140 days, from May to December. Rainfall recorded between January and September 1992 is as shown in figure 4.

The site was a secondary mangrove forest characterized by a young mixed stand of *C. tagal* and *R. mucronata* and a few *A. marina* and *B. gymnorrhiza* resting on black sandy soil. It was well stocked with about 25% mother trees with an average height of 4-5 m. Though the site was not flooded daily, there was little drainage of the soil between tides. Gazi Bay mangal is part of the major East African Mangal Group (Chapman 1977). This group is characterized by the predominance of *R. mucronata, A. marina, B. gymnorrhiza, S. alba* and *C. tagal* and is not very rich in species. According to Gallins *et al.,* (1989) four types of mangal can be individualized in the study site. The lowermost zone, closest to the sea is formed by *S. alba*. Around rivermouths (e.g. Mkurumuji river) *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* mangal is a zone characterized by a mixed vegetation (with six of the seven species described in Gazi Bay) consisting of *R. mucronata* closest to the channel and *C. tagal, B. gymnorrhiza* and some *X. granatum* occurring some 15-20 m landward. This mangal is developed on an area with varied sediments. Pneumatophores, the rhizosphere and knee roots in these two zones are covered by epiphytic algae (Coppejan and Gallins 1989; De Schryver 1990). The highest zone covered by mangal is sandy and almost horizontal. It is inundated by seawater only at spring tides. The tree layer is composed solely by *A. marina,* no epiphytes, but halophytes such as *Salicornia herbacea* and *Sesuvium portulacastrum* locally cover the sand. *L. racemosa* shrubs form a narrow fringe towards the Poaceae-Cyperaceae dominated vegetation which 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. The depressions are flooded from the northern side (where dunes are absent). The more inland depressions have a central permanent seawater pool. The northern part of the dune-depression system is flooded during mean and spring high tide; the most inland and the southern part are exclusively flooded at spring high tide. Vegetation in the dunes is composed of dense mixed shrub thickets, including *Pandanus kirkii* **Rendle** and *Hyphaene coriacea* **Gaertn**.

For local economies this mangal is useful for the wood it provides, particularly from *R. mucronata, B. gynomrrhiza* and *C. tagal*. Some years ago, the most useful specimens for wood and posts in Gazi were cut by a soap factory at Gazi, the Kenya Calcium Products factory at Tiwi (Kwale district) and presently by the Rio bakery at Gazi and now only big dead stumps and a lot of small trees remain growing. These trees are also being cut for the construction of houses in Gazi village while others are commercially sold in Mombasa. Because of the scarcity of mangrove firewood being currently experienced, Gazi community now mostly uses the coconut shells for fuel and mangrove wood is gathered to light the fire.

Figure 3

Mangrove forest of Gazi Bay, Kenya
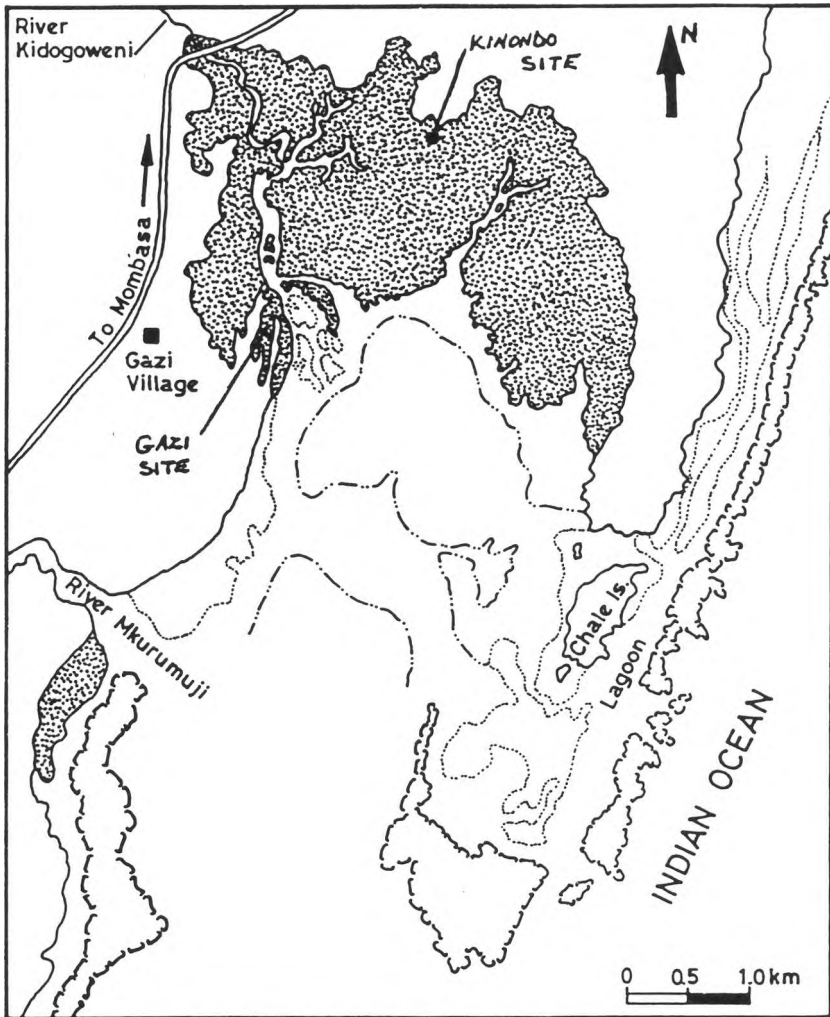
Mangrove

Reefs

Intertidal (bare)

Figure 4

Rainfall distribution at Gazi Bay from January to September 1992

24
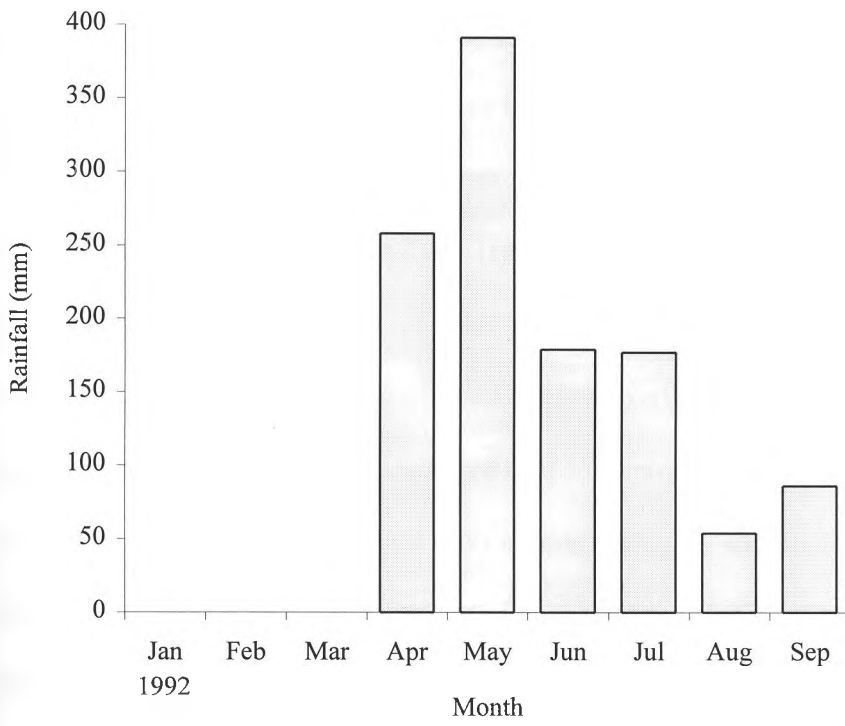
CHAPTER THREE

3.0   MATERIALS AND METHODS

3.1   MEASUREMENT OF GAS EXCHANGE BETWEEN THE LEAF AND THE AIR

Sampling was done in the mixed mangal zone on two mangrove species, *Rhizophora mucronata* and *Ceriops tagal* belonging to the family **Rhizophoraceae** in two different seasons: late dry season (between 24th February and 12th March) and wet season in the months of May (between 20th and 29th), June (between 1st and 8th), July (between 1st and 18th and 25th to 30th), and August (between 1st and 22nd) 1992. CO_2 gas exchange rates of selected leaves of the two mangrove species were measured with an ADC LCA-2 Portable Infra-red Gas Analyser (IRGA) (*The Analytical Development Co. Ltd.*, Hertfordshire, England) fitted with a modified broad leaf chamber (ADC PLC - 2(B)). During the measurements the infrared gas analyser was used in a constant flow rate variable differential method of CO_2 photosynthesis. In this method atmospheric air of measured CO_2 concentration, by the analyser reference stream, (Fig. 5), was passed at a controlled flow rate (300 ml/min) using an air supply unit into the leaf chamber. An intact, fully expanded leaf was placed into the chamber so that it covered the window area of 6.25 cm². Air from the chamber was then sampled using a restrictor T-piece at the analysis. The leaf chamber was fitted with the following sensors: a copper-constantan thermocouples for measurement of leaf and air temperature inside and outside the chamber, thermocouple psychrometry for measurement of vapour density in both air-streams, and a selenium capacitance for the measurement of photosynthetically active radiation (PAR) incident on the leaf.

Measurements were commenced at about 0800 hours, after the leaves were free of dew and continued through every hour until about 1730 hours. Access to the top of the canopy was made possible by construction of a portable 4 m tripod ladder. Because of previous cutting of the mature mangrove
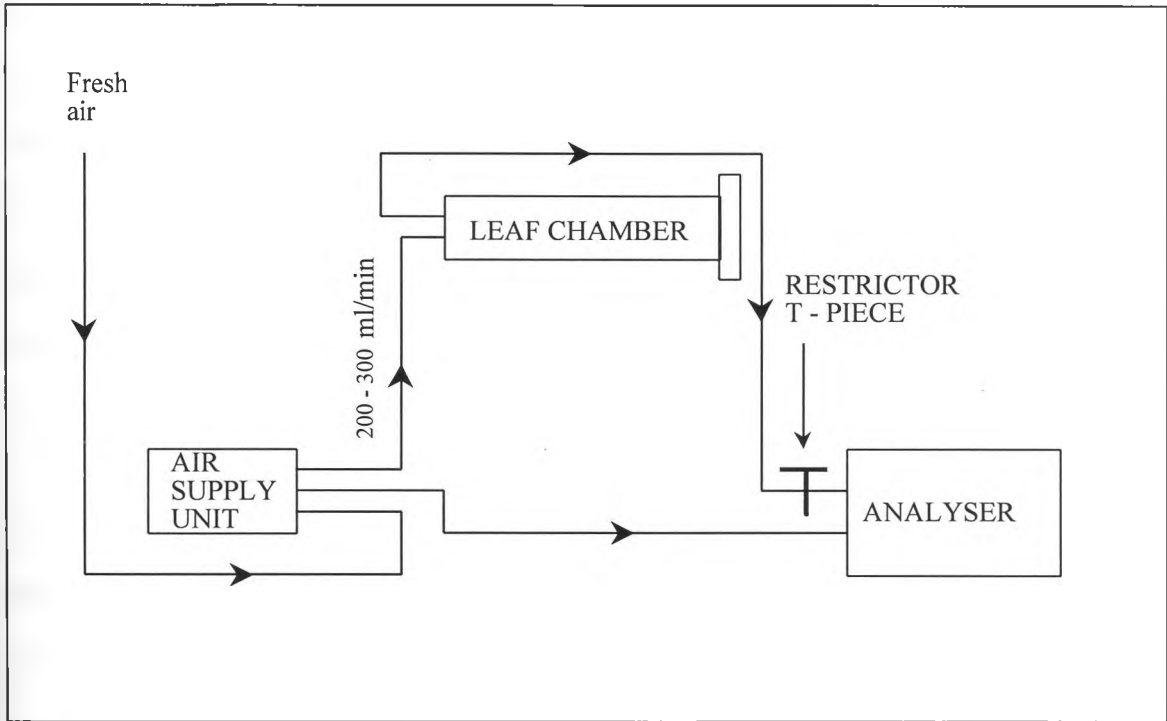
Figure 5

Schematic presentation of the flow of air in the IRGA system

trees in the study site, the open canopy enabled leaves to appear even below 1 m above the ground. Atmospheric pressure was about 950 mbar.

Measurements were made in a sequence, beginning at the bottom and working upwards through the canopy. At each leaf position one leaf was measured every hour in each species, in most cases on the same leaves, in the sun and in varying degrees of cloud cover (shade) throughout the day. Four leaf positions, 1 m apart, were designated, ranging from 1 m to 4 m above ground level. During measurement, leaves were oriented to the sun's rays to ensure they recieved maximum incident light. Other measurements were made on leaves in a nearby part of the canopy where the structure appeared to be similar.

Nursery beds, from where transplanting sapling of *Rhizophora* and *Ceriops* were obtained, were established at Gazi near the fishermen landing bay in October 1991. The nusery was constructed jointly with that of Mr. J. G. Kairo, an Msc student who was undertaking a study on the artificial regeneration of mangroves at Gazi. The nurseries were constructed under the shade of mature *Avicennia marina* trees. The *Avicennia* trees measured over 10 m in height and had a broad canopy created by the branches. The ground level of the *Avicenia* trees was inundated with sea water when a tide of 2.7 m high approached the shoreline. The nursery bed was first ploughed and all vegetation and other debris removed. Plastic pots (27 cm height x 12 cm diameter) were filled with fertile mangrove soil and placed side by side in a nursery bed dug to the level of the paper pots. Side drains with greater depth and width were made around the nursery beds to control the inflow and outflow of tidal water and to reduce waterlogging in the nursery beds.

