Transpirational Characteristics of Mangrove Species in Southern Thailand

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In order to investigate the seasonal change of transpiration in mangrove species, the sap flow rates (F_s) in *Bruguiera cylindrica* were measured in southern Thailand, with a stem heat balance method. From the result, the transpiration rates (T_r) normalized by leaf area in wet and dry seasons were estimated to be 0.50 and 1.04 kg m⁻² d⁻¹ on the average, respectively. T_r in the dry season was rather high compared to that in the wet season. This was probably caused by the difference of meteorological conditions, such as solar radiation and air humidity. Moreover, stomatal conductance (g_s) in 4 species, *Rhizophora apiculata*, *Ceriops decandra*, *Xylocarpus moluccensis* and *B. cylindrica*, was measured in the wet season with a porometry to investigate its interspecific difference. In all the species, g_s reached a plateau at the PPFD of 200 to 400 $\mu\text{mol m}^{-2} \text{s}^{-1}$. The plateau in *R. apiculata* was estimated to be between 150 and 250 mmol m⁻² s⁻¹; the level is similar to that in evergreen trees in Japan. However, g_s in the remaining 3 species was rather low.

INTRODUCTION

“Mangrove” is the general term given to halophytic trees and shrubs which grow in intertidal zone along tropical and subtropical coasts. In many developing countries in Southeast Asia, people have depended on mangrove forests, because the trees are a major source of firewood and building materials, and because rich mangrove ecosystems grow commercially important fishes, crabs and prawns (Clough, 1984; Aksornkoae *et al.*, 1990). At present, however, many mangrove forests face a serious problem of deterioration. In Thailand, about half of mangrove forests have already been destroyed by conversion to aquaculture, industrial site, urbanization, tin mining, salt pan, harbor and agriculture (Jintana, 1994).

One striking feature of mangroves is their ability to grow in muddy tidal flats, where the soil is under saline and anaerobic conditions. This feature has interested many plant physiologists and ecophysiologists for a long time (Tomlinson, 1994). They have studied the salt balance, water relation, photosynthesis and functional root systems to explain the mechanisms to adapt to the unique environment (e.g., Clough, 1984; Yabuki *et al.*, 1990a, b; Aiga *et al.*, 1995; Hirano *et al.* 1996). On the water relation, there are some field studies on transpiration rates (T_r) and stomatal conductance (g_s) in some species in North America and Australia (e.g., Moore *et al.*, 1972, 1973; Andrews and Muller, 1985). In these studies, the seasonal change and interspecific difference in T_r and g_s were reported. In Southeast Asia, however, there is little knowledge of T_r and g_s in mangroves owing to insufficient field studies (Ong *et al.*,

1995).

In this study, sap mass flow rates (F_s) in *Bruguiera cylindrica* were measured continuously with a stem heat balance method (Sakuratani, 1981) in wet and dry seasons in Phangnga Bay, southern Thailand. T_r in *B. cylindrica* was evaluated from F_s , and the relationship between T_r and meteorological elements, such as solar radiation and humidity, was investigated. Moreover, g_s in 4 species was measured with a porometry in the wet season and its interspecific difference was discussed.

METHODS

1. *Study site*: The measurement was conducted in a homogeneous secondary mangrove forest (8°20' N, 98°27' E) in the Phangnga Bay National Park, southern Thailand, which has a tropical monsoon climate with clearly defined wet and dry seasons. The study site was located inside of the forest, about 1 km away from its seaward front, and was submerged with the spring high tide. From a survey of every tree with the height above 1.3 m in a 20 m × 20 m plot, the density of 16,675 trees ha⁻¹ and the average height of 3.86 m were obtained. Dominant species were *B. cylindrica* and *Ceriops decandra*, which occupied 70% and 14% of total trees, respectively.

