Photosynthesis and Water-Use Characteristics in Indian Mangroves

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Photosynthesis and water efflux were measured in different PAR and stomatal conductance in members of Avicenniaceae and Rhizophoraceae. Trend of leaf temperature with irradiance and its effect on photosynthesis were also estimated. In most of the studied species, photosynthesis and stomatal conductance followed similar trends with increase in irradiance. The rate of net photosynthesis and stomatal conductance were higher in members of Avicenniaceae than in Rhizophoraceae. In Avicenniaceae, the optimum PAR for maximum photosynthesis ranged between 1340-1685 μmol m^{-2}s^{-1}, which was also higher than that of Rhizophoraceae (840-1557 μmol m^{-2}s^{-1}). Almost in all the studied taxa, transpiration and stomatal conductance followed similar trends and reached the maximal peaks at the same PAR value. The range of breakeven leaf temperature was almost the same in both the families (34-36°C in Avicenniaceae and 33.5-36.3°C in Rhizophoraceae), beyond which assimilation rate declined.

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

Mangroves are a group of halophytes growing in tropical and subtropical estuaries. Despite regular tidal inundation, these plants have to face physiologically dry soil condition due to high salinity in soil. Besides, in a mangrove swamp, change in the microclimate, i.e. irradiance, temperature and precipitation, occurs regularly surrounding the leaves. This phenomenon has a direct and immediate effect on diurnal water use in relation to carbon gain (Ball, 1988).

Considerable amount of incident sunlight is lost owing to absorption and scattering. The residual irradiance that is utilized in photosynthesis is called photosynthetically active radiation (PAR; McCree, 1981). A leaf exposed to full sunlight may not be completely efficient to utilize light energy, and according to Mavi (1994), the maximum photosynthetic efficiency is usually obtained only at low irradiance levels. Golley et al. (1962) published an account of productivity of a mangrove forest in the Caribbean and reported that light saturation occurs at about 5000 f.c., which is about 50% of the incident light in the tropics. Later, this report was supported by Ball and Critchley (1982), Björkman et al. (1988) and Cheeseman et al. (1991), who found a wider range, i.e. 25%-50% as saturation flux density.

During assimilation, CO_2 influx needs opened stomata that allow escape of considerably high amount of water vapor from leaf cells. To prevent dehydration of protoplast, plants often decrease stomatal conductance leading to lower transpiration rate and consequently slower CO_2 assimilation (Heldt, 1999). Mangrove roots take up water very slowly, primarily via the symplastic pathway to exclude excess amount of salt intake (Lin and Sternberg, 1993). Thus, soil salinity enhances gradually and rapid transpiration rates in such a condition may increase the salt concentration to such an extent that may severely retard water uptake by roots. On the other hand, when water flow is limited, rapid transpiration rate may induce considerably high osmotic potential in 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. Hence, mangroves have to restrict excess water efflux, and stomatal opening is therefore regulated by reducing stomatal conductance. Passioura et al. (1992) calculated the limiting rate of transpiration in mangroves to be about 1 mm per day.

The effect of temperature on photosynthesis depends on the species and the environmental conditions. The photosynthetic rate usually increases with temperature to a maximum value and the value is maintained over a wide range of temperature when the promotional effect is nearly balanced by increased respiration and photorespiration rates (Salisbury and Ross, 1995). Leaf temperature also has a major effect on enzymatic reactions and membrane processes that in turn affects photosynthesis.

Although ample studies have been carried out on ecophysiology of mangroves throughout the world

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(Björkman et al., 1988; Cheeseman et al., 1991; Ball and Passioura, 1993), very few data are yet available on the mangrove plant community of the Indian subcontinent, especially the Sundarbans forest. Aim of the present study is to estimate the effect of microclimates (irradiance and temperature) on photosynthesis and water efflux in two Indian mangrove families, viz. Avicenniaceae and Rhizophoraceae, which is an extension work of Nandy and Ghose (2001).

