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Photosynthesis and Water-Use Efficiency of Some Mangroves from Sundarbans, India

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We studied seasonal fluctuations in the rates of photosynthesis, transpiration, PAR, and stomatal conductance for 16 species of true mangroves from the Sundarbans region of West Bengal. Soil salinity and pH were also measured. Leaf temperatures were almost always higher than the ambient temperature. We observed considerable seasonal (summer vs winter) as well as interspecific variations in photosynthesis, with the highest rates occurring in *Heritiera fomes* (13.21 μmol $m^{-2}s^{-1}$) and *Avicennia marina* (11.8 μmol $m^{-2}s^{-1}$), and the lowest in *Nypa fruticans* (1.56 μmol $m^{-2}s^{-1}$) and *Ceriops decandra* (2.32 μmol $m^{-2}s^{-1}$). In many species, an abrupt rise in leaf temperature retarded the photosynthetic process. In winter, the rate of transpiration and stomatal conductance reached their maxima in *A. marina* (4.83 mmol $m^{-2}s^{-1}$ and 124.23 mmol $m^{-2}s^{-1}$, respectively) and their mimima in *Excoecaria agallocha* (1.85 mmol $m^{-2}s^{-1}$ and 49.19 mmol $m^{-2}s^{-1}$, respectively). In contrast, the maximum summer readings were recorded in *E. agallocha* (6.07 mmol $m^{-2}s^{-1}$ and 192.74 mmol $m^{-2}s^{-1}$ respectively).

Keywords: leaf, mangrove, PAR, photosynthesis, salinity, stomatal conductance, transpiration

Photosynthesis is the only mechanism for energy input into the living world. Approximately 112,000 calories of energy are required to reduce 1 mole of CO_2 to a carbon-storage form (Mavi, 1994). Light is made available for this process as photons (discrete packets of energy), each with an energy content of about 41,000 calories mol^{-1}. Eight to twelve quanta are absorbed during photosynthesis (Mavi, 1994).

As sunlight passes through atmosphere to the earth's surface, considerable energy is lost from absorption and scattering caused by water vapor, dust, CO_2, and O_3. The residual that reaches the plants comprises approximately 50% infrared and 5% UV. The balance (approx. 400 J $m^{-2}s^{-1}$), which is capable of driving photosynthesis, is photosynthetically active radiation (PAR; McCree, 1981). PAR is further defined by the Dutch Committee on Plant Irradiation (Wassink, 1953) as the third (0.70 to 0.61 μm), fourth (0.61 to 0.51 μm), and fifth (0.51 to 0.40 μm) bands of the solar spectrum.

Of the total absorbed PAR, >95% is usually lost as heat, so that <5% is captured during photosynthesis (Salisbury and Ross, 1995). During that process, the excess excitation energy is dissipated via the thylakoid pH gradient (Krause and Behrend, 1986), and by xanthophyll cycle pigments. Such an energy release can be followed by photoinhibition, which enables "down regulation" to balance the light energy received by Photosystem II with its capacity to use it (Chow, 1994). Hence, a leaf exposed to full sunlight may not be completely efficient in utilizing light energy, so that maximum photosynthetic efficiency is usually obtained only at low irradiance levels (Mavi, 1994).

Light is collected primarily by chlorophyll pigments that absorb light at wavelengths <480 nm and between 550- and 700 nm. Although chlorophyll a is the only constituent of the photosynthetic reaction center, it does not absorb light over a wide range of the visible spectrum. However, chlorophyll b does absorb and efficiently transfer light energy to chlorophyll a, and enhances the plant's efficiency for utilizing sunlight (Heldt, 1999).

The effect of temperature on photosynthesis depends on the species and the environmental conditions under which a plant is grown and measured (Salisbury and Ross, 1995). The photosynthetic rate usually increases with temperature, to a maximum value. This value is maintained over a broad temperature range, for which its promotional effect is nearly balanced by increased respiration and photorespiration rates. At extremely high temperatures, metabolic enzymes become denatured, and ATP and NADPH are not produced quickly enough to allow increase in CO_2 fixation, thus leading to a rapid decline in the photosynthetic process (Salisbury and Ross, 1995).