2. *Measurement of sap flow rate*: In order to evaluate transpiration, F_s in *B. cylindrica* was measured with a stem heat balance method (Sakuratani, 1981), which is an absolute measuring technique and does not need calibration. In this method, F_s is calculated by solving heat balance of the stem heated at a constant power (Van Bavel and Van Bavel, 1990). The measurements were conducted with stem gauges (Dynagage SGA13, Dynamax Inc., USA) in a wet season, from Jul. 28 to Aug. 7 in 1994, and a late dry season, from Mar. 30 to Apr. 17 in 1995. The numbers of trees measured in the wet and dry seasons were 1 and 2, respectively; the trees with the height between 2.0 and 3.0 m, leaf area between 1.0 and 1.4 m², and leaf area index (LAI) between 2.2 and 2.4, were selected in a sunny place. The gauges were mounted on the stems at the height of 0.8 m to prevent submergence; leaf areas above the gauges were between 0.6 and 1.0 m². Power for the heater of the gauge was provided by alkaline dry batteries with a voltage range between 4.1 and 4.6 V. The gauges and the stems at 40 mm above and below the gauges were wrapped in a plastic film for waterproofing, and were wrapped fourfold in aluminum foil with a thickness of 15 μm to shield against radiation. Gauge output signals were measured every 15 s and recorded as 10 min average, with a data logger (Micrologger 21X, Campbell Scientific Corp., USA). According to Van Bavel and Van Bavel (1990), gauge sheath conductance (K_{sh}) was determined from gauge outputs measured on a night, after removing all leaves and enclosing the remaining branches in a plastic bag. The range of K_{sh} observed was between 0.95 and 0.99 W mV⁻¹. Thermal conductivity (K_{st}) of the stems was assumed to be constant with an average value of 0.42 W m⁻¹ °C⁻¹ (Steinberg *et al.*, 1989).

3. *Measurement of stomatal conductance*: One tree of each *Rhizophora apiculata*, *C. decandra* and *Xylocarpus moluccensis* and three trees of *B. cylindrica* were selected; these 4 species are all evergreen trees. The heights of these trees were between 2 and 4 m. Stomatal conductance (g_s) to water vapour in abaxial surfaces of 4 sunlit leaves, at the height of 1 m, of each tree was measured every 2 h from 10:00 to 18:00 during 5 d in the wet season, with a steady-state porometer (LI-1600, LI-COR Inc., USA).

4. *Meteorological data*: In the dry season, wet and dry bulb temperature (handmade ventilated thermocouple thermometer), wind speed (handmade cup anemometer), global radiation (pyranometer, MŞ-100, Eko, Japan), net radiation (net radiometer, CN-11, Eko, Japan) and amount of precipitation (tipping bucket type, Isuzu Co., Japan) were measured on

a 15 m high tower built in the study site, and tide level (handmade float type tide gauge) was measured in a nearby creek. These were recorded every 30 s with a personal computer system. In this study, from daily averages of these meteorological data, Penman potential evapotranspiration (PET) was calculated by using the following equations (Penman, 1956, 1963),

$$E_T = 10 \frac{\Delta}{\Delta + \gamma} \frac{R_n + G}{L} + E_a \frac{\gamma}{\Delta + \gamma}, \quad (1)$$

$$E_a = f(u)(e_s - e), \quad (2)$$

$$f(u) = 0.26 (0.5 + 0.54u), \quad (3)$$

where E_T is PET (mm d^{-1}), Δ rate of change of saturation water vapour pressure with temperature ($\text{hPa } ^\circ\text{C}^{-1}$), γ psychrometric constant ($\text{hPa } ^\circ\text{C}^{-1}$), R_n net radiation ($\text{J cm}^{-2} \text{d}^{-1}$), G heat storage component ($\text{J cm}^{-2} \text{d}^{-1}$), L heat of evaporation (J cm^{-3}), E_a drying power of the air (mm d^{-1}), $e_s(T)$ saturation water vapour pressure at $T^\circ\text{C}$ (hPa), e water vapour pressure (hPa), u wind speed (m s^{-1}) and $f(u)$ function of wind speed ($\text{mm d}^{-1} \text{hPa}^{-1}$). Here, the daily value of G was assumed to be zero. While $f(u)$ is the function derived empirically on the basis of observations at a height of 2 m over short grass, wind speed and wet and dry bulb temperature used for the calculation were the measurements at 8 m, about 2 m higher than the forest canopy top.