Mature propagules were harvested from mother trees or litter under trees. Propagules were collected from numerous individuals either by shaking fruiting branches and picking the fall or by collecting recently fallen propagules from the ground litter. Field collections were made over wide areas from Gazi, Kinondo and Chale Island. A distinct ring like mark (cotyledonary collar) in the hypocotyl, proximate to the plumate, differentiated the young propagules from mature propagules. A mature propagule of

Rhizophora or *Ceriops* has a distinctly longer cotyledonary collar that is yellow in colour. After collection, the propagules were kept in moist plastic bags and stored for not more than three days. In most cases, they were planted in the day of collection. 240 healthy propagules of *R. mucronata* and 280 of *C. tagal* were sworn in the pots at the rate of one propagule per pot.

Transplanting of the propagules from the nurseries began in April, soon after the onset of the long rains that characterize the wet season at Gazi. Planting was done during low tide in marked reforestation sites, at Gazi (mixed mangal zone) and Kinondo, where a second hole was dug to receive each sapling. In most cases the interspace was kept at 1.5 x 1.5 m. Both these sites had similar inundation levels and received tidal water only during spring tides. Due to favourable climatic conditions in April, and minimal transplanting shock of the saplings from the nursery beds to the reforestation sites, very few mortality cases were detected. Measurements of the transplanted saplings (seedlings) of *R. mucronata* and *C. tagal* were made in the wet season from the late month of May 1992. The height of saplings was at or below 1 m above the ground.

In all cases leaves were carefully selected for measurements, usually the third or fourth leaf from the apex of the tree or branch. In the entire study period 575 leaves of adult *R. mucronata* trees were sampled of which 451 leaves had light saturated rates of photosythesis (received photon flux density greater than 800 μmol m^{-2} s^{-1}) and were used in subsequent statistical analysis. Similarly in *C. tagal* trees 563 leaves were sampled of which 437 leaves were used in statistical analysis. Amongst the saplings, 204 leaves of *R. mucronata* and 200 leaves of *C. tagal* were sampled in the wet season of which 173 and 161 leaves of *R. mucronata and C. tagal* respectively, were used in statistical analysis.

Raw data accumulated from the IRGA were transferred into a computer and flux rates of CO_2 assimilation (**A**), stomatal conductance to water (**g$_s$**), transpiration (**E**), intercellular CO_2 concentration (Ci), leaf temperature (T$_l$) and leaf to air vapour pressure deficit (VPD) were calculated using the following

equations adapted from von Cammerer and Farquhar (1981) and as modified by Long and Hällgren (1985):

CO_2 assimilation rate (Fc) (μmol m^{-2} s^{-1}) :

$$Fc = \frac{f}{s} \cdot \Delta c$$

where,

f = mole flow of air (mol s^{-1})

s = leaf surface area (m^2)

Δc = CO_2 differential between reference and analysis streams (mol mol^{-1}).

However, a correction for the increase in water vapour by transpiration was necessary, thus:

$$Fc = \frac{f}{s} \cdot \Delta c \cdot \frac{(1 - Xe)}{(1 - Xo)}$$

where,

X_O = mole fraction of water vapour at leaf chamber outlet (mol mol^{-1})

X_e = mole fraction of water vapour at leaf chamber inlet (mol mol^{-1})

X_O and X_e were calculated from saturated vapour pressure (X_S) at the measured leaf temperature, given the relative humidity (RH) from the analyser:

$$Xo \text{ or } Xe = Xs \cdot \frac{RH}{100}$$

Since all the above equations were in moles, the following equation was used to convert the measured volumetric flow to mole flow of air:

$$f = \frac{fv}{1000} \cdot \frac{1}{22.4} \cdot \frac{273.15}{273.15 + T} \cdot \frac{P}{101.3} \cdot \frac{1}{60}$$

where,

f = mole flow of air (mol s^{-1})

fv = volumetric flow of air (cm^3 min^{-1})

22. 4 = volume in dm^3 of one mole of air at S.T.P.

T = temperature recorded during measurement (°C)

P = atmospheric pressure during measurement (KPa)

Transpiration rate, **E** (mol m^{-2} s^{-1}):

$$E = \frac{f}{s} \cdot \frac{(Xo - Xe)}{(1 - Xo)}$$

Stomatal conductance (g_S) (mol m^{-2} s^{-1}):

$$gs = \frac{E}{Xs \cdot Tl - Xo}$$

where,

Xs = mole fraction of water vapour at saturation assuming the leaf is saturated with water vapour at the actual leaf temperature Tl

Internal CO_2 concentration, Ci:

$$Ci = Co - \frac{(Fc \times 1.6)}{gs}$$

where,

Co = mole fraction of CO_2 in outlet air from leaf chamber given by (Ce-Δc) from reference and differential measurements (μmol mol^{-1})

1.6 = ratio of diffusivity of CO_2 and water in the air.

Calculations of vapour pressure deficit (VPD) followed the method of Buck (1981):

$$VPD = e_o - e_s$$

where,

e_0 = vapour pressure of water of air in the chamber

e_S = saturated vapour pressure at chamber air temperature given by:

$$es = 6.13753. Exp\left[ta(18.564 - \frac{ta}{2544.4}) \div (ta + 255.57)\right]10^{-3}$$
where,

ta = air temperature

$$e_o = e_s \cdot \frac{he}{100}$$

hc = % relative humidity in chamber.

Water use efficiency (mol of carbon gained per mol of water lost) was calculated using the method developed by Farquhar *et al*., (1982):

$$WUE = \frac{A}{E} = \frac{(ca - ci)}{\Delta w \times 1.6}$$

where,

Ca = ambient CO_2 concentration

Ci = intercellular CO_2 concentration

Δw = vapour pressure difference between the leaf and air

1.6 = ratio of diffusivity of CO_2 and water in the air

3.2 EFFECTS OF LIGHT ON PHOTOSYNTHESIS AND RELATED VARIABLES

Effect of light on photosynthesis was carried out on clear days in August between 9:00 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. A white filter paper was placed on the leaf chamber so that it covered the whole window area and photosynthetically active radiation (PAR) sensor area. After CO_2 differential had stabilized gas exchange parameters, photon flux density, and temperature were recorded and a second filter paper placed on top of the first. This procedure was repeated until PAR recorded was almost nil. Effects of light on photosynthesis, stomatal conductance, leaf temperature, transpiration and internal CO_2 concentration were assesed by fitting regression lines.

3.3 WATER RELATIONS IN MANGROVES

Studies were made of the water relations of the two mangrove species in the wet season when nitrogen gas became available from the East African Oxygen Company, Mombasa. The studies were made in

order to assess some of the more important environmental and ecophysiological parameters influencing primary productivity. Changes in the xylem pressure potential of *R. mucronata* and *C. tagal* leaves on days with different weather patterns during daylight hours were measured with a pressure bomb (*PMS Instrument Co.* USA model 1000) and the initial balancing pressure determined. In this technique a detached shoot is enclosed within a sealed pressure bomb and a measured positive pressure is progressively applied until leakage from the cut xylem begins. This critical positive pressure is assumed to represent the negative pressure that was in the xylem at the time the shoot was detached, since it restores water to the previous volume state. Leaves previously used for determination of gas exchange parameters were detached at each leaf position and used for determination of leaf water potentials.

Statistical analysis (ANOVA) was performed on data collected at saturating light during the study period. The significantly different parameters at the 95% level of confidence were separated using Tukey's Multiple Range Test (Zar, 1984). Regression lines were used to correlate various relationships.

3.4   MEASUREMENT OF SOIL SALINITY

Soil salinity was measured in the mixed mangal zone during neap tides in the wet season. Soil samples were collected from designated randomly distributed plots between 5cm to 30cm in depth where mangrove roots develop. In each of the 9 plots selected (measuring 10m x 10m) 5 holes were dug randomly using a soil auger and the soil samples mixed together. The samples fresh weights were determined using an electronic, portable weighing balance before they were taken to the Kenya Marine and Fisheries Research Institute laboratories, Mombasa, for drying. Soil samples were dissolved in distilled water in the ratio of 1:4 and after mixing thoroughly salinity of the solution was measured with a hand held reflectometer (Kogo, 1985).

CHAPTER FOUR

4.0 RESULTS

4.1 CO_2 ASSIMILATION AND STOMATAL CONDUCTANCES RATES OF   ADULT MANGROVE TREES

Overall, rates of photosynthesis were significantly (P<0.001) higher in *R. mucronata* (degrees of freedom, d.f.$(3, 451)$ (n = 451) than in *C. tagal* (d.f.$(3, 437)$ (n = 437) during the entire study period. *R. mucronata* had an average rate of photosynthesis of about 3.9 µmol m^{-2} s^{-1} while *C. tagal* had values of about 2.55 µmol m^{-2} s^{-1}. In both species photosynthetic rates were significantly (P<0.0001) lower in the dry season than in the wet season. In *R. mucronata* mean rate of photosynthesis was 1.53 µmol m^{-2} s^{-1} in the dry season, increasing to 4.04 µmol m^{-2} s^{-1} in the wet season. Similarly in *C. tagal* mean photosynthetic rate in the dry season was 1.25 µmol m^{-2} s^{-1}, but increased to about 3.20 µmol m^{-2} s^{-1} 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*. Mean Values of photosynthesis varied from 1.34 to 1.79 µmol m^{-2} s^{-1} in the dry season and from 3.87 to 4.15 µmol m^{-2} s^{-1} in the wet season (Table 1a). 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 µmol m^{-2} s^{-1} for the exposed leaves to 1.70 µmol m^{-2} s^{-1} for the bottom leaves (Table 1a).

Variations in leaf stomatal conductance to water between the two species were insignificant (P>0.05), remaining at a mean value of about 0.039 mol m^{-2} s^{-1} in *C. tagal* and 0.041 mol m^{-2} s^{-1} in *R. mucronata* during the study period. Comparatively, however, rates of stomatal conductance were significantly (P<0.001) low in the dry season than in the wet season. In *C. tagal* stomatal conductances were stable at about 0.029 mol m^{-2} s^{-1} in the dry season increasing to about 0.044 mol m^{-2} s^{-1} in the wet season, while in *R. mucronata* leaf stomatal conductances were 0.033 and 0.044 mol m^{-2} s^{-1} in the dry and wet season

respectively. Because CO_2 influx into the leaf mesophyll is partly a function of stomatal aperture, differences in stomatal conductance between the dry and wet seasons were positively reflected in the variations of intercellular CO_2 concentration (Ci). During the dry season Ci in the leaf mesophylls of both species were in the range of 65-100 µbars whereas in the wet season Ci was in the range of 120-160 µbars (Table 1a).

There were no significant (P>0.05) differences in leaf stomatal conductance of leaves at different levels of tree canopy during the two seasons in both species (Table 1a). In *R. mucronata* rates of stomatal conductance remained at a mean value of about 0.033 mol m^{-2} s^{-1} in the dry season. However, during the wet season, stomatal conductance varied from 0.040 to 0.047 mol m^{-2} s^{-1}, with the lower values being obtained from the uppermost leaves at the top of the canopy. In *C. tagal* conductances varied from 0.026 to 0.032 mol m^{-2} s^{-1} in the dry season and from 0.042 to 0.048 mol m^{-2} s^{-1} in the wet season. Relatively, the topmost leaves, like those of *R. mucronata*, had lower levels of stomatal conductance than the bottom leaves (Table 1a).

4.2 CO$_2$ ASSIMILATION RATES OF MANGROVE SAPLINGS

Saplings of both species had greater photosynthetic and stomatal conductance rates than their adult mangrove counterparts in the wet season. Maximum rates of light saturated photosynthesis in saplings of *R. mucronata* ranged from 0.26-13.37 µmol m^{-2} s^{-1} and from 0.34-8.70 µmol m^{-2} s^{-1} in *C. tagal* with an average of 5.82 and 3.70 µmol m^{-2} s^{-1} respectively. Mean leaf stomatal conductance in *R. mucronata* was 0.063 mol m^{-2} s^{-1} and 0.048 mol m^{-2} s^{-1} in *C. tagal* in the wet season. Photosynthetic and stomatal conductance rates of the saplings of *R. mucronata* were significantly (P < 0.0001) higher than those of *C. tagal* in the wet season (Table 1b) and although the saplings were located in two distant locations about 4 km apart, no significant differences (P > 0.05) were detected in the rates of photosynthesis and stomatal conductances. For example, average rate of photosynthesis for *R. mucronata* saplings were 5.81 µmol m^{-2} s^{-1} at Gazi site and 5.63 µmol m^{-2} s^{-1} at Kinondo site, while the corresponding stomatal conductances

were 0.066 and 0.058 mol m^{-2} s^{-1} respectively. Similarly, average photosynthetic rate in the saplings of *C. tagal* at Gazi was 2.84 μmol m^{-2} s^{-1} and 3.27 μmol m^{-2} s^{-1} at Kinondo with corresponding conductances of 0.054 and 0.044 mol m^{-2} s^{-1} respectively.   Comparatively, variables such as transpiration rates, intercellular CO_2 concentration and water use efficiencies were significantly different from those of the adult mangrove trees counterparts in the wet season.