Even though only an insignificant amount of water is needed for CO_2 assimilation (700 to 1300 mole to

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fix 1 mole CO_2 (Heldt, 1999)), water stress may seriously retard the rate of photosynthesis. Loss of water is unavoidable because CO_2 uptake requires the stomata to be open. The much higher concentration of water vapor in leaf cells (~31000 ppm) than in the air (~350 ppm) means that a considerably high amount of water escapes during CO_2 influx (Heldt, 1999). Therefore, the opening of the stomata is regulated to minimize water loss by restricting the vapor pressure gradient that drives transpiration from the leaf interior through the stomatal pores. To prevent dehydration of the protoplast, plants often decrease stomatal conductance, which leads to a lower transpiration rate and consequently, slower CO_2 assimilation (Heldt, 1999).

In the tidal wetlands along tropical and subtropical coasts, high-saline soils force the dominating mangrove vegetation to cope with physiologically dry conditions despite an abundant water supply. To exclude excessive salt intake, mangrove roots take up water very slowly, primarily via the symplastic pathway (Moon et al., 1986; Lin et al., 1993). As a result, salinity in the water continues to rise until a sufficiently large concentration gradient develops to diffuse the salt back to the soil surface. In such situations, rapid transpiration rates may cause soil-bound salt to become so concentrated that water uptake by the roots is severely restricted. In contrast, when water flow is limited, rapid transpiration rates induce considerably low water potential in the leaves. This causes excessive accumulation of salt in leaf cells to maintain turgor that, in turn, may dehydrate the cytosol and denature several essential metabolic enzymes. Furthermore, rapid induction of a very low water potential can strain the xylem cavity, leading to embolism (Ball and Passioura, 1993).

The capacity for plants to function under low stomatal conductance makes it possible to maintain water potential above a threshold value that generally would induce substantial embolism (Sperry et al., 1988). Salinity varies both temporally and spatially in a mangrove swamp, but soil salt contents around the roots change more slowly than does the microclimate surrounding the leaves. This phenomenon has a direct and immediate effect on diurnal water use in relation to carbon gain (Ball, 1988). Levels of both salt and light also may interact, thereby reducing the capacity for photosynthetic carbon assimilation under conditions of high salinity combined with high irradiance (Björkman et al., 1988). Nonetheless, Cheeseman et al. (1991) have found no evidence of photoinhibition in exposed leaves of *Bruguiera parviflora* growing under natural illumination. Likewise, no ill effects were seen in *Rhizophora mangle* produced in the greenhouse under water-stressed conditions (Cheeseman, 1994). Therefore, Cheeseman et al. (1997) have questioned the occurrence of photoinhibition in mangroves.

Although photosynthesis and water use efficiency of mangroves has been studied throughout the world, few data are available on the mangroves of Sundarbans, India. In the study presented here, we investigated rates of photosynthesis, transpiration, stomatal conductance, and leaf temperature for some true mangrove species. Our research compared physiological parameters during two different seasons in order to determine the influence of salinity and irradiance.

MATERIALS AND METHODS

We measured the rates of photosynthesis, transpiration, stomatal conductance, and leaf temperature in 16 species of true mangroves belonging to nine families (Table 1). In addition, we recorded ambient temperature and PAR values during summer (May) and winter (November), using a Photosynthesis System (CI-301PS, CID, Inc., USA). The CO_2 gas analyzer (comprising an internal container of soda lime, a CO_2 absorbent, four valves, and two pumps) included an electronic mass flow meter to monitor the airflow rate. A built-in microprocessor controlled the valves and pumps. Measurements of photosynthesis, transpiration, and stomatal conductance also required a leaf chamber in conjunction with the analyzer. The rate of photosynthesis was determined by measuring the rate at which a particular concentration of CO_2 was assimilated by a known leaf area. The net photosynthesis rate was then calculated as:

$$P_n = -W \times (C_o - C_i)$$
$$= -2005.39 \times \{(V \times P)/(T_a \times A)\} \times (C_o - C_i);$$

where, C_o (C_i) = outlet (inlet) CO_2 concentrations (ppm or μmol/mol) and T_a = air temperature (K).