In the wet season, however, only global radiation (R_s) was measured continuously. Air temperature and humidity were monitored irregularly with the porometer.

RESULTS

1. Sap flow and transpiration

Hourly F_s per leaf area in *B. cylindrica* and R_s are shown in Fig. 1. In the dry season, F_s is an average of two measurements. In both the wet and dry seasons, F_s changed together with R_s during the daytime and F_s was almost less than $10 \text{ g m}^{-2} \text{h}^{-1}$ during the nighttime.

It was reported that F_s integrated for a day or longer agrees well with T_r (Steinberg *et al.*, 1989), while F_s is not usually equal to T_r because of a change in water contents of leaves, branches and stems. Thus, daily F_s per leaf area is used below to evaluate transpiration.

In Fig. 2, F_s in two individual trees named A and B for convenience is compared; these were the measurements in the dry season. F_s in the tree B was larger than that in the tree A by 10 to 20% throughout the period. Since there was the same difference in hourly values between the trees A and B, this difference seems to be caused by individual variation and/or an instrumental error.

The relationship between F_s and R_s is shown in Fig. 3 to clarify the seasonal difference in F_s ; R_s was selected as a parameter because it was measured continuously in both the seasons. Although F_s increased according to R_s which promotes transpiration mainly by increasing leaf temperature, the values of F_s and R_s were rather different between the seasons. The averages of F_s and R_s were $0.50 \text{ kg m}^{-2} \text{d}^{-1}$ and $15.8 \text{ MJ m}^{-2} \text{d}^{-1}$ in the wet season, and $1.04 \text{ kg m}^{-2} \text{d}^{-1}$ and $24.3 \text{ MJ m}^{-2} \text{d}^{-1}$ in the dry season. The averaged F_s and R_s in the wet season were 48 and 65% of those in the dry season, respectively. When F_s was averaged within the defined R_s between 20 and $25 \text{ MJ m}^{-2} \text{d}^{-1}$, the value ($1.05 \text{ kg m}^{-2} \text{d}^{-1}$) in the dry season was 1.4 times higher than that ($0.75 \text{ kg m}^{-2} \text{d}^{-1}$) in the wet season. This seasonal difference under the same level of R_s is probably caused by that in the air humidity, which is described in the discussion.

In the dry season, the relationship between F_s and R_s in the former 4 d from Apr. 2 to 5, denoted by an asterisk, differed from that in the latter 10 d from Apr. 6 to 15. In order to

Fig. 1 Hourly sap flow rate per leaf area in *B. cylindrica* and global radiation in the wet and dry seasons. In the dry season, the sap flow rate is the average of two measurements.

Fig. 2 Comparison between daily sap flow rates in two individual trees named A and B, of *B. cylindrica* in the dry season.

Fig. 3 Relationship between daily sap flow rate and global radiation. Each daily value in the dry season is the average of two measurements, and each point denoted by an asterisk refers to a day of Apr. 2 to 5.

discuss this difference, the change of the daily F_s is shown in Fig. 4, together with PET and some meteorological elements (net radiation, precipitation, water vapour pressure deficit (VPD) and wind speed), and the relationship between F_s and PET is shown in Fig. 5; F_s was calculated in the same unit (mm d^{-1}) as PET by using the average LAI of 2.33. Since PET is the evapotranspiration from vegetation when water is rich in its rhizosphere, it depends on meteorological conditions (Eqs. (1)–(3)). The value of F_s ranged from 1.76 to 2.86 mm d^{-1}

Fig. 4 Daily change of sap flow rate, PET and some meteorological elements, such as net radiation, precipitation, water vapour pressure deficit (VPD) and wind speed, in the dry season. The VPD and wind speed are the measurements at a height of 8 m.

with the average of 2.42 mm d^{-1} , while PET ranged from 4.53 to 6.56 mm d^{-1} with the average of 5.88 mm d^{-1} . F_s changed according to PET for the days after Apr. 5; this shows that the transpiration was almost independent of physiological conditions, such as stomatal aperture. On the other hand, F_s increased gradually until Apr. 5, although PET was nearly constant. This discrepancy between the time courses of F_s and PET suggests the process of release from water stress. The trees under water stress for the previous dry days probably recovered through the precipitation of 38.5 mm from Mar. 31 to Apr. 4.