Average diurnal trends in photon flux density, leaf temperature, vapour pressure deficit, and measured gas parameters for mangrove saplings are shown in figure 6. In *R. mucronata* significant differences ($P <$ 0.05) d.f.$_{(9, 172)}$ n = 172) were found in all the related parameters except transpiration. As expected photon flux densities were highest at midday (1652 μmol m^{-2} s^{-1}) than in the morning or in the evening. Corresponding parameters, namely leaf temperature and vapour pressure deficit were also highest at midday. Leaf temperatures were about 33 °C at midday, rising from 31.5 °C at 8 hours before dropping to 28.6 °C at 17 hours. Vapour pressure deficit trend increased from about 14.5 mbars at 8 hours to 22.0 mbars at midday and then dropping to 14.0 mbars in the evening. Rates of photosynthesis and stomatal conductances were significantly higher in the morning between 8 and 9 hours, dropping to low values thereafter before increasing slightly for a short period at around 15 hours. Maximum rate of transpiration varied from 0.34-1.92 mmol m^{-2} s^{-1} with an average mean value of 0.98 mmol m^{-2} s^{-1} throughout most of the day.

In *C. tagal* diurnal trends in irradiance, leaf temperature and vapour pressure deficit between the leaf and air were similar and very close to those of *R. mucronata* during the course of a day. However rates of photosynthesis, stomatal conductance and transpiration rates did not exhibit significant ($P > 0.05$) diurnal variations in the wet season. Photosynthesis and conductance rates were stable at about 3.70 μmol m^{-2} s^{-1} and 0.048 mol m^{-2} s^{-1} respectively, while transpiration rate was about 0.67 mmol m^{-2} s^{-1} throughout most of the day. Rates of photosynthesis, stomatal conductance and leaf temperatures responded similarly to rainfall trends in the wet season, being highest in May and lowest in August (Fig. 7).

Table 1a (above)

Photosynthetic characteristics of mangrove trees in the dry and wet seasons at Gazi. All data are the mean ± S.E. of n measurements at irradiances greater than 800 μmol m^{-2} s^{-1}. **A**, maximum rate of photosynthesis (μmol m^{-2} s^{-1}), gs, leaf stomatal conductance to water (mol m^{-2} s^{-1}), **E**, rate of transpiration (mmol m^{-2} s^{-1}), Ci, intercellular CO_2 concentration (μbar), WUE, water use efficiency (dimensionless, see text for definition).

Table 1b (below)

Photosynthetic characteristics of mangrove saplings in the wet season at Gazi. All data are the mean ± S.E. of n measurements at irradiances greater than 800 μmol m^{-2} s^{-1}. Units of measure are as in Table 1a.

(A)

Adult trees	n	A	g_S	E	Ci	WUE
DRY SEASON						
R. mucronata						
Height at 1 m	32	1.792±0.238	0.0332±0.0032	0.889±0.076	104±14	0.0023±0.0003
Height at 2 m	35	1.341±0.131	0.0329±0.0027	0.876±0.064	77±10	0.0018±0.0002
Height at 3 m	40	1.508±0.211	0.0331±0.0027	0.868±0.054	79±10	0.0020±0.0002
Height at 4 m	46	1.474±0.196	0.0328±0.0023	0.881±0.031	80±10	0.0019±0.0003
WET SEASON						
R. mucronata						
Height at 1 m	68	4.150±0.310	0.0457±0.0026	0.940±0.043	128±10	0.0040±0.0008
Height at 2 m	72	4.148±0.333	0.0471±0.0032	0.928±0.050	148±10	0.0046±0.0011
Height at 3 m	79	3.985±0.287	0.0452±0.0029	0.923±0.052	148±9	0.0045±0.0007
Height at 4 m	80	3.867±0.334	0.0395±0.0030	0.853±0.053	159±9	0.0046±0.0006
DRY SEASON						
Ceriops tagal						
Height at 1 m	30	1.703±0.276	0.0316±0.0027	0.862±0.057	102±14	0.0021±0.0005
Height at 2 m	34	1.241±0.141	0.0286±0.0021	0.790±0.047	79±9	0.0017±0.0004
Height at 3 m	42	1.119±0.101	0.0263±0.0097	0.783±0.044	73±8	0.0016±0.0003
Height at 4 m	40	0.963±0.101	0.0279±0.0029	0.803±0.061	65±8	0.0014±0.0003
WET SEASON						
Ceriops tagal						
Height at 1 m	60	3.396±0.303	0.0475±0.0042	0.874±0.049	126±10	0.0038±0.0003
Height at 2 m	75	3.247±0.295	0.0423±0.0037	0.819±0.051	136±10	0.0040±0.0003
Height at 3 m	75	3.089±0.243	0.0434±0.0033	0.857±0.048	124±8	0.0039±0.0003
Height at 4 m	82	3.064±0.262	0.0430±0.0037	0.874±0.053	119±10	0.0038±0.0003

(B)

Saplings	n	A	E	gs	Ci	WUE
R. mucronata	173	5.824±0.207	0.798±0.029	0.063±0.0029	168±6	0.0159±0.0006
C. tagal	161	3.701±0.121	0.676±0.037	0.048±0.0003	173±8	0.0151±0.0006

Figure 6

Mean changes in photon flux density (PFD), vapour pressure deficit (vpd), leaf temperature and measured gas exchange parameters:- Assimilation rate, stomatal conductance and transpiration rate in leaves of *Rhizophora mucronata* and *Ceriops tagal* saplings in the field during the course of the days in the wet season. n measurements for each species in every hour are as follows with n values in brackets: *C. tagal* 8:00 (14), 9:00 (14), 10:00 (22), 11:00 (17), 12:00 (19), 13:00 (18), 14:00 (19), 15:00 (19), 16:00 (19). Vertical bars are standard errors for means.
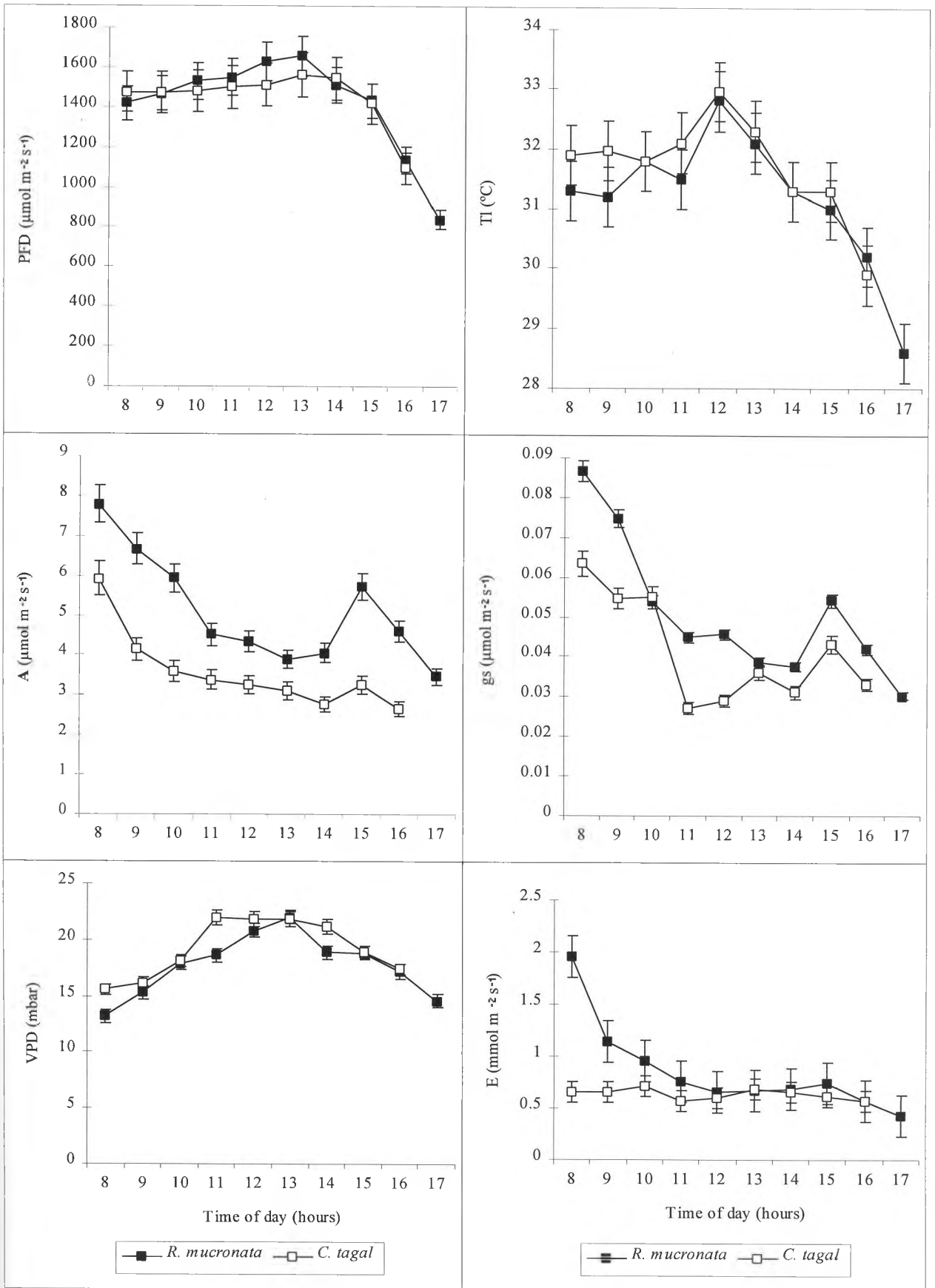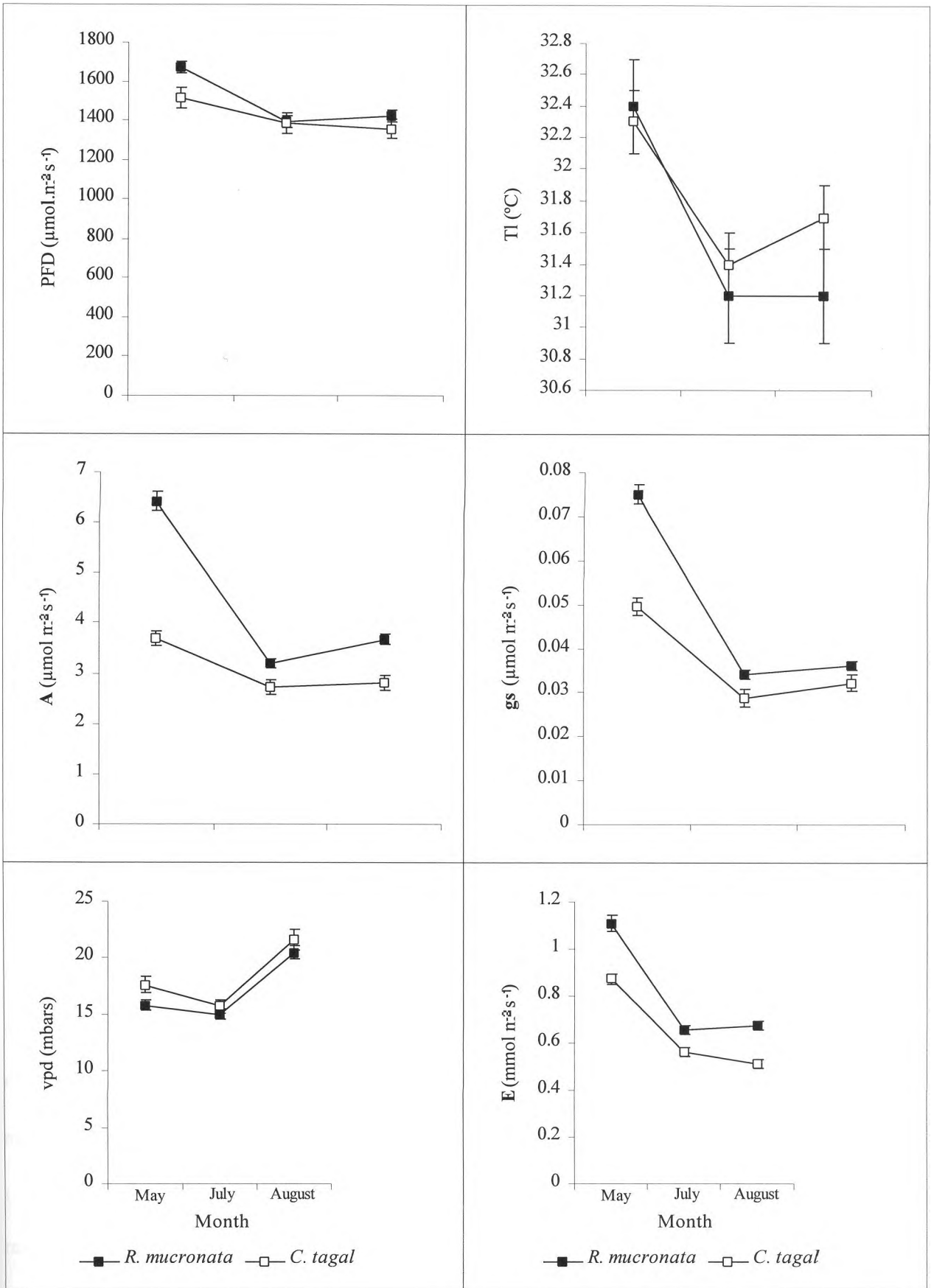
Figure 7

Mean monthly trends in PFD, T_1 , vpd and measured gas exchange parameters; A, g_S and E in leaves of *R. mucronata* and *C. tagal* saplings in the field. n measurements (in brackets) for *R. mucronata* and *C. tagal* respectively are as follows: May (53, 52), July (76, 62), August (44, 47). Vertical bars are standard error for means.