The transpiration rate was measured from the water vapor flux per one-sided leaf area, following the formula:

$$E = \{(e_o - e_i) / (P - e_o)\} \times W \times 10^3;$$

where, e_o (e_i) = outlet (inlet) water vapors (bar); P = atmospheric pressure (bar); and W = mass flow rate per leaf area (mol $m^{-2}s^{-1}$).

Stomatal conductance was calculated from transpiration rates and leaf-surface temperatures, according to:

Table 1. Physiological parameters measured to determine the response to light, temperature, and salinity by various mangrove species.

Species (Family)	Season	PAR (m mol $m^{-2}s^{-1}$) (±SE)	Air temp. (°C) (±SE)	Leaf temp. (°C) (±SE)	P (μmol $m^{-2}s^{1}$) (±SE)	T (mmol $m^{-2}s^{-1}$) (±SE)	S.C. (mmol $m^{-2}s^{-1}$) (±SE)	Salinity (PPT) (±SE)	Soil pH⁺ (±SE)
Aegialitis rotundifolia Roxb. *(Plumbaginaceae)*	Summer	1.50(0.47)	37.43(0.07)	39.77(0.64)	8.97(0.19)	3.51(0.18)	93.13(12.09)	18(0.20)	7.45(0.01)
	Winter	0.90(0.19)	33.38(0.30)	36.68(0.49)	6.06(1.95)	3.04(0.83)	80.42(24.35)	19(0.03)	7.50(0.16)
Aegiceras corniculatum (L) Blan *(Myrsinaceae)*	Summer	1.18(0.11)	36.43(0.14)	39.80(1.41)	6.25(4.74)	3.43(0.93)	98.17(43.77)	24(1.76)	7.76(0.19)
	Winter	0.79(0.33)	32.65(1.49)	32.91(3.31)	7.24(6.15)	3.44(1.68)	104.54(50.16)	15(0.06)	6.80(0.18)
Avicennia alba Blume (Avicenniaceae)	Summer	1.78(0.41)	37.05(0.78)	37.20(2.69)	9.58(4.09)	3.21(1.53)	108.65(27.37)	15(0.06)	6.80(0.18)
	Winter	1.18(0.19)	25.25(0.28)	38.10(1.72)	11.11(3.38)	4.32(0.91)	106.49(31.75)	15(0.06)	6.80(0.18)
Avicennia marina (Forsk) Vierh (Avicenniaceae)	Summer	0.98(0.36)	37.13(0.98)	37.63(3.87)	8.98(3.18)	3.42(0.44)	128.30(8.72)	16(1.21)	6.80(0.18)
	Winter	1.43(0.20)	32.27(0.95)	37.37(1.87)	11.80(3.18)	4.83(0.44)	124.23(8.72)	24(1.76)	7.73(1.35)
Avicennia officinalis L. (Avicenniaceae)	Summer	1.46(0.89)	37.53(0.49)	38.93(2.89)	8.22(1.42)	3.38(0.21)	106.67(40.25)	15(0.06)	6.80(0.18)
	Winter	0.65(0.33)	30.00(0.87)	31.45(1.39)	8.56(3.94)	2.02(0.33)	89.53(24.33)	24(1.76)	7.76(0.19)
