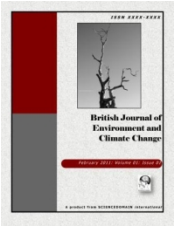

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Wind Speed Response of Sap Flow in Five Subtropical Trees Based on Wind Tunnel Experiments

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Authors' contributions

This work was carried out in collaboration between all authors. Author SL performed the experiments and statistical analyses and drafted the manuscript. Authors TK and CRC designed the study and wrote the protocol. Authors SL and HK performed the literature searches. All authors read and approved the final manuscript.

Research Article

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ABSTRACT

Aims: We evaluated the responses of tree sap flow to wind speeds in coniferous and broad-leaved plants under steady and unsteady wind conditions.
Study Design: We performed sap flow and micro-meteorological measurements on two conifers, *Chamaecyparis obtusa* var. *formosana* and *Araucaria cunninghamii*, and three broadleaved species, *Swietenia mahagoni*, *Michelia formosana* and *Plumeria acutifolia* in a wind tunnel.
Place and Duration of Study: Civil Engineering Department, National Central University, Zhongli, Taiwan, China, between May and July 2011.
Methodology: In a wind tunnel, wind speed was increased incrementally from 0 to 2, 4, 6, and 8 m s^{-1}, then decreased from 8 to 0 m s^{-1}. To examine how sap flow responded to unsteady wind, we estimated the time constant of each individual for each step change in wind speed. Moreover, we examined differences in transpiration rate and leaf conductance among individuals under stable wind speeds.
Results: The time constant was generally about 30 min in both conifers and broadleaved

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individuals. Interestingly, under steady winds, transpiration rate showed two different response patterns to increased wind speed: linear and saturated. The two patterns may be a consequence of different stomatal conductance values, but not of different leaf shapes.

Conclusion: Our results suggested that neither hydraulic system nor leaf shape differences between coniferous and broad-leaved trees was an ultimate factor affecting the transient response of tree sap flux and transpiration to wind speed, and that stomatal conductance played an important role in transpiration regulation in response to wind speed.

Keywords: Transient response; transpiration rate; stomatal conductance; conifers; broadleaved tree species.

ABBREVIATIONS

a, n	*regression constants (Granier, 1985); $a = 1.123$, $n = 1.19 \times 10^2$*
ΔT_m	*maximum temperature difference between heated and non-heated probes at $V = 0$ (°C)*
ΔT	*temperature difference between heated and non heated probes at a given V (°C)*
E	*rate of leaf transpiration (g m^{-2} s^{-1})*
g_a	*boundary layer conductance (m s^{-1})*
g_s	*stomatal conductance (m s^{-1})*
g_w	*leaf conductance for vapor transport (mol m^{-2} s^{-1})*
LA	*total leaf area (m^2)*
Q	*whole water use amount (g m^{-1} s^{-1}); $Q = Fd \times As$, where $Fd = V \times 1.0 \times 10^6$ g m^{-3} and As is the stem sectional area at sensor height (m^2)*
r_a	*boundary layer resistance (m^2 s mol^{-1})*
r_w	*leaf resistance for vapor transport (m^2 s mol^{-1})*
Tc	*time constant (min)*
U	*wind speed (m s^{-1})*
V	*sap flow (μm s^{-1})*
w_i, w_a	*mole or volume fractions of water vapor in the intercellular spaces and air, respectively (g mol^{-1}) (w_i is the saturated water vapor at a given leaf temperature)*

1. INTRODUCTION

In recent years, climate change has considerably impacted the hydrology of terrestrial ecosystems, and hence water resources [1,2]. Plant transpiration is an important hydrological process that regulates water, energy, and carbon dioxide fluxes in terrestrial ecosystems [3]. Therefore, understanding transpiration is essential to predict potential ecosystem responses to climate change. Transpiration largely depends on five environmental factors: wind, radiation, temperature, humidity, and soil moisture. Wind has especially substantial effects on transpiration [4].

To understand how wind affects transpiration, both steady and unsteady wind-speed conditions must be considered, but traditionally, only steady wind conditions have been tested in controlled-environment wind tunnels [5,6,7]. Dixon and Grace [8] clarified that wind

could significantly affect transpiration, mainly by changing the boundary layer resistance (r_a) between leaves and air. The boundary layer is strongly regulated by leaf shape [6,9]); the relatively rough leaf surfaces of coniferous needle leaves can have smaller r_a values than the relatively large, smooth leaves of broad-leaf trees. Thus, coniferous and broad-leaf trees might show systematic differences in transpiration responses to wind speed. However, few wind-tunnel studies have compared how wind speed impacts transpiration in coniferous and broad-leaf trees.