4.3 DIURNAL AND SEASONAL TRENDS IN PHOTOSYNTHESIS AND RELATED VARIABLES IN ADULT MANGROVES

Diurnal trends in irradiance, vapour pressure deficit, leaf temperature and measured gas exchange parameters for the top, exposed leaves of *R. mucronata* and *C. tagal* are shown in figures 8 and 9 respectively (from data recorded on 28 Feb 92 and 27 May 92). The two different dates are representative of 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. From figure 10 the coefficient of determination (r^2) between CO_2 assimilation and stomatal conductance on leaves of *C. tagal* on 27 May 92 (wet season) was 0.638 showing that there was a clear relationship between the two variables, but the relationship was less clear ($r^2 = 0.099$) during the dry season (on 28 Feb 92). The close positive correlation was more explicit in leaves of *R. mucronata* as $r^2 = 0.906$ on 27 May 92, but less clear on 28 Feb 92 since $r^2 = 0.224$.

Variations between the rate of transpiration and the relative position of leaf in the tree canopy and between the two species were not significant ($P > 0.05$) (Table 1a). Average mean values of transpiration were 0.894 mmol m^{-2} s^{-1} in *R. mucronata* and 0.832 mmol m^{-2} s^{-1} in *C. tagal*. In the dry season maximum rates of transpiration recorded on single leaves of *R. mucronata* ranged from 0.16 to 1.74 mmol m^{-2} s^{-1} while the rates ranged from 0.25 to 2.52 mmol m^{-2} s^{-1} in the wet season. In *C. tagal* maximum rates of transpiration recorded on single leaves ranged from 0.14 to 1.84 mmol m^{-2} s^{-1} in the dry season and from 0.22 to 2.63 mmol m^{-2} s^{-1} in the wet season. Significant variations ($P < 0.01$) were, however, evident in the wet season in both species. Rates of transpiration were highest in May when they reached a mean value of 1.27 mmol m^{-2} s^{-1} and 1.17 mmol m^{-2} s^{-1} in *R. mucronata* and *C. tagal* respectively. Lowest rates of transpiration were in August; 0.86 and 0.76 mmol m^{-2} s^{-1} in *R. mucronata* and *C. tagal* respectively.

Vapour pressure deficit (vpd) between the leaf and air was influenced to a major degree by leaf temperature and depending on the prevailing ambient relative humidity individual vpd values as high as 45 mbars were encountered. In figure 11, which is reproduced from figures 8 and 9, the diurnal trends between vpd and leaf temperature are clearly illustrated. In both species vpd and T_l were positively and closely correlated (fig. 12). For example, on 28 Feb 1992 (dry season) the coefficient of determination (r^2) in *C. tagal* was 0.972 while r^2 was 0.565 on 27 May 1992 (wet season). In *R. mucronata* $r^2 = 0.858$ on 28 Feb 1992, but the relationship was less obvious on 27 May 1992 as r^2 was 0.258.

Seasonal trends in photon flux density, leaf temperature, vapour pressure deficit and measured gas parameters are as shown in figure 13 depicting a close association between leaf temperature, photosynthesis, transpiration, stomatal conductance and trends in rainfall. It is apparently clear in Fig. 13 that vapour pressure deficit remained relatively high in the dry season, being at or above 30 mbars. In the wet season, however, optimal vpd values of about 20 mbars and below persisted. PFD values in the dry season were in the range of 1500 μmol m^{-2} s^{-1} dropping to the range of 1100 μmol m^{-2} s^{-1} in the wet season. Clear skies characterised the dry months of February and March while days of the months of the wet season had varying degrees of cloud cover.

In both species, there were significant differences ($P < 0.001$) in leaf water potential (Ψ_l) in relation to the position of the leaf in the canopy. The topmost leaves were always more negative than the bottom leaves: Ψ_l varied from -2.5 to -1.6 MPa in *C. tagal* and from -2.7 to -1.7 MPa in *R. mucronata,* the lower values being for the top leaves (Fig. 14). Leaf water potential showed significant diurnal variations (P<0.001) in both species, and whereas solar radiation fluctuated markedly throughout most of the day in May-July period, there was relatively little short term fluctuations in solar radiation in August 1992. An example of the daily course in leaf water potential collected on 20 August 1992 is shown in Figure 15 for leaves at the top of the canopy. On this day (which was similar to most other days in August 1992) leaf water potential fell from a value of -2.8 and -3.1 MPa at 9 hours (for *C. tagal* and *R. mucronata* respectively) to a low value of -4.3 MPa in the early afternoon and then rose again rapidly after about 16

hours when solar radiation had started to show a significant fall. From the data presented in Fig. 15 leaf water potential recovered (rose) rapidly from about -4.3 MPa to about -3.2 MPa when incoming solar radiation fell from about 1960 μmol m^{-2} s^{-1} to 845 μmol m^{-2} s^{-1} for one hour between 13:00 and 14:00 hours due to cloud cover. Leaf water potentials became low (more negative) 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 leaf water potentials recorded for single leaves on clear days were as high as -4.6 MPa in *C. tagal* and -4.1 MPa in *R. mucronata*, but net photosynthesis remained positive in leaves at all levels in the canopy in both species albeit at lower photosynthetic values. This phenomenon is clearly shown by data collected on 11 August 1992 in the curvelinear lines relationships between assimilation, stomatal conductance, and leaf temperature with water potential values for the top leaves of both species in figure 16. It is evidently clear that CO_2 assimilation and stomatal conductance improved as Ψ_l became less negative and as T_l decreased towards evening.

Soil salinity recorded during neap tides on days of clear skies is shown in Table 2 below. Soil salinity was on average about 30 ‰ salt.

Table 2.

Soil salinity in parts per thousand in randomly selected sites in the mixed mangal zone

Plot No.	7	8	9	10	11	12	13	14	15
Soil salinity (‰)	23	36	20	29	39	27	16	41	37

Figure 8

Changes in photon flux density, leaf temperature, vapour pressure deficit and measured gas exchange parameters: CO_2 assimilation rate, stomatal conductance and transpiration rate in an exposed `sun' leaf of *R. mucronata* in the field during the course of the day in the dry season (28 Feb 92) and in the wet season (27 May 92).

Figure 9

Changes in photon flux density, leaf temperature, vapour pressure deficit and measured gas exchange parameters: CO_2 assimilation rate, stomatal conductance and transpiration rate in an exposed `sun' leaf of *C. tagal* in the field during the course of the day in the dry season (28 Feb 92) and in the wet season (27 May 92).
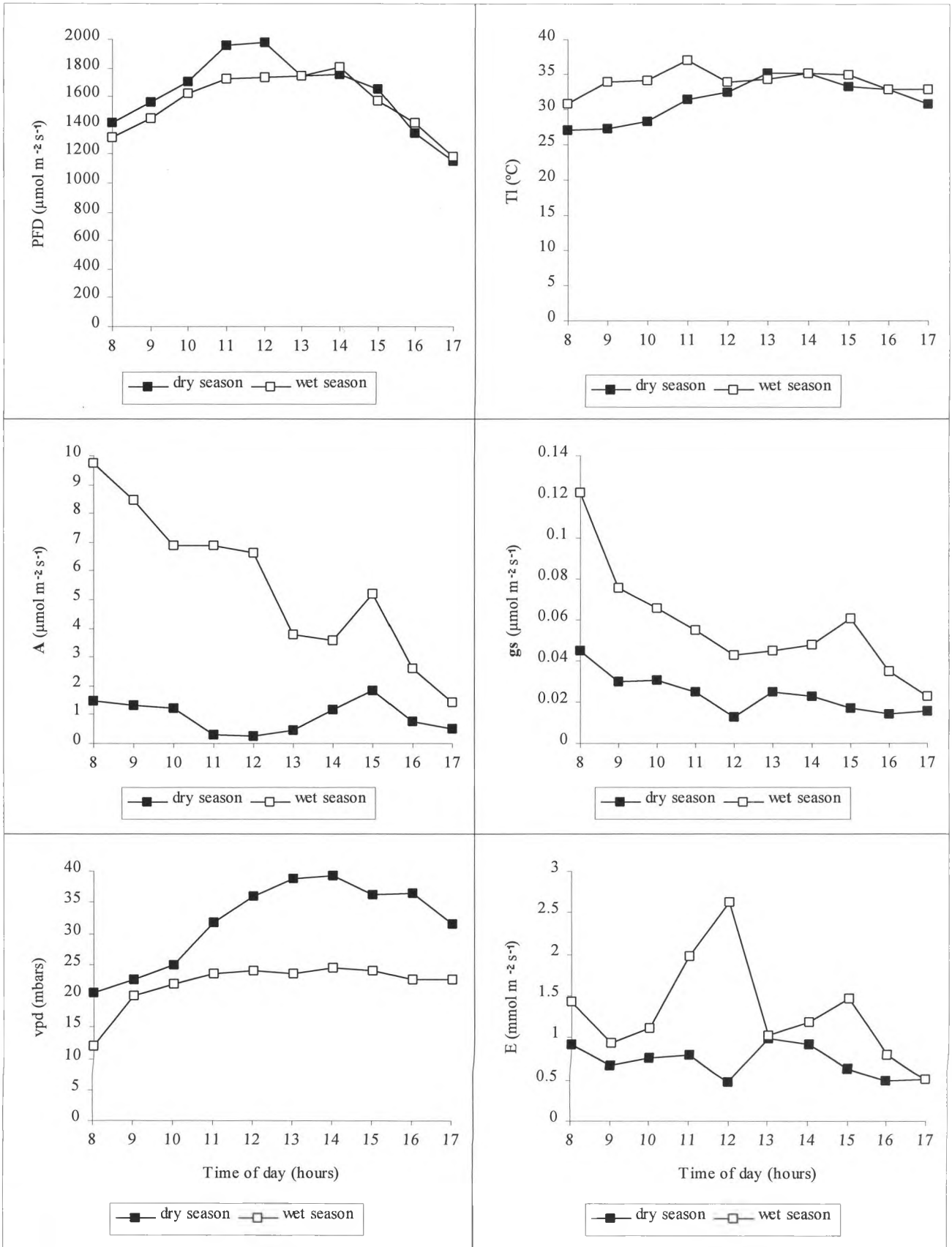
Figure 10

Relationship between CO_2 assimilation (μmol m^{-2} s^{-1}) and stomatal conductance (mol m^{-2} s^{-1}) in an exposed 'sun' leaf of *R. mucronata* and *C. tagal* in the dry (28 Feb 92) and wet season (27 May 92) under field conditions.

Dry Season (28 Feb 1992)

- ■ *R. mucronata*
- □ *C. tagal*
- – – – *C. tagal*
- ——— *R. mucronata*

Eq. *R. mucr*: y = 23.808x + 0.3078
R^2 = 0.2235

Eq. *C. tagal*: y = 17.836x + 0.5147
R^2 = 0.099

CO$_2$ assimilation (μmol m^{-2} s^{-1})

Stomatal conductance (μmol m^{-2} s^{-1})

Wet season (27 May 1992)

- □ *C. tagal*
- ■ *R. mucronata*
- ——— *R. mucronata*
- – – – *C. tagal*

Eq. *R. mucr*: y = 94.939x - 0.4074
R^2 = 0.9055

Eq. *C. tagal*: y = 38.714x + 2.1661
R^2 = 0.6377

CO$_2$ assimilation (μmol m^{-2} s^{-1})

Stomatal conductance (μmol m^{-2} s^{-1})

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Figure 11.

Diurnal trends in vapour pressure deficit and leaf temperature during the dry (28 Feb 92) and wet (27 May 92) season for the topmost leaves of *R. mucronata* (A) and *C. tagal* (B) under field conditions.