Bruguiera gymnorrhiza (L) Lam (Rhizophoraceae)	Summer	1.79(0.06)	37.47(0.21)	46.10(2.42)	3.81(2.14)	2.89(0.55)	45.47(17.08)	15(0.06)	6.80(0.18)
	Winter	0.99(0.34)	29.32(1.93)	31.34(3.76)	8.05(1.12)	2.13(0.39)	117.60(55.87)	27(1.19)	7.80(0.28)
Bruguiera sexangula W & A *(Rhizophoraceae)*	Summer	0.88(0.32)	30.50(3.85)	33.42(2.15)	5.89(2.41)	1.90(0.29)	72.10(20.98)	18(0.20)	7.45(0.01)
Ceriops decandra (Grif) D.H. (Rhizophoraceae)	Summer	1.46(0.29)	36.07(4.59)	36.96(5.09)	2.32(0.09)	1.81(0.19)	66.50(2.97)	18(0.20)	7.45(0.01)
	Winter	0.94(0.27)	33.25(0.00)	36.65(1.06)	4.54(0.09)	2.25(0.06)	55.10(9.26)	15(0.06)	6.80(0.18)
Ceriops tagal (Pierr) Robins (Rhizophoraceae)	Summer	1.57(0.59)	36.63(0.35)	39.43(0.47)	4.37(0.25)	3.40(1.93)	82.00(44.37)	16(1.21)	7.40(0.07)
Excoecaria agallocha L. (Euphorbiaceae)	Summer	1.58(0.27)	36.44(0.79)	38.83(2.9)	8.47(7.00)	6.07(0.81)	192.74(97.58)	15(0.06)	7.50(0.16)
	Winter	1.23(0.33)	30.03(1.08)	36.58(2.57)	5.57(3.12)	1.85(0.51)	49.19(14.35)	19(0.03)	7.50(0.16)
Heritiera fomes (Buch) Ham (Sterculiaceae)	Winter	1.21(0.16)	30.19(0.84)	33.39(2.18)	13.21(3.57)	2.95(0.53)	119.06(35.19)	24(1.76)	7.76(0.19)
Nypa fruticans# (Thunb) Wurmb (Arecaceae)	Summer	0.11(0.38)	24.90(2.05)	24.35(2.33)	1.56(0.42)	0.14(0.71)	2.95(1.98)	15(0.06)	7.40(0.07)
	Winter	1.23(0.26)	30.65(1.77)	35.10(3.92)	8.56(3.71)	2.70(0.51)	87.60(45.69)	27(1.19)	7.80(0.28)
Phoenix paludosa# Roxb. (Arecaceae)	Summer	2.02(0.09)	38.43(0.74)	45.80(2.32)	3.69(2.12)	2.26(0.63)	30.23(5.36)	16(1.21)	7.40(0.07)
Rhizophora mucronata Lam *(Rhizophoraceae)*	Summer	0.69(0.69)	34.97(0.14)	35.73(0.07)	5.96(2.71)	2.23(0.55)	89.67(21.35)	27(1.19)	7.80(0.28)
	Winter	0.71(0.15)	31.88(0.46)	34.25(1.79)	5.48(1.08)	2.45(0.19)	56.97(24.25)	18(0.20)	7.45(0.01)
Xylocarpus granatum Konig. *(Meliaceae)*	Summer	1.41(0.15)	36.50(0.49)	40.97(1.91)	3.47(0.81)	1.89(0.19)	44.23(0.78)	16(1.21)	7.40(0.07)
Xylocarpus mekongensis Piere. *(Meliaceae)*	Summer	1.46(0.47)	35.92(1.97)	41.02(5.66)	3.96(1.69)	1.74(0.74)	41.56(23.65)	18(0.20)	7.45(0.01)
	Winter	0.78(0.07)	32.35(1.97)	34.02(5.66)	6.75(1.69)	2.63(0.74)	86.88(23.65)	15(0.06)	6.80(0.18)