Wind typically varies substantially over time. Variable wind speeds cause unsteady sap flow because of internal water-dynamics responses in plants. Sap flow (i.e., water uptake) has been reported to lag behind leaf transpiration [10,11]. The time lag is regulated by hydraulic resistance and capacitance in plants and is often characterized using a time constant parameter (*Tc*) defined as the time taken for sap flow to reach 63.2% of its steady velocity after a step change in transpiration [11]. Coniferous and broad-leaf trees use different xylem cells to transport water (tracheids and vessel elements, respectively) which might affect *Tc*. However, few studies have examined *Tc* in a variety of species because of difficulty in measuring it *in situ*. Previously, *Tc* of conifers was derived from a combination of field measurements and models [12,13]. In contrast, Chu et al. (2009) [14] successfully used a wind tunnel and sap flux measurements to determine *Tc* in a broad-leaf individual; however, wind tunnel experiments are usually limited to potted individuals of small size. Previous studies performed in wind tunnels estimated transpiration using weighing methods [6,7,8] that are unsuitable for unsteady wind conditions.

The present study aimed to clarify the response of tree sap flow and, hence, transpiration to wind speed in coniferous and broad-leaved plants in a wind tunnel. We measured the *Tc* of sap flow in five subtropical species, including broad-leaf and coniferous species, using step changes in wind speed. Moreover, differences in transpiration rate and leaf conductance between species were also evaluated under stable wind speeds.

2. MATERIALS AND METHODS

2.1 Wind Tunnel

Wind speed experiments were carried out in the open-circuit suction-type wind tunnel of the Department of Civil Engineering, National Central University, Zhongli, Taiwan (Fig. 1a). The total tunnel length was 30 m, and the test section was 18.5 m long, 3.0 m wide, and 2.1 m high. Constant wind speeds of 1–20 m s^{-1} could be set by adjusting the rotation speed of a fan of 1.8 m diameter, with steady wind speed in the test section reached within 1–2 min. Wind speeds of 0, 2, 4, 6, and 8 m s^{-1} were used in these experiments.

Fig. 1. Experimental set-up. a) External view of wind tunnel; b) *Chamaecyparis obtusa* var. *formosa*; c) *Araucaria cunninghamii*; d) *Swietenia mahagoni*; e) *Michelia formosana*; and f) *Plumeria acutifolia*

2.2 Trees Species

Five subtropical forest tree species from Taiwan were studied (Fig. 1b–f), including two conifers, *Chamaecyparis obtusa* var. *formosana* (Cupressaceae) and *Araucaria cunninghamii* (Araucariaceae), and three broad-leaved species, *Swietenia mahagoni* (Meliaceae), *Michelia formosana* (Magnoliaceae), and *Plumeria acutifolia* (Apocynaceae). Three specimens of each species were used. Trunk diameter at a height of 8 cm ranged from 2.0–3.0 cm in *C. obtusa* var. *formosana*, *A. cunninghamii*, and *P. acutifolia*; in *S. mahagoni* and *M. formosana*, trunk diameter at a height of 3 cm ranged from 1.0–1.5 cm (Table 1). Individuals of all species ranged in height from 80–130 cm, except *A cunninghamii*, which were 160–180 cm tall.

Table 1. Tree characteristics

Species	Leaf shape	Tree height (cm)	Sensor height (cm)	Diameter* (cm)	*LA* (m^2)	g_s** ($m\ s^{-1}$)
C. obtusa	needle	1 128	18	1.74	0.73	
		2 138		1.99	0.81	6.11
		3 132		17.8	0.82	
A. cunninghamii	needle	1 183	18	3.28	0.76	
		2 178		2.61	0.71	19.62
		3 161		1.80	0.53	
S. mahagoni	broad leaf	1 102	13	1.48	0.14	
		2 95		1.31	0.15	35.79
		3 112		1.17	0.1	
M. formosana	broad leaf	1 90	13	1.15	0.03	
		2 86		1.15	0.01	822.45
		3 88		1.13	0.05	
P. acutifolia	broad leaf	1 120	18	3.29	0.49	
		2 114		3.20	0.49	12.09
		3 113		2.71	0.48	

**: Diameter at the height that sap flow sensors were installed.*
***: g_s was derived from g_w under the condition of U = 6 m s^{-1} (See Section 2.7)*