(A) **(B)**

53
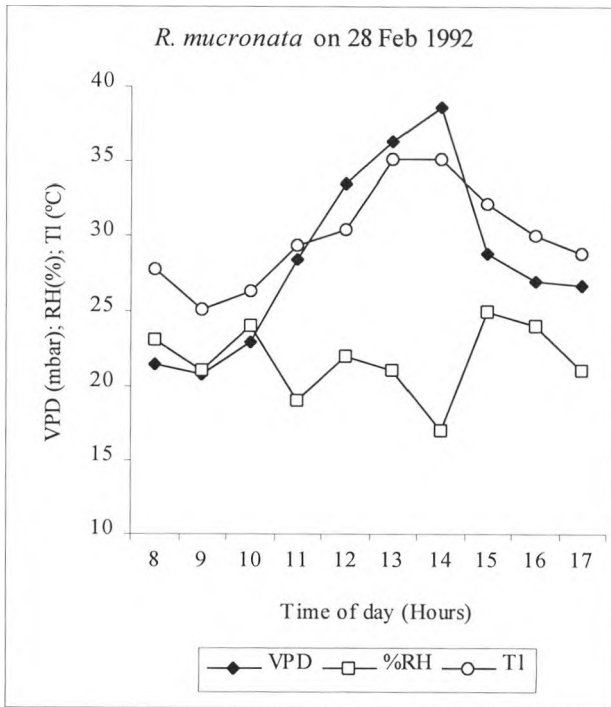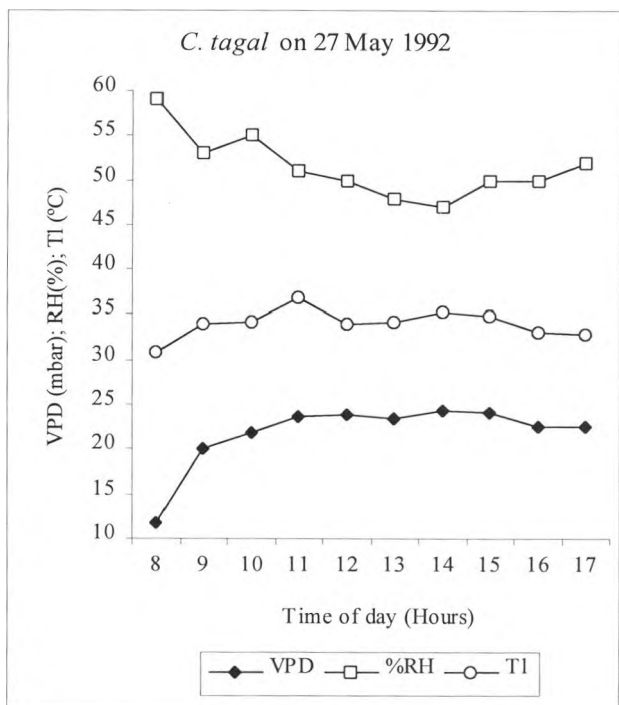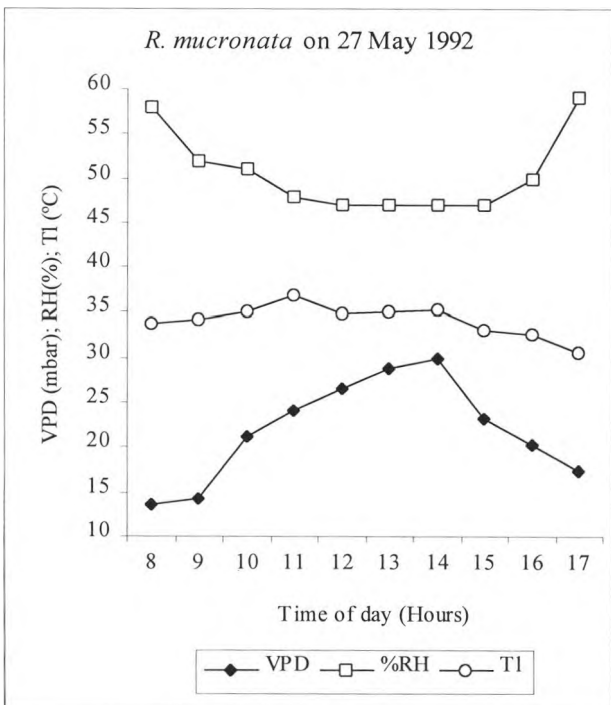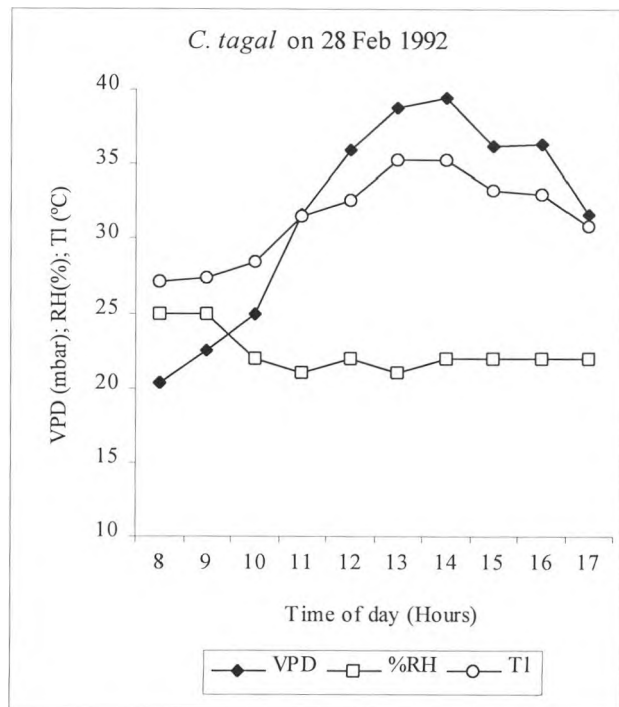
Figure 12

Relationship between leaf temperature and vapour pressure deficit for the top leaves of R. mucronata and Ceriops tagal on 28 Feb 1992 (dry season) and on 27 May 1992 (wet season) under field conditions

Dry Season (28 Feb 1992)

Eq.: *R. mucronata*
$y = 1.6673x - 21.643$
$R^2 = 0.858$

Eq.: *C. tagal*
$y = 2.246x - 38.87$
$R^2 = 0.972$

Wet Season (27 May 1992)

Eq.: *C. tagal*
$y = 1.7046x - 36.17$
$R^2 = 0.5652$

Eq.: *R. mucronata*
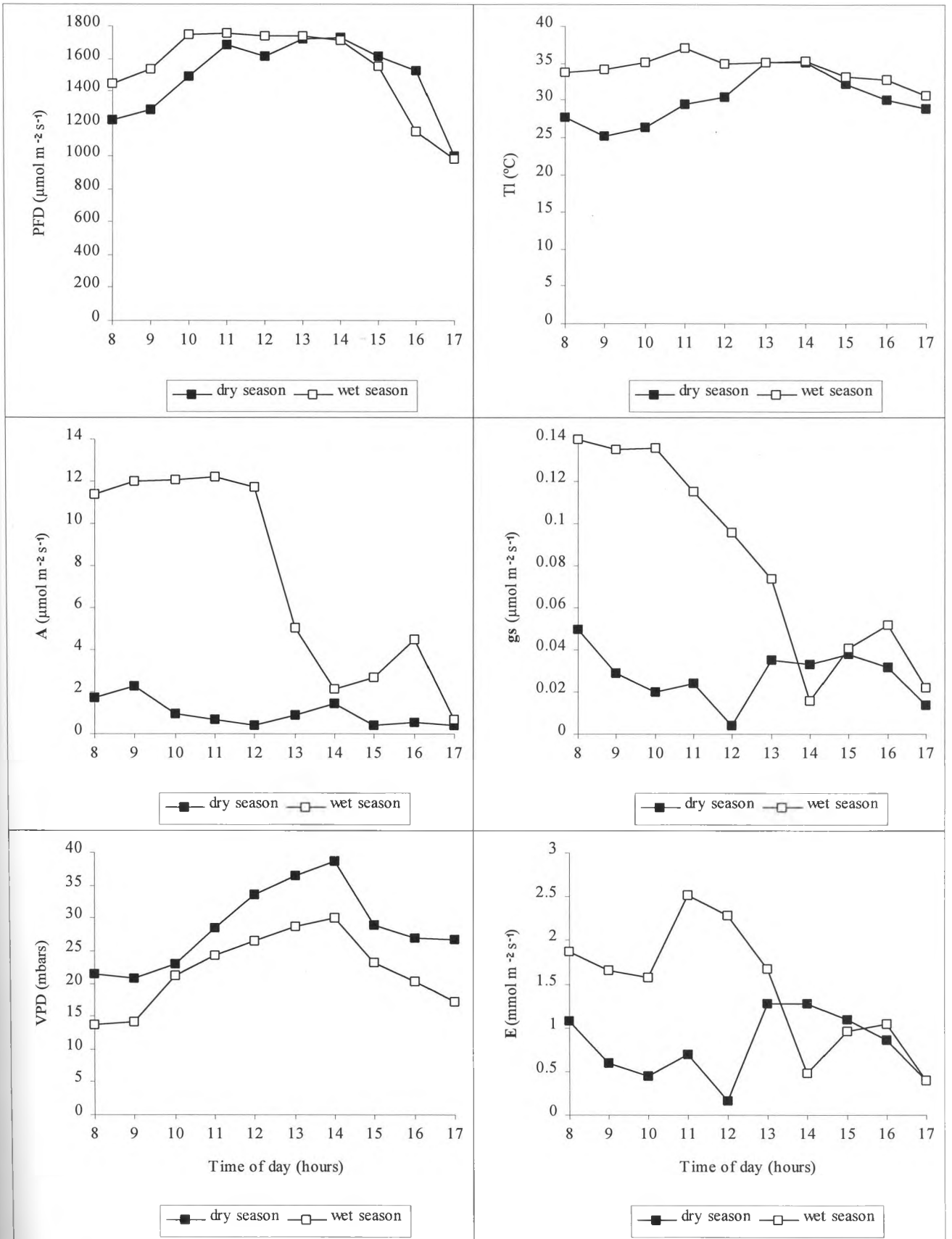$y = 1.6568x - 34.7$
$R^2 = 0.2578$

55
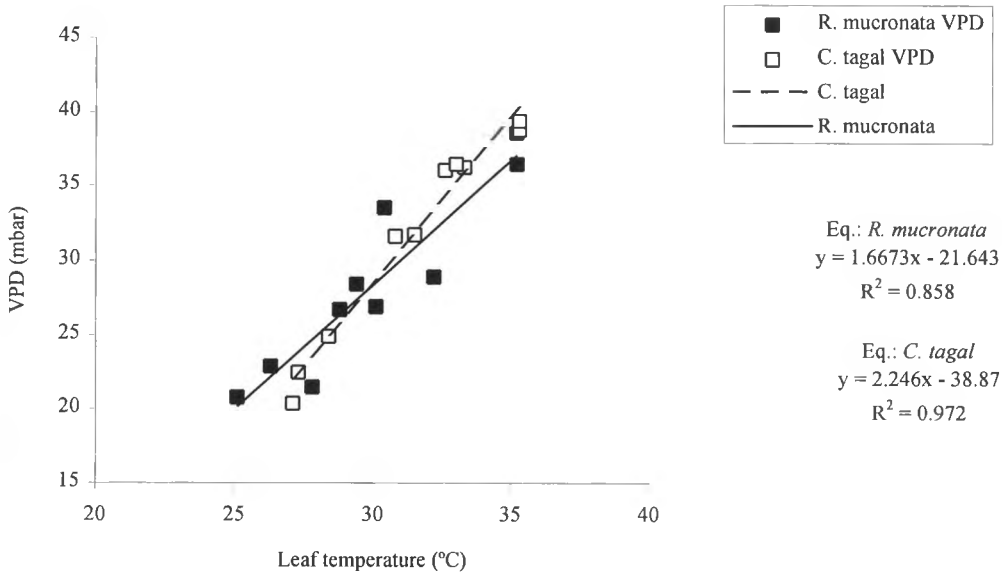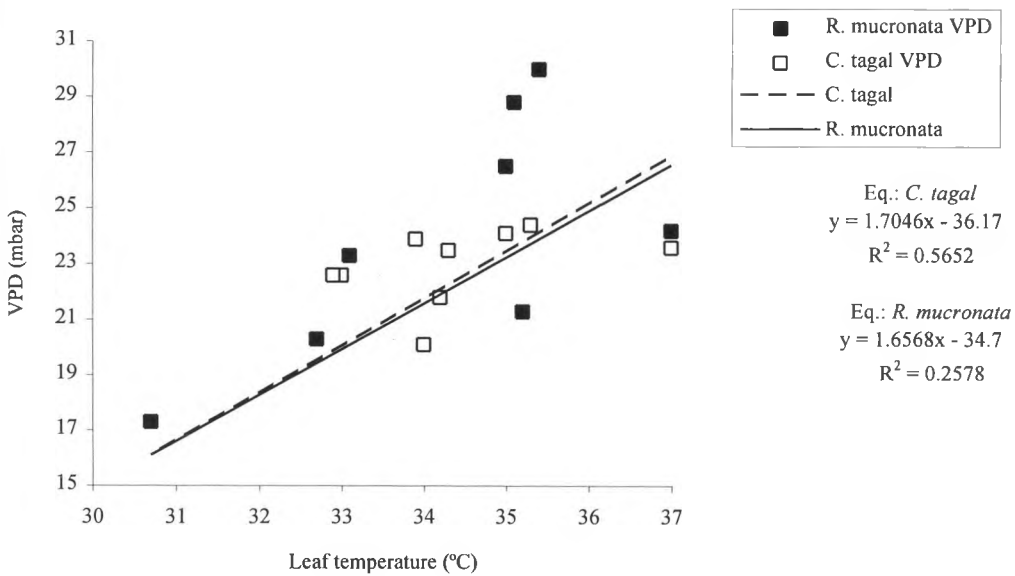
Figure 13