N.B. P, T, and S.C. indicate rate of photosynthesis, transpiration, and stomatal conductance, respectively.
#Monocot species..
Values within parentheses indicate +/− Standard Error (SE).
Each data entry is the average of the values measured from three leaves in each plant and three plants from each species..

$$C_{leaf} = W / [\{(e_{leaf} - e_o) / (e_o - e_i)\} \times \{(P - e_o) / P\} - R_b W] \times 1000;$$

where, e_{leaf} = saturated water vapor at leaf temperature (bar); R_b = leaf boundary layer resistance (m^2s^{-1}/mol); P = atmospheric pressure (bar); and W = mass flow rate per leaf area (mol $m^{-2}s^{-1}$).

For each parameter, data were collected from three individual leaves at the upper, middle, and lower portions of each plant. Because of cloudy weather and extremely low PAR levels, the values for photosynthetic rates in some species were zero or negative and, therefore, were eliminated from our study. We used analyses of variance (ANOVA) to evaluate data for photosynthesis, transpiration, and stomatal conductance during summer and winter, and to identify any statistically significant differences among species.

Soil salinity and pH were estimated according to the standard method of Jackson (1973), using air-dried soil samples collected near each plant. Data were recorded for three plants of each species growing in different locations in the Sundarbans.

RESULTS AND DISCUSSION

Levels of PAR varied significantly between summer and winter (Table 1). In the summer, the highest PAR values were recorded in *Phoenix paludosa* (2.02 mmol $m^{-2}s^{-1}$) and *Bruguiera gymnorrhiza* (1.79 mmol

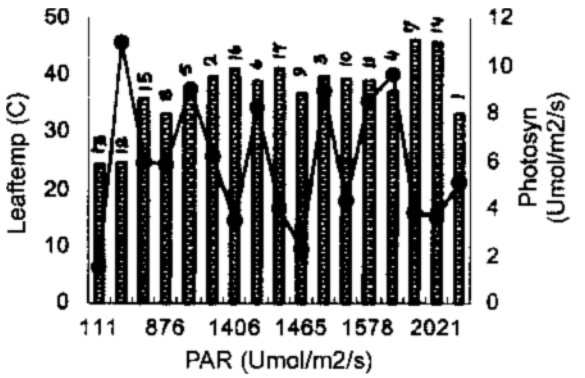

Figure 1. Relation between rate of photosynthesis and leaf temperature during summer at specific PAR values. ▦, air temp; -●-, leaf temp. (N.B. Value over each histogram indicates individual species: 1, *Acanthus ilicifolius*; 2, *Aegiceras corniculatum*; 3, *Aegialitis rotundifolia*; 4, *Avicennia alba*; 5, *Avicennia marina*; 6, *Avicennia officinalis*; 7, *Bruguiera gymnorrhiza*; 8, *Bruguiera sexangula*; 9, *Ceriops decandra*; 10, *Ceriops fagal*; 11, *Excoecaria agallocha*; 12, *Heritiera fomes*; 13, *Nypa fruticans*; 14, *Phoenix paludosa*; 15, *Rhizophora mucronata*; 16, *Xylocarpus granatum*; 17, *Xylocarpus mekongensis*).

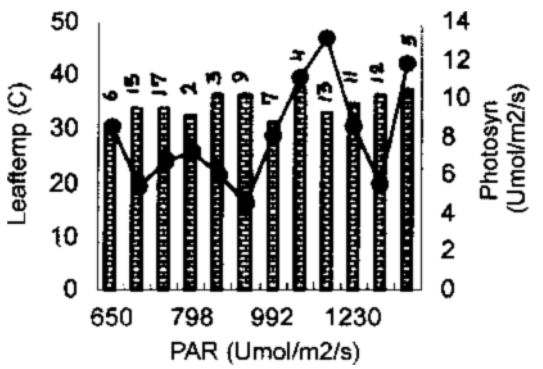

Figure 2. Relation between leaf temperature and rate of photosynthesis during winter at specific PAR values. ▦, air temp; -●-, leaf temp. (N.B. Value over each histogram indicates individual species: 2, *Aegiceras corniculatum*; 3, *Aegialitis rotundifolia*; 4, *Avicennia alba*; 5, *Avicennia marina*; 6, *Avicennia officinalis*; 7, *Bruguiera gymnorrhiza*; 9, *Ceriops decandra*; 11, *Excoecaria agallocha*; 12, *Heritiera fomes*; 13, *Nypa fruticans*; 15, *Rhizophora mucronata*; 17, *Xylocarpus mekongensis*).

$m^{-2}s^{-1}$). In winter, the maximum PAR was measured from *Avicennia marina* (1.43 mmol $m^{-2}s^{-1}$). Interestingly, rates of photosynthesis did not rise significantly with the concomitant increase in PAR (Figs. 1 and 2). For example, a summertime photosynthetic rate for *B. gymnorrhiza* of 3.81 µmol $m^{-2}s^{-1}$ was paired with a PAR value of 1.79 mmol $m^{-2}s^{-1}$. In the winter, however, photosynthesis was measured at 8.05 µmol $m^{-2}s^{-1}$, but with a PAR of only 0.99 mmol $m^{-2}s^{-1}$.