MATERIALS AND METHODS

Eight species of true mangroves belonging to two different families (Avicenniaceae and Rhizophoraceae) were studied in vivo for the rate of net photosynthesis, transpiration and stomatal conductance in different PAR and leaf temperatures. A CO_2 gas analyser (PS 301 CID, USA) with an electronic mass flow meter was used to monitor airflow rate. Measurements were taken from the exposed surface of leaves from top, middle and bottom of each plant. The rate of net photosynthesis (P_n) was determined by measuring assimilated CO_2 concentration at a given time at a known leaf area.

$P_n = -W \times (C_o - C_i) = -2005.39 \times \{(V \times P) / (T_a \times A)\} \times (C_o - C_i)$ .... $[C_o (C_i) =$ outlet (inlet) CO_2 conc. (μmol m^{-2}s^{-1}) and $T_a =$ air temp. (K)].

Transpiration rate (E) was measured from the water vapor flux per one-sided leaf area.

$E = \{(e_o - e_i) / (P - e_o)\} \times W \times 10^3$ .... $[e_o$ $(e_i) =$ outlet (inlet) water vapour (bar); P = atm. pressure (bar) and W = mass flow rate per leaf area (mmol m^{-2}s^{-1})].

Stomatal conductance (C_{leaf}) was obtained by measuring transpiration and leaf surface temperature.

$C_{leaf} = W / [\{e_{leaf} - e_o) / (e_o - e_i)\} \times \{(P - e_o) / P\} - R_bW]$ $\times 1000$ .... $[e_{leaf} =$ saturated water vapour at leaf temperature (bar); $R_b =$ leaf boundary layer resistance (m^{2}s / mol); P = atm. pressure (bar) and W = mass flow rate per leaf area (mmol m^{-2}s^{-1})].

The data recorded and stored in the instrument were dumped out and computed through the RS 232 Port (a software provided with the instrument PS 301 CID, for downloading on the computer from the microchip of the instrument and makes it readable).

RESULTS AND DISCUSSION

In members of Avicenniaceae, photosynthesis increased with increase in PAR up to certain extent,

and then declined gradually (Fig. 1A-C). The optimum PAR for maximum photosynthesis was 1340 μmol m^{-2}s^{-1} in Avicennia alba, 1685 μmol m^{-2}s^{-1} in Avicennia marina and 1526 μmol m^{-2}s^{-1} in Avicennia officinalis. In A. alba and A. officinalis, maximum photosynthesis was measured at the leaf temperature of 34.1°C and 34.4°C, respectively (Fig. 3A and C), while in A. marina photosynthesis increased till 36.6°C (Fig. 3B). In A. marina, transpiration and stomatal conductance rose continuously to 1860 μmol m^{-2}s^{-1} PAR. In A. alba and A. officinalis, the trends were almost similar to that of photosynthesis, the maximal peak being noticed at 1383 and 1012 μmol m^{-2}s^{-1}.

In A. officinalis, photosynthesis continued to rise even after CO_2 influx was restricted beyond 1012 μmol m^{-2}s^{-1} PAR due to stomatal closure (Fig. 1C). It was probably the enhanced CO_2 partial pressure inside mesophyll cells that maintained considerably high assimilation rate up to 1526 μmol m^{-2}s^{-1} PAR, above which photosynthesis dropped. On the other hand, in A. alba photosynthesis declined much before stomatal closure restricted CO_2 influx (Fig. 1A). In A. marina, however, photosynthesis declined beyond 1685 μmol m^{-2}s^{-1} PAR even though stomatal conductance increased with irradiance (Fig. 1B). However, photosynthesis and stomatal conductance followed similar trends in A. alba and A. officinalis. On the other hand, leaf temperature was maximum at 1175, 1383 and 1597 μmol m^{-2}s^{-1} PAR in A. alba, A. marina and A. officinalis, respectively (Fig. 2A-C), while the optimum PAR for maximum photosynthesis ranged between 1340-1685 μmol m^{-2}s^{-1}. Thus, heat-regulated inhibition of photosynthesis did not occur in Avicenniaceae. It contradicts the view of Osmond (1981) that under full sunlight, photosynthesis becomes light saturated, and the excess of excitation energy produced leads to photoinhibition in mangroves. The present observation rather points similar to Cheeseman et al. (1991) that there is no evidence of photoinhibition in naturally illuminated leaves of Bruguiera parviflora and Cheeseman (1994) who nullified any possibility of photoinhibition in Rhizophora mangle grown in greenhouse under water-stressed conditions. However, photosynthesis dropped down as leaf temperature exceeded 34-36°C (Fig. 3A-C).