Monthly changes in photon flux density, leaf temperature, vapour pressure deficit, and measured gas exchange parameters: CO_2 assimilation rates, stomatal conductance, and transpiration rates in leaves of *R. mucronata* and *C. tagal* under conditions in the field. n measurements in every month for *R. mucronata* and *C. tagal* respectively (values in brackets) are as follows: February (88, 89), March (55, 57), May (60, 59), June (68, 53), July (72, 73), August (109, 107). Vertical bars are the S.E. for means.
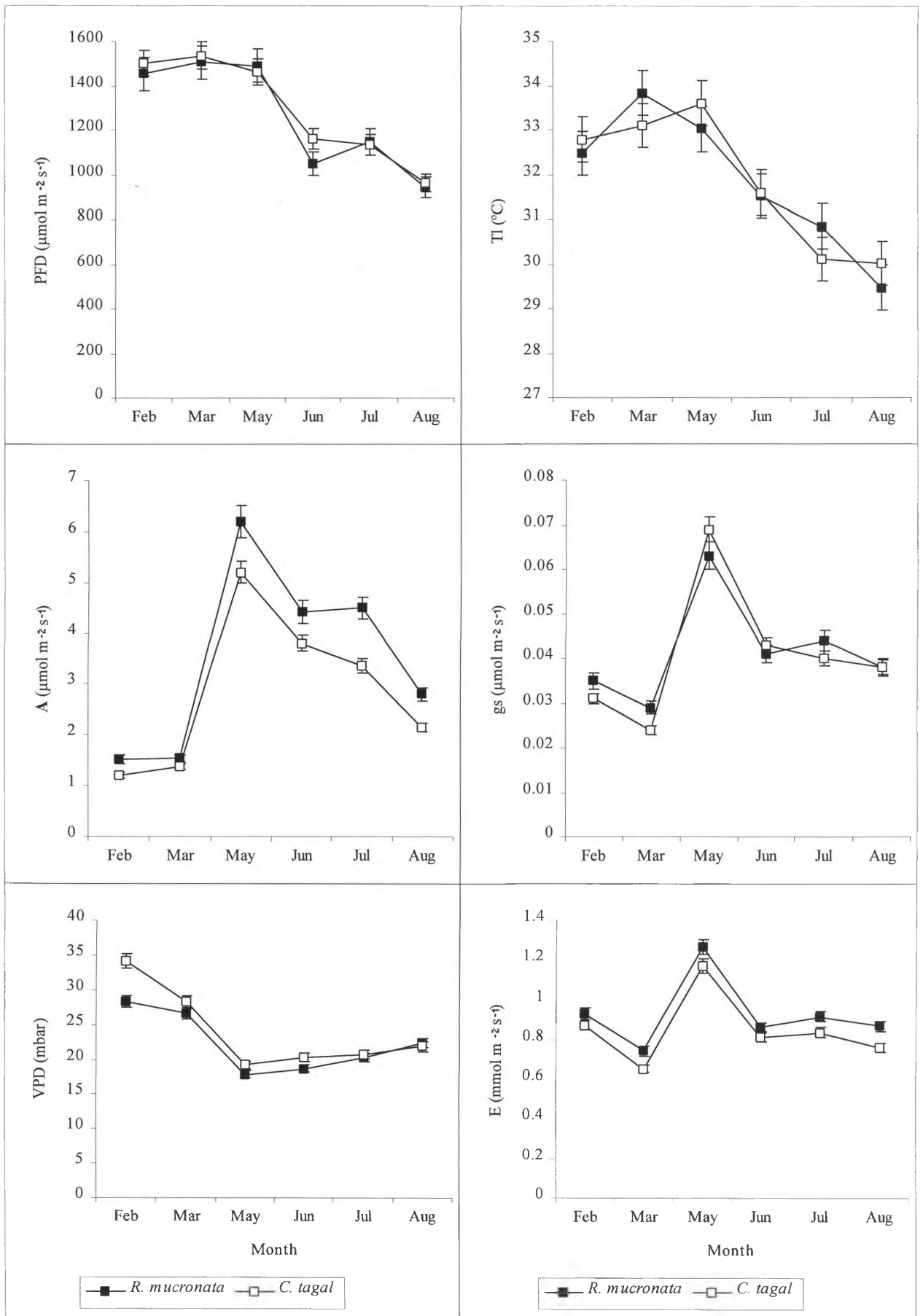
Figure 14

Relationship between leaf position in the canopy and the corresponding mean leaf water potential in *R. mucronata* and *C. tagal* under field conditions in the wet season. Vertical bars are the S.E. for means.

59
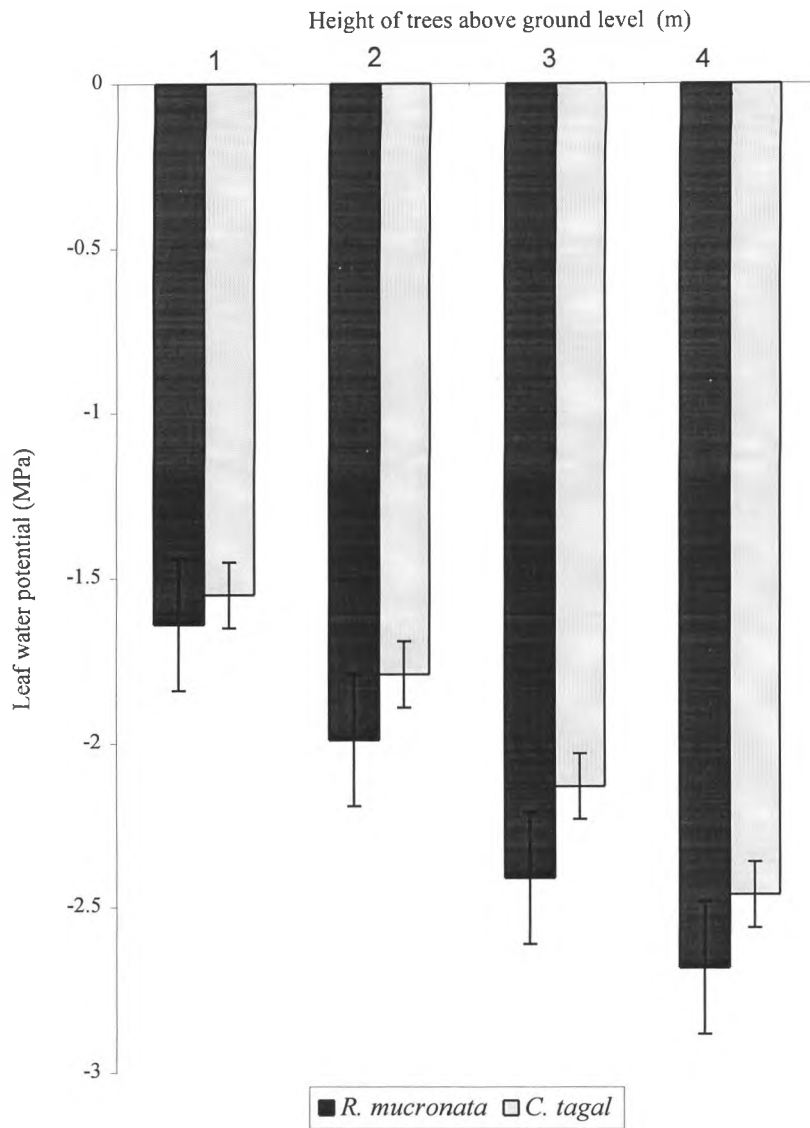
Figure 15

Changes in photon flux density and leaf water potential in an exposed 'sun' leaf of

R. mucronata and *C. tagal* in the course of the day on 20 August 92
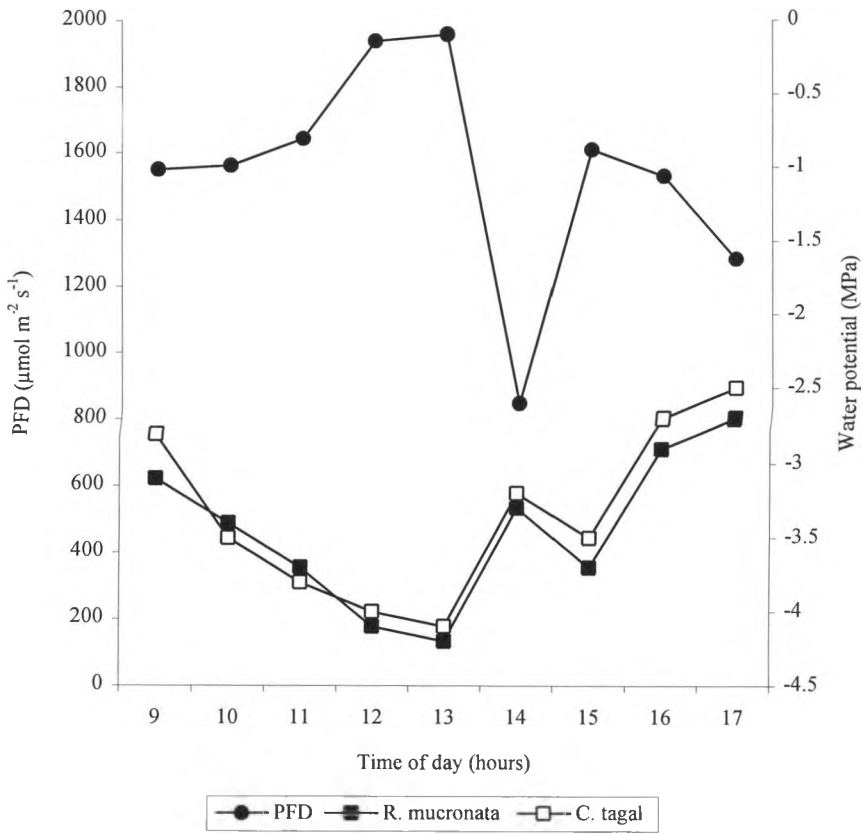
Figure 16

Relationship between CO_2 assimilation (μmol m^{-2} s^{-1}), stomatal conductance

(mol m^{-2} s^{-1}) and leaf water potential (MPa) for the sun leaves of *C. tagal* and

R. mucronata during the course of the day (11 Aug 92) in the wet season

Plot 1 (top): CO$_2$ assimilation (μmol m^{-2} s^{-1}) vs Water potential (MPa)

Legend:
- ■ *R. mucronata*
- □ *C. tagal*
- —— *R. mucronata*
- — — *C. tagal*

Eq. *R. mucronata*
$y = -2.4436x^2 - 15.936x - 21.941$
$R^2 = 0.7268$

Eq. *C. tagal*
$y = -0.9168x^2 - 5.3373x - 4.8555$
$R^2 = 0.5862$

Plot 2 (middle): Stomatal conductance (μmol m^{-2} s^{-1}) vs Water potential (MPa)

Legend:
- ■ *R. mucronata*
- □ *C. tagal*
- — — *C. tagal*
- —— *R. mucronata*

Eq. *R. mucronata*
$y = -0.0097x^2 - 0.0584x - 0.0433$
$R^2 = 0.4414$

Eq. *C. tagal*
$y = -0.0189x^2 - 0.121x - 0.1496$
$R^2 = 0.7353$

Plot 3 (bottom): Leaf temperature (°C) vs Water potential (MPa)

Legend:
- ■ *R. mucronata*
- □ *C. tagal*
- —— *R. mucronata*
- — — *C. tagal*

Eq. *R. mucronata*
$y = -1.4048x^2 - 13.596x + 3.9674$
$R^2 = 0.9684$

Eq. *C. tagal*
$y = -0.8204x^2 - 9.4573x + 11.313$
$R^2 = 0.7607$

3.4   WATER USE EFFICIENCY

Water use efficiency varied with vapour pressure deficit during the study period and was comparatively over 50% more conservative in the dry season. Water use efficiency (WUE) in *C. tagal* was on average 0.0017 in the dry season while in the wet season WUE improved to significantly (P < 0.05) favourable mean value of 0.0039. Average WUE in *R. mucronata* was 0.0020 and 0.0044 in the dry and wet season respectively. Comparatively, WUE in *R. mucronata* was significantly (P < 0.05) favourable than that of *C. tagal* during the wet season. Variations in water use efficiency in relation to the relative leaf position in the tree canopy were not significant (P> 0.05) in either of the dry or wet season. In *R. mucronata* WUE varied from 0.0018 to 0.0023 in the dry season and from 0.0040 to 0.0046 in the wet season while in *C. tagal* water use efficiency varied from 0.0014 to 0.0021 in the dry season and from 0.0038 to 0.0040 in the wet season (Table 1a).

Water use efficiency of both mangroves species was indeed reflected in the restriction of carbon dioxide influx into the leaf mesophyll. As noted earlier, intercellular CO_2 concentration in *C. tagal* was 80 µbars in the dry season increasing to about 129 µbars in the wet season. Similarly, in *R. mucronata* Ci was 85 µbars in the dry season and 146 µbars in the wet season. Differences in WUE between the two species was not significant (P > 0.05) in the dry season as was the case with Ci.   In the mangrove saplings WUE was more favourable for carbon dioxide influx in the wet season when compared with that of the adult mangroves counterparts. In *C. tagal* saplings WUE was 0.0151 and Ci was 173 µbars while in *R. mucronata* WUE was 0.0159 at an average Ci of 168 µbars (Table 1b). These WUE values of the saplings were almost three times higher than those of the adult mangroves in the wet season (Table 1a and 1b).

3.5 RESPONSE OF PHOTOSYNTHESIS, LEAF TEMPERATURE AND INTERNAL CO_2 TO LIGHT

A typical light response curve for *R. mucronata* and *C. tagal* at leaf temperature of between 33 - 34 °C is shown in figures 17. At low light levels net photosynthesis increased more or less linearly with photon flux density (PFD) giving an incident quantum efficiency (A/PFD) of about 0.017 in both species. There was little linear increase in photosynthesis beyond photon flux density of about 800 μmol m^{-2} s^{-1}. In figure 10 and figure 17, photosynthesis initially increased almost linearly with Ci and with PFD, the relationship apparently becoming nonlinear at values of Ci beyond 130 μbars in the wet season. Similarly, in figure 17, leaf temperature, stomatal conductance and Ci increased almost linearly with increase in irradiance, although that of leaf temperature was not explicitly clear.