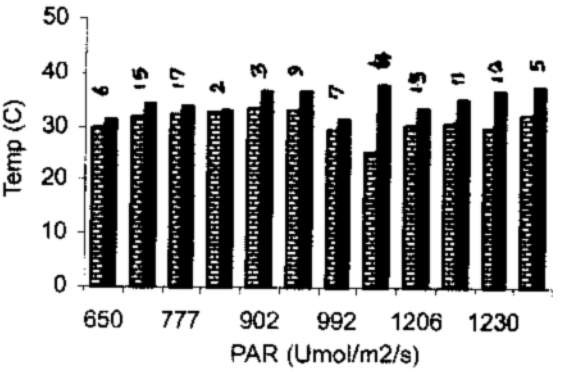

Figure 3. Difference in leaf temp and air temp at specific PAR values during winter. ▦, air temp; ■, leaf temp. (N.B. Value over each histogram indicates individual species: 2, *Aegiceras corniculatum*; 3, *Aegialitis rotundifolia*; 4, *Avicennia alba*; 5, *Avicennia marina*; 6, *Avicennia officinalis*; 7, *Bruguiera gymnorrhiza*; 9, *Ceriops decandra*; 11, *Excoecaria agallocha*; 12, *Heritiera fomes*; 13, *Nypa fruticans*; 15, *Rhizophora mucronata*; 17, *Xylocarpus mekongensis*).

Indeed, compared with summertime, considerably higher rates of photosynthesis were measured in the winter for some species (i.e., *Aegiceras corniculatum*, *Avicennia officinalis*, *B. gymnorrhiza*, and *Xylocarpus mekongensis*), despite their lower levels of PAR (0.65 to 0.99 mmol m^{-2} s^{-1}) (Figs. 1 and 3). Thus, the optimum PAR required for photosynthesis in mangroves may be lower than that absorbed on a bright, sunny day. This observation also supports the findings of Ball and Critchley (1982) and Cheeseman et al. (1991). The leaves of field-grown mangroves generally become light saturated at incident quantum flux densities ranging from 25 to 50% of full sunlight. However, our ANOVA results also indicated that during summer, the difference in the rate of photosynthesis among species was not significant, but the difference was clearly significant in the winter (Tables 2 and 3).

For all our tested species, leaf temperature exceeded ambient temperature during both the seasons (Figs. 3 and 4). Heat dissipation was not adequate from the mangrove leaves, probably because transpiration was restricted. This then resulted in relatively higher leaf temperatures. In some species, *viz. B. gymnorrhiza*, *Ceriops decandra*, *P. paludosa*, *Xylocarpus granatum*, and *Xylocarpus mekongensis*, the rate of photosynthesis decreased significantly during the summer when leaf temperatures abruptly arose to >36 ^{0}C (Table 1). Cowan (1982) has shown that shading mangrove leaves from high light intensities allows them to maintain fairly constant, but low, assimilation rates throughout the day. In this way, a greater net gain of carbon is

Table 2. ANOVA for rate of photosynthesis in summer.

Source	Degree of freedom	Mean square	F
Treatment	14	21.60	1.80***
Error	42	11.98	

***not significant.

Table 3. ANOVA for rate of photosynthesis in winter.

Source	Degree of freedom	Mean square	F
Treatment	11	32.61	2.89*
Error	58	11.27	

*significant to 1% level.