The study site was submerged 2 times a day with high tide for the days from Apr. 2 to 5 and Apr. 13 to 15, respectively. It was difficult to estimate the effects of the inundation by the high tide on the transpiration, from the data obtained in this study. To estimate this, further experiments are needed.

2. Stomatal conductance

The relationships between g_s and photosynthetic photon flux density (PPFD) are shown in Fig. 6; these were determined in the wet season. In all the 4 species, g_s almost reached a plateau at the PPFD between 200 and $400 \mu\text{mol m}^{-2} \text{ s}^{-1}$, while the range of PPFD during the measurement differ from each other. Within the defined PPFD between 200 and $400 \mu\text{mol m}^{-2} \text{ s}^{-1}$, the averages of g_s in *R. apiculata*, *X. moluccensis*, *C. decandra* and *B. cylindrica* were 166 , 46 , 112 and $74 \text{ mmol m}^{-2} \text{ s}^{-1}$, respectively. Since g_s in *R. apiculata* was 2 times higher than that in *B. cylindrica*, it was estimated that T_r in *R. apiculata* was also higher. By the way, no effects of the inundation by the high tide on g_s were recognized, as described by

Fig. 5 Relationship between daily sap flow rate and PET in the dry season.

Fig. 6 Relationship between stomatal conductance and PPFD in the wet season. Each value is the average of the measurements from 4 individual leaves. In *B. cylindrica*, different symbols refer to different trees.

Attiwill and Clough (1980).

DISCUSSION

The characteristics of transpiration in mangrove species are discussed by comparison between the results obtained here and reported by the other researchers.

When daily F_s is assumed to be equal to T_r (Steinberg *et al.*, 1989), the averaged T_r in *B. cylindrica* was estimated to be $0.50 \text{ kg m}^{-1} \text{ d}^{-1}$ (1.20 mm d^{-1}) in the wet season and $1.04 \text{ kg m}^{-2} \text{ d}^{-1}$ (2.42 mm d^{-1}) in the dry season. In the dry season, T_r was 41% of the average of PET. These T_r values are rather high compared to that in *R. mangle* in South Florida, which was evaluated by Miller (1972) by using a heat balance model; he reported T_r between 0.42 and 0.49 mm d^{-1} in Jan. and between 0.84 and 1.21 mm d^{-1} in Jun. This difference in T_r between *B. cylindrica* and *R. mangle* is probably caused by differences between species and/or methods, because the meteorological conditions, such as air temperature and VPD, of these 2 studies resemble each other.

The interspecific difference and seasonal change in g_s in mangrove species were reported by Moore *et al.* (1972, 1973), who conducted field experiments in South Florida. On the mangroves growing in Australia, *R. apiculata*, *Avicennia marina* and *B. gymnorhiza*, g_s was about 150, 150 and $100 \text{ mmol m}^{-2} \text{ s}^{-1}$, respectively under the PPFD of $1,000 \mu\text{mol m}^{-2} \text{ s}^{-1}$ and about 150, 100 and $50 \text{ mmol m}^{-2} \text{ s}^{-1}$ under the PPFD of $2,000 \mu\text{mol m}^{-2} \text{ s}^{-1}$, at the optimum leaf temperature (Ball *et al.*, 1988). This value of g_s in *R. apiculata* is similar to that in our study. Moreover, it was reported that g_s in mangrove species decreased as air humidity decreased (Ball and Farquhar, 1984; Andrews and Muller, 1985), in the same manner as ordinary terrestrial plants (Schulze *et al.*, 1987). In this study, g_s in the dry season was not measured. However, it estimated that g_s in the dry season was lower than that in the wet season, because the VPD averaged for daytime (10:00 to 18:00) in the dry season (17 hPa) was higher than that in the wet season (10 hPa).