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Figure 17

Effects of light (PFD, 400-700 nm, μmol m^{-2} s^{-1}) on CO_2 assimilation (μmol m^{-2} s^{-1}), stomatal conductance (mol m^{-2} s^{-1}), intercellular CO_2 concentration (μbars) and leaf temperature (Tl, °C) in an exposed 'sun' leaf of *R. mucronata* and *C. tagal* under field conditions in the wet season

Eq. *R. mucronata*
$y = -2E-06x^2 + 0.0063x - 1.1577$
$R^2 = 0.9623$
Eq. *C. tagal*
$y = -5E-07x^2 + 0.0025x - 0.5229$
$R^2 = 0.9761$

Eq. *R. mucronata*
$y = -2E-08x^2 + 6E-05x + 0.0036$
$R^2 = 0.8928$

Eq. *C. tagal*
$y = -2E-08x^2 + 5E-05x + 0.0031$
$R^2 = 0.8855$

66

Eq. *C. tagal*
$$y = 57.565 Ln(x) - 318.02$$
$$R^2 = 0.9115$$

Eq. *R. mucronata*
$$y = 56.936 Ln(x) - 303.8$$
$$R^2 = 0.8173$$

Eq. *R. mucronata*
$$y = 4E\text{-}07x^2 + 0.0002x + 33.$$
$$R^2 = 0.5043$$

Eq. *C. tagal*
$$y = -1E\text{-}08x^2 + 0.0008x + 33.3$$
$$R^2 = 0.3783$$
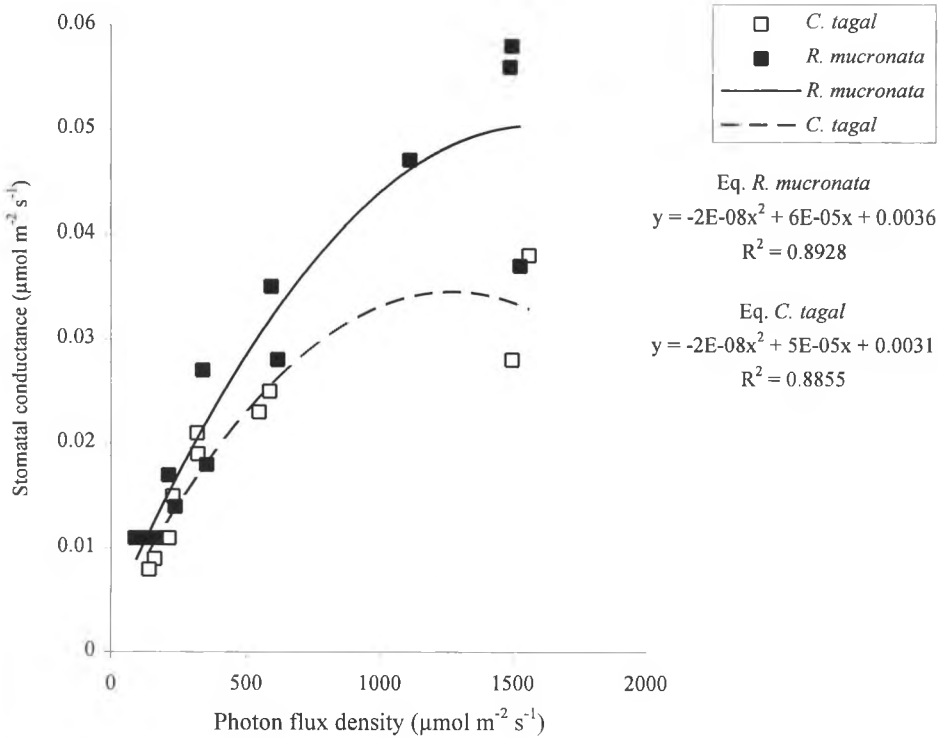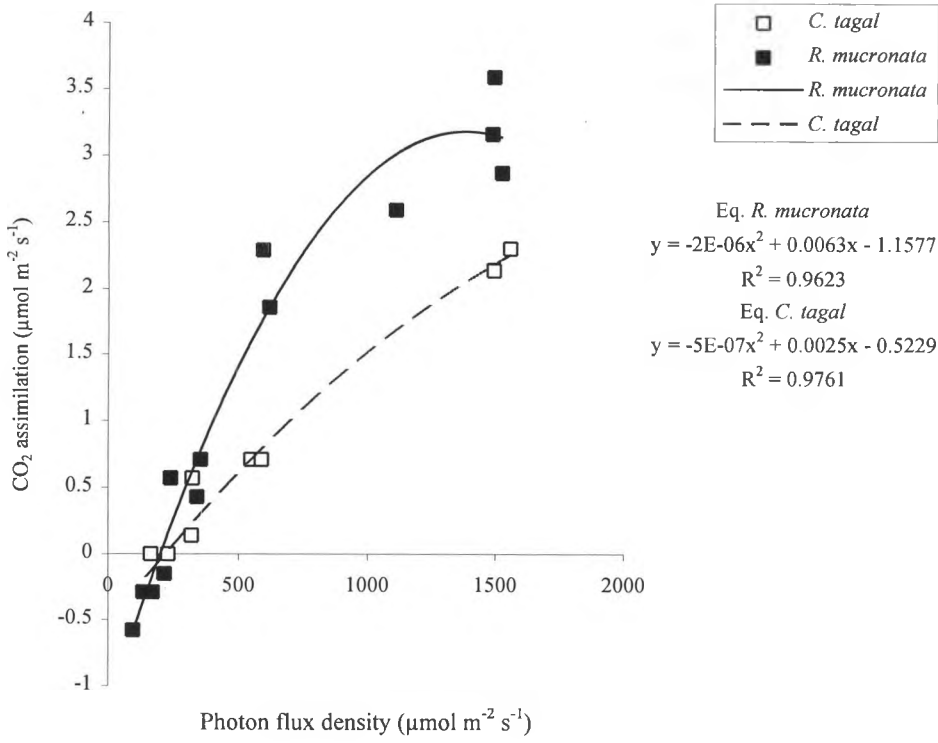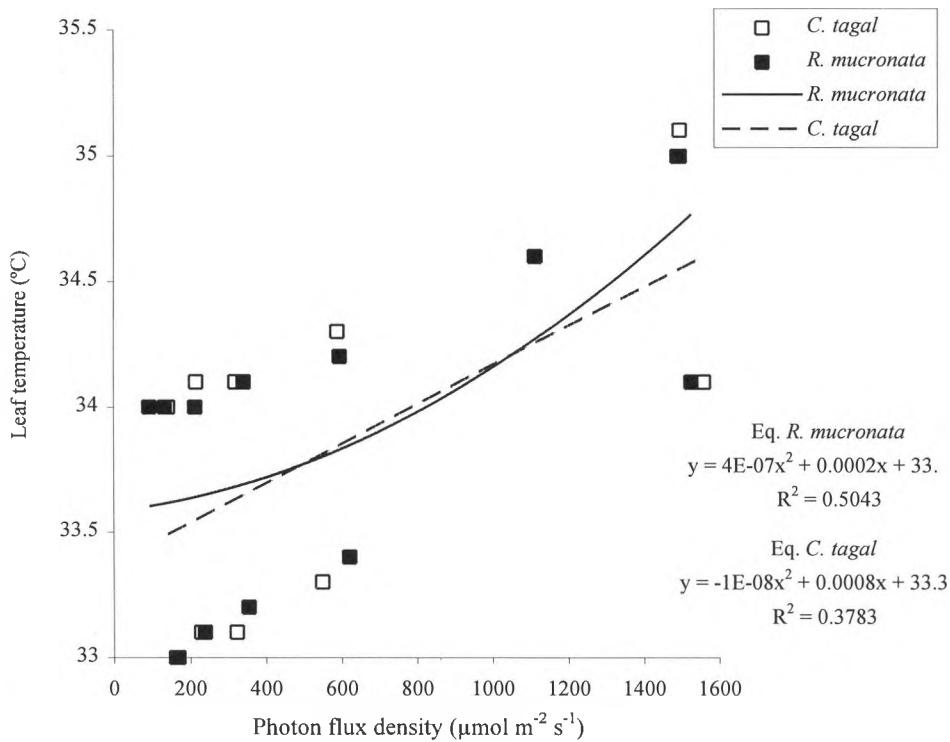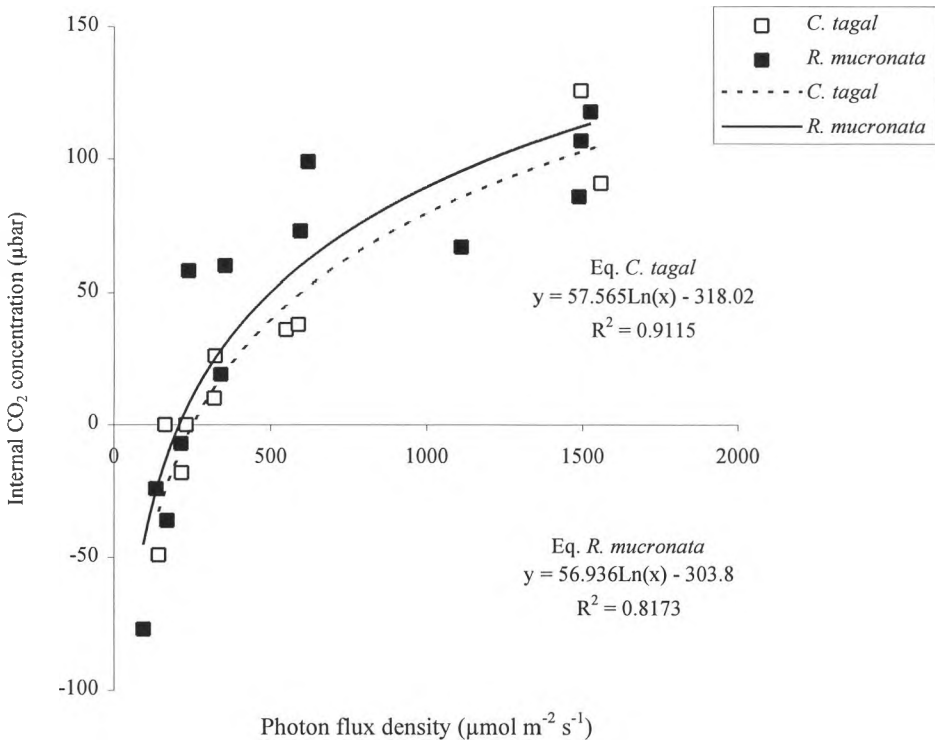
CHAPTER FIVE

5.0   DISCUSSION

The results presented above indicate that gas exchange characteristics of **Rhizophoraceae** mangroves exhibit diurnal and seasonal shifts in metabolic patterns of photosynthesis, with highest values in the morning. Seasonally, highest values occurred in the wet season. *R. mucronata* showed less resistance to CO_2 exchange than *C. tagal* due to its relatively higher rates of stomatal conductance. As a result *R. mucronata* had consistently higher rates of photosynthesis than *C. tagal*. Stomatal behaviour of the mangroves was such that the stomates were open to allow CO_2 influx in the morning up to about 10 hours. They were partially open in the afternoon, but again opened to a slight extent in the evening as evidenced by higher stomatal conductances in the morning and in the evening than in the afternoon. From the individual plant curves it appeared that much of the variability in photosynthesis 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 in the wet season, leaf water potentials were low in the afternoon primarily due to higher insolation and higher leaf temperature in the middle of the day thereby causing significant stress in the plants.

Maximum rates of photosynthesis observed in this study were moderately low, rarely rising above 5.0 $\mu mol\ m^{-2}\ s^{-1}$ in the wet season and well below 2.0 $\mu mol\ m^{-2}\ s^{-1}$ in the dry season. These rates of light-satured photosynthesis are relatively low. Rates well above 25 $\mu mol\ m^{-2}\ s^{-1}$ have been reported for field situations in the luxuriant mangrove forest of the Asia-Pacific Region. More commonly, rates of net photosynthesis in the field lie in the range of 5-20 $\mu mol\ m^{-2}\ s^{-1}$, the lower values being recorded in the Florida mangrove species (Moore *et al*., 1972; 1973; Atiwill and Clough, 1980; Ball and Critcheley, 1982; Andrews *et al*., 1984; Andrews and Muller, 1985; Clough and Sim, 1989; Cheeseman *et al*., 1991). The calculated quantum efficiency for both species from figure 17 was 0.017. Aksornkoae *et al*., (1991) found a quantum efficiency value of 0.019 for *B. parviflora* and *R.. apiculata* in Thailand. Normally, for

Rhizophora species, values of 0.03 or higher would be expected (Tsilemanis, 1988). Presently there is no data available on photosynthetic gas exchange characteristics of mangroves in East Africa which can be used for direct comparison with those obtained in this study. However, Table 3 shows comparable data on mangrove photosynthesis, containing data for other tree species other than mangroves. The present data seems realistic by comparison with data from Florida mangrove species.

SPECIES		PHOTOSYNTHESIS maximum (μmol m^{-2} s^{-1})	SOURCES
Rhizophora mucronata	dry season	1.53	Present study
	wet season	4.04	Present study
	wet season saplings	5.82	Present study
Ceriops tagal	dry season	1.25	Present study
	wet season	3.20	Present study
	wet season saplings	3.97	Present study
Avicennia marina		5.30	Atiwill and Clough (1980)
Rhizophora mangle		4.27	Moore *et al*. (1973)
Avicennia germinans		3.59	Moore *et al*. (1973)
Languncularia racemosa		4.27	Moore *et al*. (1973)
Rhizophora mangle		5.32	Golley *et al*. (1962)
Bruguiera parviflora		4.45	Aksornkoae *et al*. (1991)
Rhizophora apiculata		4.50 - 6.10	Aksornkoae *et al*. (1991)
Rhizophora mucronata	dry season saplings	10.77	Aksornkoae *et al*. (1991)
	wet season saplings	17.33	Aksornkoae *et al*. (1991)
Other tree species			
Conifers		0.96 - 12.64	Larcher (1969)
Deciduous		2.52 - 15.80	Larcher (1969)
Temperate evergreen		4.43 - 10.75	Larcher (1969)
Maple		3.80	Hesketh and Baker (1967)
Oak		6.32	Hesketh and Baker (1967)

Table 3. A comparison of photosynthetic gas exchange for *R. mucronata* and *C. tagal* with those obtained in other studies.