2.3 Sap Flow Measurements: the Granier Sensors

To measure sap flow, we used a dual-probe sap flow measuring system [15,17], commonly referred to as the thermal dissipation probe (TDP) method. Sensors consisted of two cylindrical probes 10 mm long and 2 mm diameter inserted radially into the stem 10 cm apart. The upper probe included a heating element wound around a steel needle enclosing a T-type thermocouple (copper-constantan); it was continuously heated at constant power (0.15 W). The lower probe was unheated to measure the temperature of the wood tissue. Both thermocouples were connected to a data logger (CR1000, Campbell Scientific, Logan, UT, USA), and the temperature difference at the ends of the copper probe wires was recorded. Sap flux density (V) was calculated as:

$$V = 119 \times [\frac{\Delta T_m - \Delta T}{\Delta T}]^{1.231} \quad (1)$$

where: V is the sap flux density (g m^{-2} s^{-1}); ΔT_m is the maximum temperature difference between heated and unheated probes at $V = 0$ (K); ΔT is the temperature difference between the heated and unheated probes at a given V (K), respectively. For each experiment, we estimated the maximum temperature difference using measurements taking during the night (18:00 to 6:00) preceding experiments.

The sensors were installed 18 cm high into stems of *C. obtusa* var. *formosana*, *A. cunninghamii,* and *P. acutifolia* and 13 cm high into *S. mahagoni* and *M. formosana*. The sensors were covered with aluminium to insulate them from radiation and potential cooling effects of the wind.

2.4 Meteorological Measurements

A hygrotransmitter (HD9008TR, Delta Ohm, Padua, Italy) was placed near samples to measure air temperature and relative humidity. A soil moisture sensor (EC10, Decagon Devices, Pullman, WA, USA) was inserted in the soil of one sample per species. A quantum sensor (LI-190SZ, LI-COR Scientific, Lincoln, NE, USA) was installed on the ground upwind of the samples to measure photosynthetically active radiation. These meteorological data were recorded during all experiments using a data logger (CR10X, Campbell Scientific). Copper-constantan thermocouples (Type copper-constantan, Omega Engineering, Stamford, CT, USA) were used to measure the temperature difference between tree leaf surfaces and the air. One thermocouple tip was in constant contact with a leaf blade, avoiding the midrib; the other was in contact with the air. Leaf temperature was then calculated using the temperature difference and the measured air temperature inside the wind tunnel. Two to three pairs of thermocouples were installed on each tree in all experiments.

2.5 Procedure of Wind Speed Experiment

Three individuals of the one species were positioned in the test section of the wind tunnel 30 cm from one other in a row perpendicular to the wind direction. Five halogen lamps above them operated at the same intensity during all experiments. The potting soil was saturated before each experiment and covered with plastic film to prevent surface evaporation. The wind speed was increased stepwise from 0 m s^{-1} to 2.0, 4.0, 6.0, and 8.0 m s^{-1}, then decreased from 8.0 to 0 m s^{-1}. Each wind speed was maintained for 1–3 h and changed only after sap flow had stabilized. The experiment was repeated for each tree species.

2.6 Time Constant (*Tc*)

To explain the unsteady water flow through plants, resistance-capacitance models derived from the SPAC (Soil Plant Atmosphere Continuum) concept have been used to determine how water transport lags behind transpiration [11]. In the SPAC model, *Tc* can be determined by the following simplified equation [13,14]:

$$V(t) = V_s \left[1 + \left(\frac{1}{\beta} - 1\right) \exp\left(-\frac{t}{T_c}\right)\right] \quad (2)$$

where: $V(t)$ is the sap flux density (g m^{-2} s^{-1}); V_s is the steady sap flux density after the change ($t = \infty$) (g m^{-2} s^{-1}); T_c is the time constant (s); and $\beta = (R_c+R_s)/R_c$ where R_s and R_c are axial hydraulic resistance and tissue resistance associated with storage and withdrawal of water in xylem tissue, respectively.

Based on the least-square method, *Tc* and β were determined from the measured *Vs* and $V(t)$ at each wind speed treatment.

Because broad-leaf vessels have better water conductivity than conifer tracheids [16,19], the time response of sap flux is expected to be faster in broad-leaf plants. Thus, we hypothesized that *Tc* would be smaller in the broad-leaf trees than in the conifers.

2.7 Transpiration Rate (*E*) and Leaf Conductance (g_w)

The transpiration rate *E* (g m^{-2} s^{-1}) at the leaf area basis was calculated with the following equation:

$$E = \frac{Q}{LA} \tag{3}$$

where: *Q* is the sap flux (total water use: g s^{-1}) and *LA* is the total leaf area (m^2). Total water use $Q = V \times As$, *where As* is the sectional area of the stem at the height of sensors (m^2). After the experiments, we scanned each leaf with an area meter (Li-3000 scanning head with LI-3050C Transparent Belt Conveyor Accessory, LI-COR Scientific) and obtained the accumulated *LA* for all individuals. In this study, we assumed that a 1-cm-long sensor could cover the radial variation in *V* across the cross-section because of the small stem radius (< 1.6 cm) in our sample trees.