In Bruguiera gymnorrhiza, photosynthesis and stomatal conductance followed almost similar trends (Fig. 2D). The assimilation rate is maximum at 840 μmol m^{-2}s^{-1} and stomatal conductance at 1078 μmol m^{-2}s^{-1} PAR. On the contrary, in Bruguiera sexangula
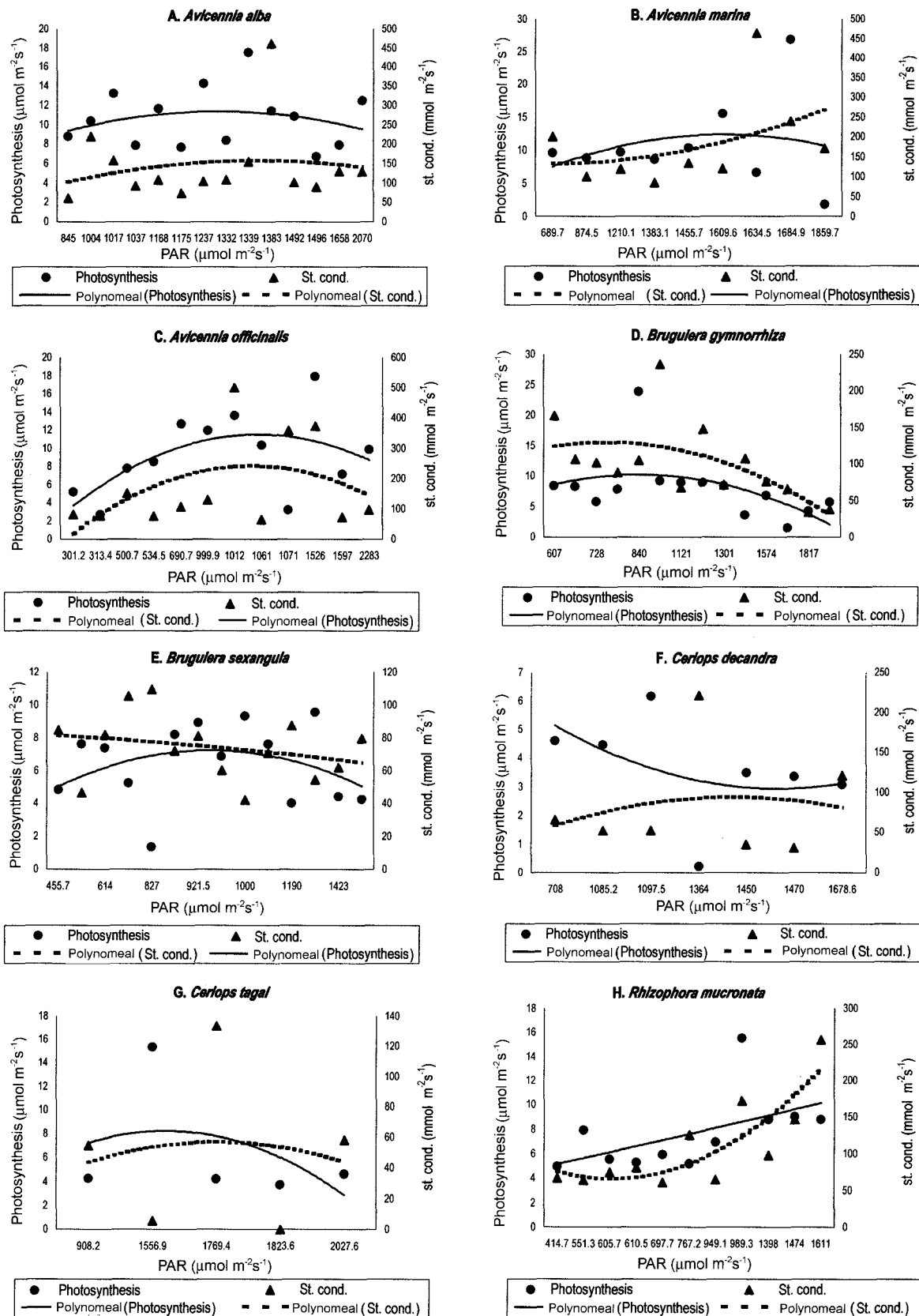
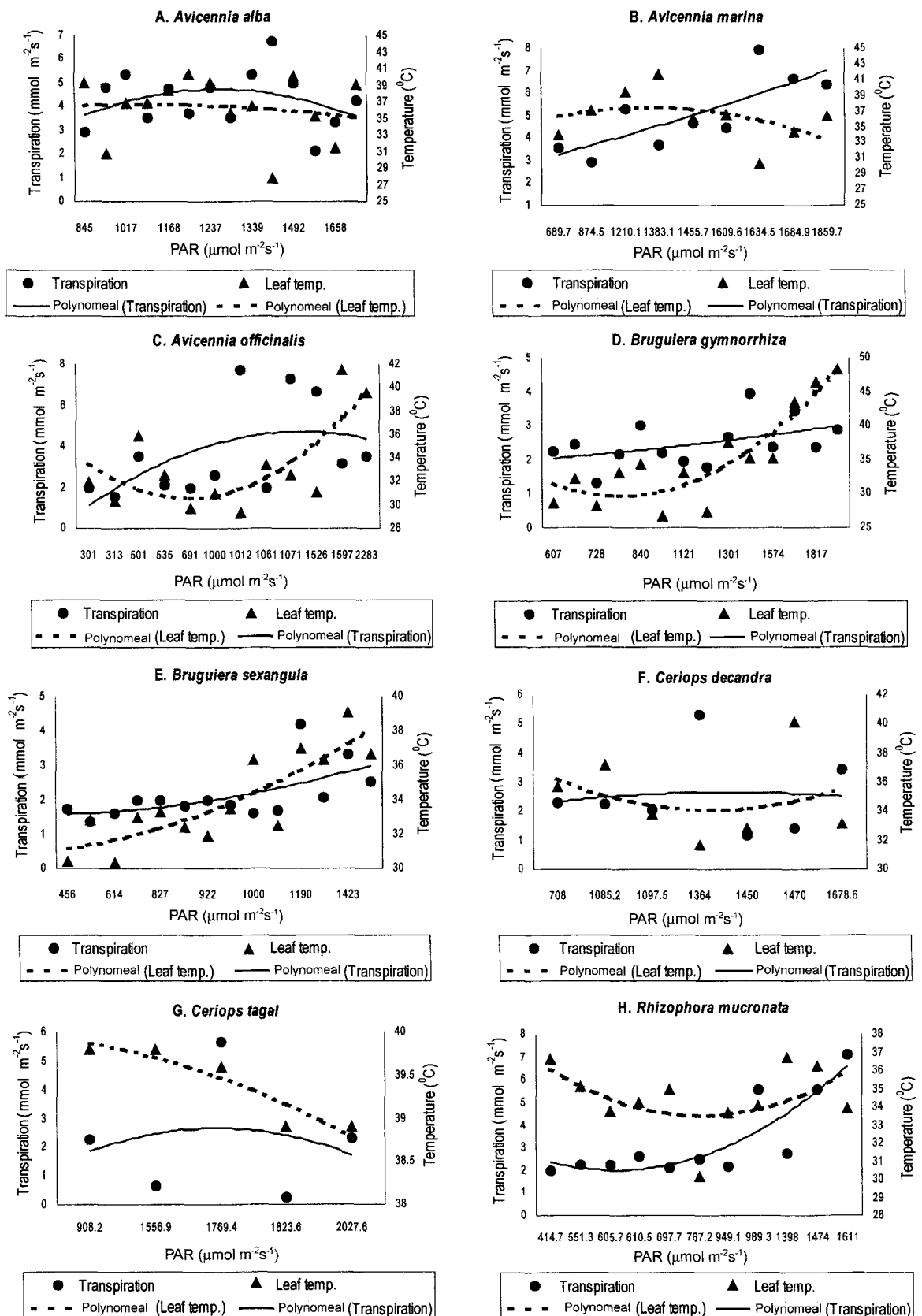**Figure 1.** PAR vs photosynthesis and stomatal conductance.