A noteworthy point in this study was the observation that leaves fully exposed to sun during their development did not have significantly higher light saturated rates of photosynthesis than leaves which had developed in the shade. In fact the shade leaves of *C. tagal* had significantly higher rates of photosynthesis than the exposed leaves at the top of the canopy during the dry season.   Similarly,

maximum values for leaf conductance to water vapour were rarely above 0.05 mol m^{-2} s^{-1} in the mangrove trees and 0.08 mol m^{-2} s^{-1} in saplings. Usually conductances in mangroves when stomata are widest open are typically less than 0.13 mol m^{-2} s^{-1} (Clough *et al.*, 1982) and maximum conductances considerably smaller than this value, comparable to those encountered in this study, have been reported for the Florida species (Moore *et al.*, 1973).

Anatomically, the stomata of mangroves are adapted so that gaseous exchange between the air space inside the leaf and external air is considerably restricted to prevent excessive water losses (Ball 1988b). 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 carbon dioxide influx. At the biochemical level the amount and properties of CO_2 carboxylation enzyme ribulose-1,5-bisphosphate carboxlyase/oxygenase (RuBisCO) strongly influences gas exchange characteristics in mangroves. RuBisCO catalyses the combination of CO_2 with the acceptor molecule ribulose-1,5 bisphosphate (RuBP). Under RuBP saturating conditions, the rate of photosynthesis will be determined largely by the amount and activity of RuBisCO as well as the relative amount of O_2 and CO_2 in the leaf. Under RuBP limiting conditions, the rate of photosynthesis will be determined by the rate of RuBP regeneration, which requires both photochemically derived energy and the series of reactions comprising the photosynthetic carbon reduction cycle (Calvin pathway). 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 directly related to levels of stomatal conductance (fig. 8 and 9). The stomata adjusted such that the leaves expended an amount of water consistent with maintenance of the assimilation rate at or very near the maximum capacity for photosynthesis. This phenomenon ensured that water loss in relation to carbon gain was minimum. In general, transpiration rates depend on both leaf conductance to water vapour and the vapour pressure gradient between the leaf

and the air (vpd). Substantial regulation of transpiration by sensitive stomatal responses has been observed with several conifers and some herbaceous angiosperms (Jarvis, 1980). Stomatal responses to humidity may reflect a mechanism which 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 was mediated by cuticular transpiration of the outer epidermis. Naturally, vapour pressure deficit is influenced to a major degree by leaf temperature and partly by the ambient relative humidity (Ball, 1986), and in this study, vpd of as high as 45 mbars were recorded.

Photosynthetic capacity was closely and positively correlated with maximum stomatal conductance in both species (fig.10). The way in which CO_2 assimilation and leaf conductance are correlated appears to have great ecological significance. Schulze and Hall (1982) documented that if during variations of environmental or plant internal conditions, A and g_S change proportionally in a straight line relationship which passes through the origin, Ci remains constant. Further, if leaf temperature and atmospheric vapour pressure do not vary, water use efficiency (an index of the amount of carbon fixed in photosynthesis per unit amount of water lost by leaves) also remains constant. In this case stomatal movements do not change the conditions of CO_2 fixation in the mesophyll. In this study, the linear relations did not pass through the origin indicating that either stomatal conductance or CO_2 assimilation responded more strongly than the other parameter to changes of environmental or plant internal conditions. As such Ci and water use efficiency are not maintained constant; Ci decreases whenever g_S is more affected by changes of environmental or plant internal conditions than A.

Differences in the slope of relationship between A and g_S are indicative of differences in water use efficiency. The steeper the slope of the relationship between photosynthesis and stomatal conductance, the higher the water use efficiency. Water use efficiency (WUE) in the two mangrove species varied between the seasons and between the species and reflected appreciably trends in carbon fixation. In an analysis of the gas exchange characteristics of mangroves Clough and Sim (1989) found that the slope of the relationship between photosynthesis rate and stomatal conductance increased with increasing salinity

and with increasing vapour pressure deficit between the leaf and air, implying that the water use efficiency increases with increasing salinity and increasing aridity. Indeed in this study, WUE varied between the two seasons mainly due to variations in vapour pressure deficit with the plants showing a more conservative WUE in the dry season.

Water use efficiency is one outstanding feature of the gas exchange characteristics in mangroves and when compared with other C_3 plants grown 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. The problem arises because mangroves only partially exclude salts from entry into the transpiration stream which supplies water to the leaves. According to Ball (1988b) the high water use efficiency 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 C_3 non-halophytes.

Restriction of water efflux from the leaves, and hence high water use efficiency, also restricted the rates of CO_2 influx into the leaves causing the leaves to operate at low internal CO_2 concentrations, Ci. Indeed leaf internal CO_2 concentrations in the dry season were almost half those encountered in the wet season in the adult mangrove trees. As stated above, water use efficiency in mangroves increases with decrease in Ci for a given set of environmental conditions such as leaf temperature, sustained high insolation and vapour pressure deficit. Healthy leaves of mangroves operate at Ci around 170 µbars (Andrew *et al.*, 1984; Ball and Farquhar, 1984a and b), as was the case with the saplings in this study, whereas the operational Ci for C_3 crop plants averages 220 µbars (Farquhar and Sharkey, 1982), consistent with the differences in water use efficiency between these two groups. Thus, conservative water use within the constraints of C_3 photosynthetic metabolism is at the expense of the assimilation rate and hence also the growth rate in mangroves.

Most C_3 plant species operate with high transpiration rates and thereby take advantage of the high irradiances required to maintain high photosynthetic rates with minimal increase in leaf temperature over air temperatures. Mangrove leaves, however, operate with more conservative expenditure of water. In this study, leaf temperatures at light saturated rates of photosynthesis were commonly in the range of 31.4° to 35.1°C even in the wet season and photosynthetically active radiation was well above 1400 μmol m^{-2} s^{-1}. Clough and Andrew (1981) documented that leaf temperature is a critical factor influencing the rate of assimilation in mangroves. CO_2 assimilation is relatively unaffected by temperatures in the range of 17-30°C, and maximum rates of photosynthesis and stomatal conductance occur at leaf temperatures ranging from 25° to 30°C. Assimilation rates fall sharply at temperatures above 35°C with very little or no photosynthesis at 40°. The gradual reduction in assimilation at leaf temperatures above 30°C is explained by a concomitant decrease in leaf conductance and reduced efficiency of carboxylation enzyme RuBisCO. The high leaf temperatures encountered in this study may partly account for the low photosynthetic and stomatal conductance levels observed.

Mangroves avoid high irradiances to maintain leaf temperatures within physiologically acceptable ranges. To prevent excessively high temperatures, mangrove leaves in exposed positions at the top of the canopy are steeply inclined, almost nearly vertical (erectophile), while those in the shade are horizontal (planophile). This strategy in leaf angle inclination results in reduced thermal input per unit leaf area for the top canopy leaves and occurs as well in other halophytes and glycophytes where irradiances are high. In this way mangrove leaves can maintain relatively constant, albeit low, assimilation rates throughout the photoperiod. This explains why the shade leaves of *C. tagal* recorded higher rates of photosynthesis than leaves at the top of the canopy. Thus, maximizing carbon gain for a fixed total expenditure of water by mangrove leaves involves a complex balance between stomatal behaviour in relation to photosynthesis and variation in leaf properties in relation to light interception and evaporation demand.

In the analysis of light response curve (Fig. 17) photosynthesis was apparently saturated at photon flux density of about 800 μmol m^{-2} 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, presumably as a result of differences in age, orientation and degree of exposure of the leaf. Another feature of the data shown in figure 17 was that the decline in assimilation at low light fluxes was related to decrease in stomatal closure. Whereas leaf stomatal conductance fell from about 0.06 mol m^{-2} s^{-1} to around 0.01 mol m^{-2} s^{-1} as photon flux density was reduced from about 1500 to 200 μmol m^{-2} s^{-1}, the reduction in assimilation was roughly proportional to the reduction in conductance. This is consistent with the correlation between assimilation and stomatal conductance (Fig. 10). Generally mangroves become light saturated at moderate light intensities 30% to 50% incident light in the tropics (600-1000 μmol m^{-2} s^{-1}) (Atiwill and Clough, 1980). Because of the low stomatal conductances and associated low light-saturated CO_2 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 implies 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 this 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 at high irradiances, thereby protecting the photosystems from damage (Björkman *et al.*, 1988) and enabling photosynthesis to continue, but at low values, during the photoperiod.

Water potentials of **Rhizophoraceae** mangrove species and their diurnal variations were similar with those previously reported for mangroves in the intertidal zone (Scholander *et al.*, 1966). Leaf water potentials, particularly in August, were commonly in the order -2.5 to -4.6 MPa. 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 water potential of leaves at the top of the canopy from those sampled at the bottom of the canopy is attributed to hydrostatic pressure gradients along the xylem. The hydrostatic pressure gradients are analogous to the voltage drop across a resistor through which an electric current is flowing. A notable

feature in mangroves is that a small increase in tissue water content resulting, for example, from reduced light intensity and hence reduced rate of evaporational demand, gives rise to a large change in both water potential and turgor potential. This apparently means that leaves or shoots of mangroves have to gain only a small amount of water from the saline environment to bring about a large rise (recovery) in water potential (Aksornkoae *et al.,* 1991). This aspect was clearly manifested in this study as exemplified by figure 15 when solar radiation dropped significantly for one hour in the afternoon, resulting into a significant rise in water potential. Although the minimum water potential recorded in this study (-4.6 MPa) are able to induce stomatal closure (Arksornkoae *et al.*, 1991), this was not the case in this study, and net photosynthesis remained positive in leaves at all levels in the canopy.

In the foregoing discussion, it is now evidently clear that photosynthesis and hence net primary production and growth rate of mangrove forests is greatly influenced by climatic conditions. The solar radiation regime, daylength, temperature, rainfall, potential evapotranspiration, and the seasonal variability of these factors operate at all levels of plant organism to influence the ecophysiological responses of mangroves. Mangroves show luxuriant growth in persistently wet equatorial climates than in seasonally monsoonal or arid climates. Wet equatorial climates are characterized by moderately high temperature, moderate to high rainfall, persistent cloudy conditions and low ratio of precipitation to evapotranspiration. In these climates, solar radiation fluxes are not extreme and seasonal variability in climate is small. Moreover, persistent cloud cover in wet equatorial climates protect the forest canopy from high solar insolation. Due to high ambient relative humidity, mangroves in wet equatorial climates have less stress on the water and salt balance which reduces the need for an unusually high conservative water use. It is in such favourable conditions of low vpd (<22 mbar), low salinity (<15‰) and moderate light (>800 $\mu mol\ m^{-2}\ s^{-1}$) that the rate of photosynthesis exceeds 25 $\mu mol\ m^{-2}\ s^{-1}$ (Clough and Sim, 1989). Such values compare favourably with those of terrestrial forests. At the other end of the scale, growth rates and net primary productivity may be close to zero when climatic conditions are severe and/or soil salinity is high.

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 monsoonal climates, as that occurs along the East African coast, mangrove forests experience similar arid conditions in the dry season. The Kenyan mangrove ecosystem highly respond to climatic conditions of monsoonal climate.

In summary, there were substantial differences in both the way in which photosynthetic metabolism changed with variation in environmental conditions. Rates varied widely depending on the species , the position of the leaves in the canopy and environmental conditions particularly solar radiation fluxes, vapour pressure deficit between the leaf and the air and soil salinity. Stomatal behaviour was such that the ability with which CO_2 was allowed to enter the leaf was consistent with the capacity of the leaf to assimilate CO_2 under prevailing environmental conditions. As a result water loss was minimum relative to carbon gain. Overall, rates of photosynthesis at all levels in the canopy were low by comparison and are therefore indicative of a system under stress from unfavourable climatic conditions such as excessive insolation, high leaf temperatures and high vapour pressure deficit, particularly in the dry season. Furthermore, there is evidence that even during the late wet season (from August), the mangrove trees are operating for at least part of the day at turgor potentials that are close to zero. The present condition of the mangrove forest also reflect the effect of past exploitation, particularly tree felling, in addition to natural environmental stress. It follows that the mangrove system of Kenya may not easily withstand continued or increased exploitation, or activities which further adversely affect the environmental conditions for mangroves, for example, salt extraction. Nevertheless, notwithstanding the restriction of growth and primary productivity in mangroves by high light intensity, water potential and vapour pressure deficit, there is still scope for improving the productivity of mangrove forest by more effective management. The present management strategy of Gazi Bay mangrove forest is to allow natural regeneration of clear-felled areas. This strategy has not resulted in extensive, closed canopy, even aged stands of mangrove forest.

Recent work in Malaysia and Australia (Aksornkoae, *et al*., 1991) suggest that closed canopy, even aged stands have a higher primary productivity and faster growth rate than stands with open canopies.

CHAPTER SIX

6.0   REFERENCES

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