Flick's law describes the relationship between transpiration and leaf conductance as follows [17]:

$$E = g_w(w_i - w_a) = (w_i - w_a)/r_w \tag{4}$$

where: *E* is the rate of leaf transpiration (g m^{-2} s^{-1}); g_w is the leaf conductance for vapor transport (mol m^{-2} s^{-1}); w_i and w_a are the mole or volume fractions of water vapor in the intercellular spaces and in air, respectively (g mol^{-1}) (w_i is the saturated water vapor at the given leaf temperature); and r_w is the leaf resistance for vapor transport (m^2 s mol^{-1}).

The total leaf resistance for water vapour transfer, r_w, has two components: stomatal resistance r_s and boundary layer resistance r_a. The inverse of stomatal resistance is stomatal conductance, which is influenced by stomatal density, size, and aperture [18]. Boundary layer conductance g_a varies with leaf size and shape and also wind speed [9,20].

Based on Eq.(4), we calculated g_w using each *Vs* and meteorological data (humidity and air and leaf temperatures) at the time of *Vs*. Leaf conductance can be described as $1/g_w = 1/g_s + 1/g_a$, and because g_a increases with increasing wind speed, we can assume that g_w is equivalent to g_s at higher wind speeds ($U \geq 6$ m s^{-1}).

Because conifer and broad-leaf leaves differ morphologically in both shape and texture (i.e., needle leaves with rough surface vs. broad leaves with smooth surfaces) [21] and because leaf size affects transpiration rate, we hypothesized that the transpiration rate of broad-leaf plants would be more responsive to wind speed.

3. RESULTS AND DISCUSSION

3.1 Changes in Sap Flow (*V*)

Between wind speeds of 0–8 m s^{-1}, the standard deviations of temperature and relative humidity were about 1.8°C and 3.2%, respectively. Sap flow *V* increased with wind speed (Fig. 2). At lower wind speeds (U = 2 m s^{-1}), more time (about 125 min) was needed to reach steady flow than at higher wind speeds (U = 6–8 m s^{-1}; about 40 min). A similar increase in *V* with wind speed was also found by Chu et al. [14]. Other studies showed a decline in transpiration with increased wind speed [6,8]. The Penman–Monteith equation [19] predicted

that transpiration would decrease at higher wind speeds occur under high available-energy conditions of > 400 W m^{-f}, and that transpiration would increase with wind speed under low available-energy conditions [8]. Thus, our experiments and those of Chu et al. [14] may have been conducted under lower available-energy conditions (short wave radiation of ~70 W m^{-7}; note that available energy is normally less than short wave radiation (12)) than in other studies. Here, higher wind speeds increased boundary layer conductance (g_a) possibly increasing transpiration. On the other hand, increased g_a also increases heat transfer (sensible heat), which decreased the leaf–air temperature differences (see eq.(4)), resulting in less transpiration under high available-energy conditions [8].

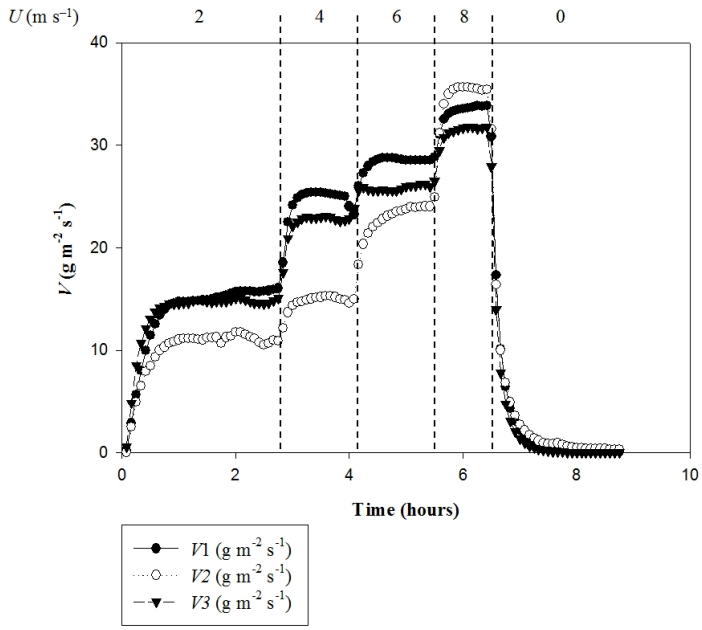

Fig. 2. *Michelia formosana* sap flow *V* (g m^{-2} s^{-1}) at different wind speeds (*U*) between 0 and 8 m s^{-1}. Different symbols indicate *V* of different individuals