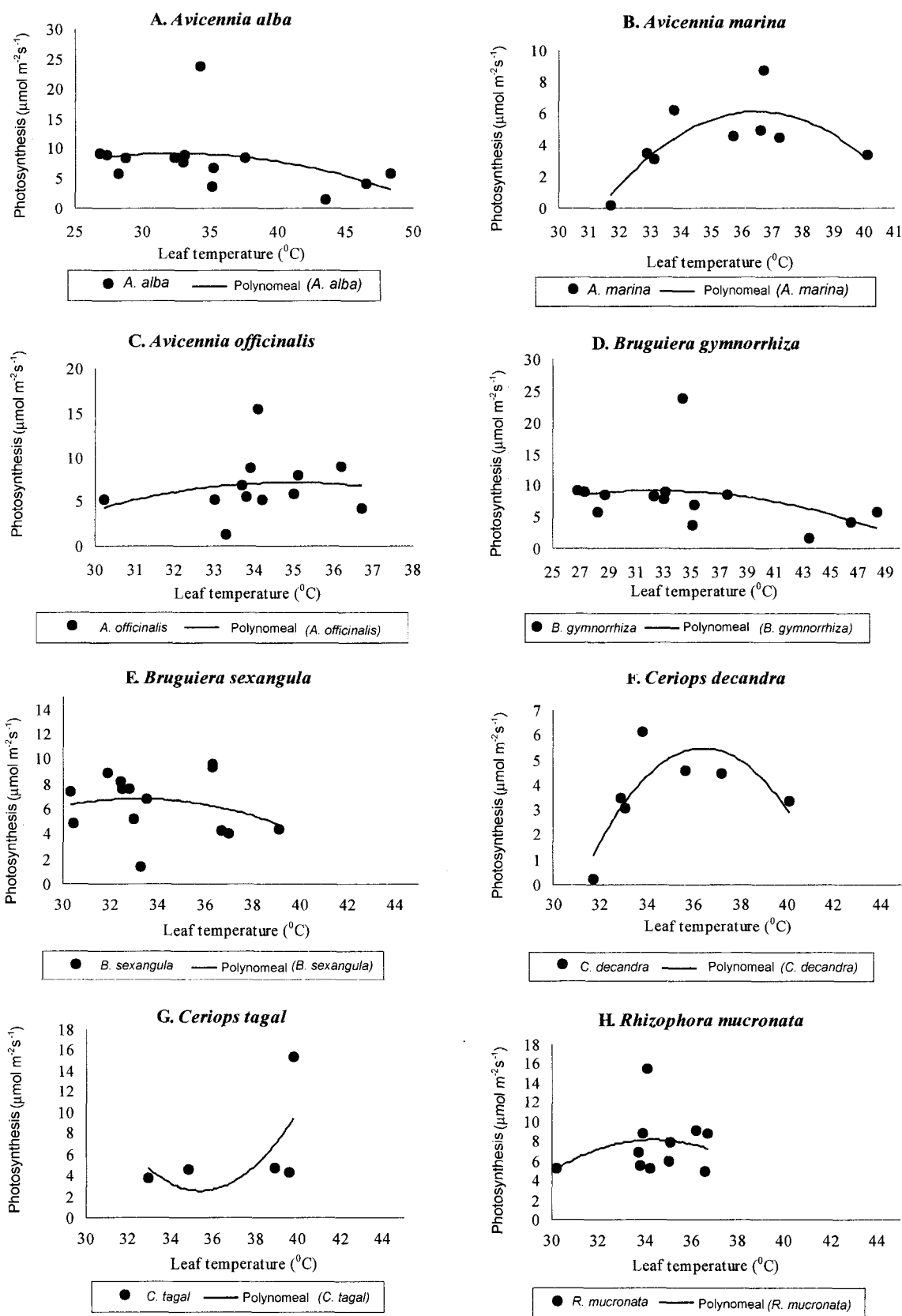**Figure 2.** PAR vs transpiration and leaf temperature.