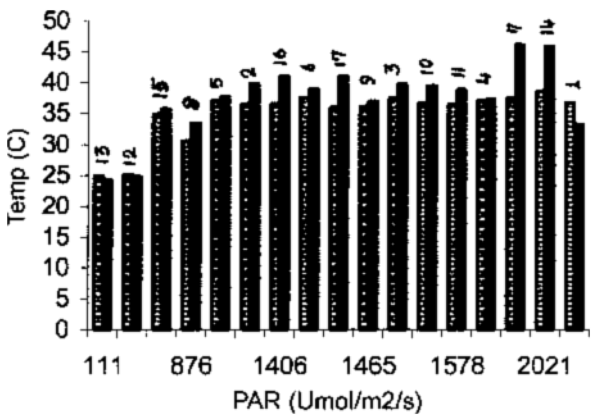

Figure 4. Difference in air temp and leaf temp at specific PAR values during summer. ▦, air temp; ■, leaf temp. (N.B. Value over each histogram indicates individual species: 1, *Acanthus ilicifolius*; 2, *Aegiceras corniculatum*; 3, *Aegialitis rotundifolia*; 4, *Avicennia alba*; 5, *Avicennia marina*; 6, *Avicennia officinalis*; 7, *Bruguiera gymnorrhiza*; 8, *Bruguiera sexangula*; 9, *Ceriops decandra*; 10, *Ceriops fagal*; 11, *Excoecaria agallocha*; 12, *Heritiera fomes*; 13, *Nypa fruticans*; 14, *Phoenix paludosa*; 15, *Rhizophora mucronata*; 16, *Xylocarpus granatum*; 17, *Xylocarpus mekongensis*).

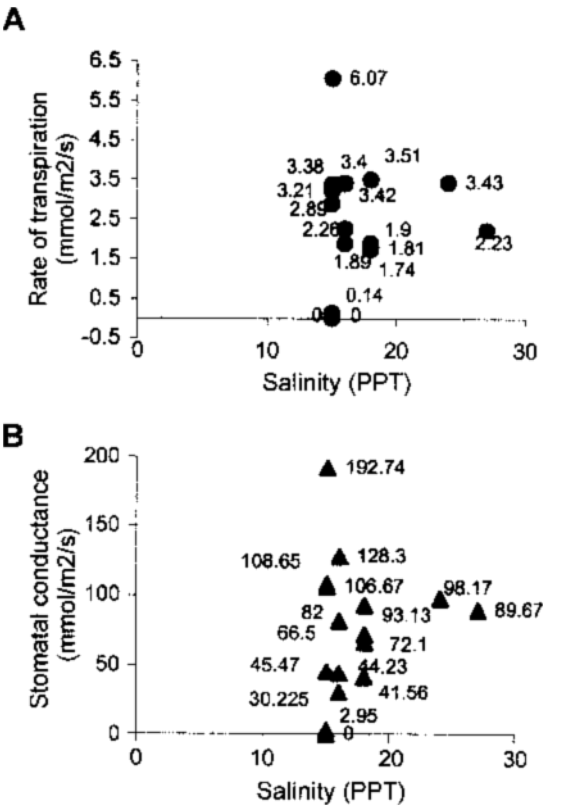

Figure 5. A. Transpiration rates at different salinity levels during summer. **B.** Stomatal conductance at different salinity levels during summer. ●, Transpiration; ▲, St. cond. (N.B. Original data of individual species shown in Table 1).

achieved than if the leaves were subject to temperature-dependent inhibition of photosynthesis for extended periods.

In both seasons, the average soil salinity in the Sundarbans ranged between 15 and 27 parts per thousand (ppt) during high tides; the higher levels were recorded near *B. gymnorrhiza*, *Nypa*, and *Rhizophora* (all 27 ppt); and near *Aegiceras*, *A. marina*, and *Heritiera* (all 24 ppt). Winter salinity often was even higher than the summer level (Table 1). During the latter, stomatal conductance varied from 30.225 mmol $m^{-2}s^{-1}$ (*P. paludosa*) to 192.74 mmol $m^{-2}s^{-1}$ (*Excoecaria agallocha*), while in the former season, the range was between 49.19 mmol $m^{-2}s^{-1}$ (*E. agallocha*) and 124.23 mmol $m^{-2}s^{-1}$ (*A. marina*) (Figs. 5B and 6B).

Transpiration rates varied from 1.74 mmol $m^{-2}s^{-1}$ (*X. mekongensis*) to 6.07 mmol $m^{-2}s^{-1}$ (*E. agallocha*) during the summer, and between 1.85 mmol $m^{-2}s^{-1}$ (*E. agallocha*) and 4.83 mmol $m^{-2}s^{-1}$ (*A. marina*) in the winter (Figs. 5A and 6A). For *A. corniculatum*, *Aegialitis rotundifolia*, and *Avicennia* sp., both transpiration and stomatal conductance were remarkably high in both seasons. However, in *E. agallocha*, those two parameters reached their maxima in summer and their minima in winter (Figs. 5 and 6). This probably occurred because the increase in soil salinity retarded the rate of transpiration, stomatal conductance, and photosynthesis of this species during the winter.