On tropical terrestrial trees, g_s between 100 and $150 \text{ mmol m}^{-2} \text{ s}^{-1}$ in *Argyrodendron perlatum* in Australian rain forests was reported (Doley *et al.*, 1988). Moreover, in seasonally dry forests with evergreen and deciduous trees in Costa Rica, the averages of g_s in some species were between 200 and $300 \text{ mmol m}^{-2} \text{ s}^{-1}$ at a moist site (10 species) and between 100

and $150 \text{ mmol m}^{-2} \text{ s}^{-1}$ at a dry site (7 species) in an early dry season (Martin *et al.*, 1994). In planted forests in Nigeria, the maximum values of g_s in *Gmelia arborea* for pulpwood and *Tectona grandis* (teak) for poles and saw timber were about 600 and $1,000 \text{ mmol m}^{-2} \text{ s}^{-1}$, respectively in a dry season (Whitehead *et al.*, 1981), and $1,200 \text{ mmol m}^{-2} \text{ s}^{-1}$ in a wet season (Grace *et al.*, 1982). Furthermore, T_r in *Guiera senegalensis* in savanna in Niger was estimated to be between 1.5 and 2.0 mm d^{-1} in a wet season, by using F_s measured with the same way as this study (Allen and Grime, 1995).

On temperate trees, Fujinuma *et al.* (1985) measured g_s in 113 deciduous species and 35 evergreen species in a summer season, in Japan, with a LI-COR's steady-state porometer. They reported that the maximum g_s ranged from 100 to $1,000 \text{ mmol m}^{-2} \text{ s}^{-1}$, and the averages of deciduous and evergreen trees were 350 and $200 \text{ mmol m}^{-2} \text{ s}^{-1}$, respectively. Moreover, by using F_s measured with a heat pulse method, T_r in Maritime pine (*Pinus pinaster*) in France was estimated to be 3.6 mm d^{-1} at maximum, which was 55% of PET (Granier *et al.*, 1990). In the study, a strong positive correlation between T_r and PET was reported.

By comparison between these terrestrial trees and the 4 mangrove species in this study, it can be said that the g_s level of *R. apiculata* in a wet season is almost similar to that in evergreen trees in Japan. However, g_s in the remaining 3 species, especially in *X. moluccensis* was rather low.

Needless to say, further field experiment with many trees is needed, because this conclusion on transpiration was derived from the result obtained with limited trees. In order to discuss the effects of tide level on transpiration, a long-term experiment is also needed. Furthermore, it is necessary to measure g_s in a dry season to investigate its seasonal change.

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タイ南部におけるマングローブの蒸散特性

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マングローブの蒸散の季節変化を調べるために、タイ南部において *Bruguiera cylindrica* の茎内流量を茎熱収支法を用いて雨季と乾季に野外測定した。その結果、*B. cylindrica* の葉面積当たりの蒸散速度は、雨季と乾季でそれぞれ 0.50 , $1.04 \text{ kg m}^{-2} \text{ d}^{-1}$ と評価された。この季節間差は、主に日射量や大気湿度の違いによるものと考えられた。また、蒸散特性の種間差を調べるために、雨季に4種類のマングローブ (*Rhizophora apiculata*, *Ceriops decandra*, *Xylocarpus moluccensis*, *B. cylindrica*) の気孔コンダクタンス (g_s) をポロメータ法により測定した。 g_s は、4樹種ともに $200 \sim 400 \mu\text{mol m}^{-2} \text{ s}^{-1}$ 以上の PPFD でほぼ一定 (光飽和) となった。そのときの *R. apiculata* の g_s は $150 \sim 250 \text{ mmol m}^{-2} \text{ s}^{-1}$ であり、日本の常緑樹での平均値とほぼ同程度であった。一方、残りの3樹種の g_s は、かなり低いレベルであった。