Figure 3. Leaf temperature vs photosynthesis.

stomatal conductance dropped down almost linearly as PAR increased. In this species, the highest photosynthesis was measured at 1280 μmol m^{-2}s^{-1} and the highest stomatal conductance was at 827 μmol m^{-2}s^{-1} PAR (Fig. 1E). Actually, in *B. gymnorrhiza*, 840 μmol m^{-2}s^{-1} was the optimum PAR value, where leaf temperature was 34.3°C, beyond which there was an increase in leaf temperature (Fig. 2D); further rise in leaf temperature caused decrease in photosynthesis rate (Fig. 3D). *B. sexangula* seemed to withstand relatively higher temperature, so that photosynthesis increased till 36.3°C (Fig. 3E); further rise in leaf temperature got into the way of net assimilation with the highest at 1280 μmol m^{-2}s^{-1} PAR (Fig. 2E). Thus, in *B. gymnorrhiza*, photosynthesis dropped much before CO_2 influx was restricted, while in *B. sexangula*, carbon assimilation continued to rise till 1280 μmol m^{-2}s^{-1} PAR even though stomatal opening was restricted at considerably low irradiance. In both the species, transpiration increased almost linearly up to the PAR value of 1817 μmol m^{-2}s^{-1} (Fig. 2D and E). In *B. gymnorrhiza*, the highest transpiration was measured at 1400 μmol m^{-2}s^{-1} and in *B. sexangula* at 1190 μmol m^{-2}s^{-1} PAR.

In *Ceriops decandra*, the maximal peaks of photosynthesis and water efflux (transpiration and stomatal conductance) were attained at 1097 and 1364 μmol m^{-2}s^{-1} PAR respectively (Fig. 1F, 2F). Figure 3F indicates that in *Ceriops. decandra* photosynthesis reached its peak at 33.8°C that in turn was attained at 1097 μmol m^{-2}s^{-1} PAR (Fig. 2F) and decreased thereafter. On the contrary, in *Ceriops tagal* the highest assimilation rate (15.54 μmol m^{-2}s^{-1}) and leaf temperature (39.8°C) were measured at 1557 μmol m^{-2}s^{-1} PAR (Fig. 1G). Thus, photosynthesis when plotted against leaf temperature formed a cusp-shaped curve that increased gradually till the leaf temperature reaches its maximum value (39.8°C) (Fig. 3G). Transpiration and stomatal conductance were maximal when the irradiance was 1770 μmol m^{-2}s^{-1} (Fig. 2G). Thus, in both the species, photosynthesis declined even though CO_2 influx continued to rise. Once started to decrease, leaf temperature regained after 1470 μmol m^{-2}s^{-1} in *C. decandra*, while it continued to decrease till 2028 μmol m^{-2}s^{-1} in *C. tagal*.

In *Rhizophora mucronata*, photosynthesis was maximum at 989 μmol m^{-2}s^{-1} (Fig. 1H), and water efflux (transpiration and stomatal conductance) was maximum at 1611 μmol m^{-2}s^{-1} PAR (Fig. 1H, 2H). Photosynthesis increased almost linearly with irradiance. Transpiration and stomatal conductance initially formed a cusp, but increased beyond 697.7 μmol

m^{-2}s^{-1} till the PAR value reached 1611 μmol m^{-2}s^{-1}. Despite the increase in transpiration rate, leaf temperature was not reduced; rather it increased beyond 767 μmol m^{-2}s^{-1} PAR (Fig. 2H). At 989 μmol m^{-2}s^{-1} PAR, leaf temperature was 34.1°C, where assimilation rate was maximum (15.49 μmol m^{-2}s^{-1}) (Fig. 3H). Like Avicenniaceae, further hike in leaf temperature did not interfere in assimilation rate.