In *A. corniculatum*, the rate of photosynthesis and the stomatal response was depressed by enhanced salinity in the substratum (Table 1), an observation shared by Ball and Farquhar (1984). Ball et al. (1988) also reported that, in a review of numerous environmental factors that could affect photosynthesis, stomatal conductance at a given assimilation rate especially

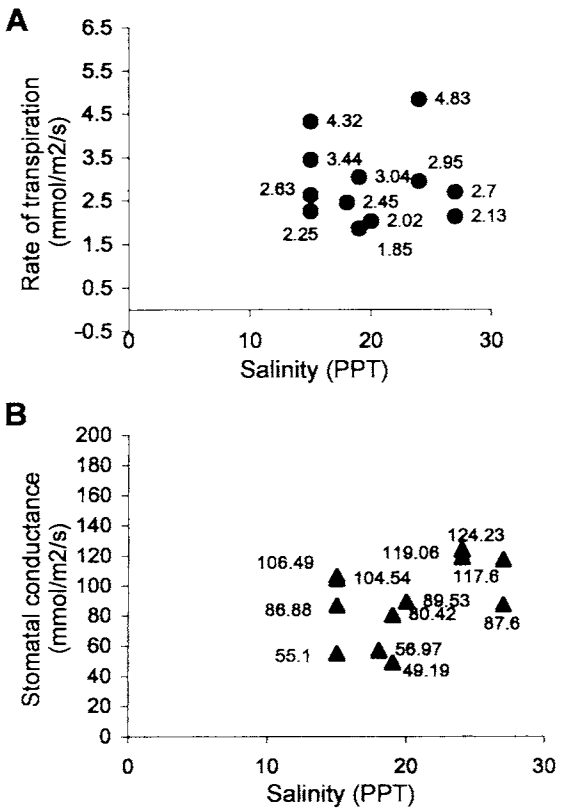

Figure 6. A. Transpiration rate at different salinity levels during winter. **B.** Stomatal conductance at different salinity levels during winter. ●, Transpiration; ▲, st. cond. (N.B. Original data of individual species shown in Table 1).

decreased when salinity tolerance increased for a particular species. Low stomatal conductance probably restricts the efflux of water, as well as the influx of CO_2. This then causes a leaf to operate under a low intercellular CO_2 concentration and a correspondingly low assimilation rate, but at a high efficiency of water-use. The results of our ANOVA indicated significant differences in transpiration and stomatal conductance among the tested species, and in both seasons (Tables 4-7).

Even under increased saline levels in the soil, the higher rate of photosynthesis for *Avicennia* sp., *B. gymnorrhiza*, *Nypa fruticans*, and *Rhizophora mucronata* demonstrates their efficiency with salt tolerance (Table 1). This was in contrast to our observations of *A. corniculatum*, *A. rotundifolia*, *C. decandra*, *E. agallocha*, and *X. mekongensis*. Although describing the complete mechanism for carbon assimilation during salinity stress was beyond the scope of our study, a detailed estimation of those physiological parameters warrants further investigation.

Table 4. ANOVA for rate of transpiration in summer.

Source	Degree of freedom	Mean square	F
Treatment	14	7.98	14.73*
Error	42	54.41	

*significant to 1% level.

Table 5. ANOVA for rate of transpiration in winter.

Source	Degree of freedom	Mean square	F
Treatment	11	4.77	9.06*
Error	58	52.63	

*significant to 1% level.

Table 6. ANOVA for stomatal conductance in summer.

Source	Degree of freedom	Mean square	F
Treatment	14	8675.6	3.28*
Error	42	2643.8	

*significant to 1% level.

Table 7. ANOVA for stomatal conductance in winter.

Source	Degree of freedom	Mean square	F
Treatment	11	3013.5	2.19**
Error	58	1375.6	

**significant to 5% level.

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