Thus, in Rhizophoraceae, the optimum PAR for maximum photosynthesis ranged between 840-1557 μmol m^{-2}s^{-1}, which was lower than that of Avicenniaceae. The rate of assimilation dropped as the leaf temperature exceeded 33.5-36.3°C amongst most of the studied members (except *C. tagal*). The limiting temperature was almost the same as that of Avicenniaceae.

The optimum PAR requirement in both the families was lower than the available irradiance in the Sundarbans forest in a bright sunny day. Nandy and Ghose (2001) also reported that in view of seasonal variation, the average values of photosynthesis do not rise significantly with the concomitant rise in PAR. This observation accords well with the explanation of Cowan (1982) that avoidance of high light intensities would allow the leaves of mangroves to maintain a fairly constant, but low, assimilation rate throughout the day, thus achieving a greater net gain of carbon than if the leaves were subjected to temperature dependent inhibition of photosynthesis for extended period.

Stomatal conductance seems to play a major role to determine net photosynthesis rate. Photosynthesis and stomatal conductance followed almost similar trends amongst the studied taxa (except *A. marina* and *C. decandra*). It is interesting to note that in *A. marina* in spite of an opposite trend between photosynthesis and stomatal conductance, their maximal peaks were similar (1684.9 and 1634.5 μmol m^{-2}s^{-1} PAR, respectively). Transpiration and stomatal conductance followed similar trends in most of the species and the maximal peaks reached at the same PAR values except in *Bruguiera* spp (Fig. 1, 2). Amongst the studied taxa, the assimilation rate either dropped down much before stomatal conductance reached the maximal peak (*A. alba*, *B. gymnorrhiza*, *C. tagal* and *R. mucronata*) or the highest photosynthesis was measured at a point where stomatal openings had already been restricted (*A. officinalis* and *B. sexangula*). This can be explained after Mulkey et al. (1996) that at lower conductance, the intercellular CO_2 concentration increases across the stomata that counteracts the decrease in stomatal conductance; photosynthesis,

therefore, does not decline as much as it was supposed to be. Stomatal conductance values were higher in members of Avicenniaceae than Rhizophoraceae, which is in conformity with Naidoo (1989). Low conductance, however, makes it possible to maintain water potential above a threshold value, thereby, protects mangrove vessels from substantial embolism.

In most of the species, leaf temperature initially formed a cusp up to certain irradiance, and then started to increase gradually. Restricted increase in leaf temperature may have an indirect benefit in terms of photosynthesis. The cooler the leaf, the larger is the stomatal conductance corresponding to any given evaporation rate, that in turn, leads to increase in CO_2 influx.

Photosynthesis started to decrease as leaf temperature exceeds 33-36°C in almost all members of the studied families (Fig. 3). The result contradicts reports of Saenger et al. (1977) that photosynthesis rates were maximal at leaf temperatures between 25-30°C, but confirms the others (Moore et al., 1972, 1973; Ball et al., 1988, Nandy and Ghose, 2001). In the Sundarbans vegetation, the prevailing air temperature is 30°C and above that is higher than the average air temperatures (25-28°C) recorded by Saenger et al. at their study site. Difference in ambient temperature can explain this dissimilarity in optimum leaf temperature with Sundarban mangroves. In view of seasonal variation, Nandy and Ghose (2001) reported that average rate of photosynthesis decreases in B. gymnorrhiza and C. decandra as leaf temperature exceeds 35°C during summer. Hence, the present study reflects a decline in the biochemical capacity of mesophyll to fix carbon with increase in irradiance and leaf temperature above certain value. It seems that the combined effects of temperature-induced increase in evaporation rate and decrease in photosynthetic capacity enhance the water cost of carbon gain drastically at leaf temperatures above 36°C, and the abrupt rise in temperature leads to denaturing photosynthetic enzymes that, in turn, cause rapid reduction in assimilation rate.

Thus, Sundarban mangroves have their own adaptive mechanism to withstand high irradiance and extreme salinity. Photosynthetic rate is decreased and transpiration regulated by restricting stomatal conductance beyond certain PAR almost in all the species. Photoinhibition therefore, can be escaped, but abrupt rise in leaf temperature has a definite negative role in assimilation rate.

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