3.2 Time Constant (*Tc*)

The *Tc* of *C. obtusa var formosa* ranged from 8.0 min (when *U* increased from 6–8 m s^{-1}) to 77.9 min (0–2 m s^{-1}), with a mean of 32.8 min. For *A. cunninghamii, Tc* ranged between 16.5 min (6–8 m s^{-1}) and 29.4 min (0–2 m s^{-1}), with a mean of 25.1 min. For *S. mahagoni*, *Tc* averaged 33.4 m and ranged between 9.7 min (4–6 m s^{-1}) and 91.7 min (0–2 m s^{-1}). For *M. formosana*, *Tc* ranged between 7.3 min (6–8 m s^{-1}) and 16.6 min (0–2 m s^{-1}) with a mean of 10.5 min. For *P. acutifolia, Tc* averaged 35.0 min and ranged from 12.8 min (4–6 m s^{-1}) to 46.1 min (0–2 m s^{-1}).

Fig. 3 shows that *Tc* of *C. obtusa* var. *formosana*, *M. formosana,* and *S. mahagoni* decreased with increasing wind speed. This means that when the wind speed was higher with a larger steady *V*, sap flow stabilized faster. In contrast, *M. formosana* and *A. cunninghamii* showed relatively conservative *Tc* values in response to changes in wind speed. The decreased *Tc* was likely to be found in the individuals with saturated trends of *E*

in response to the wind speed (Fig. 4). Here, *Tc* was defined as the multiple of total hydraulic resistance and capacitance in the plant hydraulic pathway [13,14]. In some previous studies, *Tc* values were implicitly assumed to be constant given that there was no severe soil water deficit [12,13]. In contrast, our study suggested that *Tc* in some species could change in response to wind speed and/or steady *V*, even when soil moisture was saturated, although the derived results were possibly due to an experimental artefact.

In our study, coniferous tree samples had *Tc* values of 16.5–32.8 min and broad-leaved tree samples had *Tc* values of 10.5–35.0 min. Although we expected that broad-leaved trees with vessels might have shorter *Tc* than conifers with tracheids based on previous studies [12,16], a difference was not apparent in this study. Also, at the lower wind speed of 2 m s^{-1}, the *Tc* value of the coniferous and broad-leaved trees were 29.4–77.9 and 16.6–91.7, respectively. At the higher wind speed of 8 m s^{-1}, the *Tc* values were 7.2–.9.3 and 9.4–.1.7, respectively.

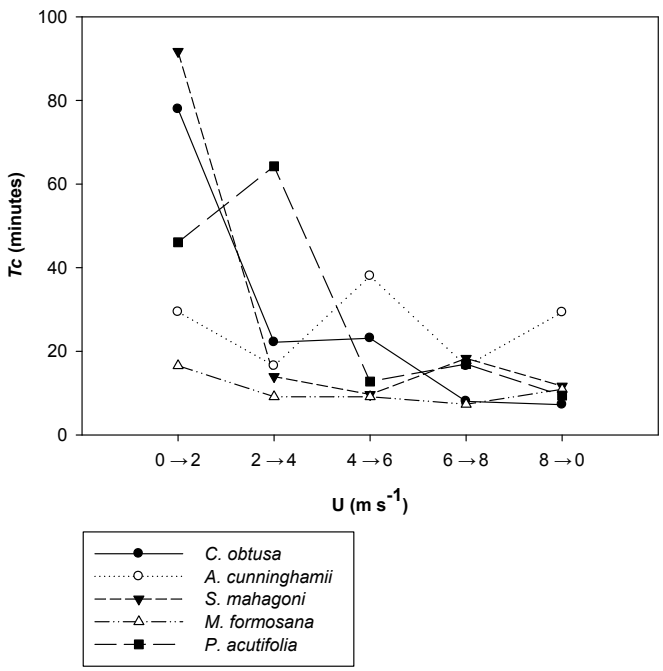

Fig. 3. Time constant (*Tc*) of each tree species for each wind speed change

3.3 Transpiration Rate (*E*), Wind Speed (*U*), and Leaf Conductance (g_w)

Fig. 4 shows the increasing in normalized *E* in response to *U*. In our samples, we found two different trends: linear curves in *S. mahagoni*, *M. formosana,* and *A. cunninghamii*, and saturated curves in *C. obtusa* var. *formosana,* and *P. acutifolia*. Because g_a is strongly affected by leaf shape [6,9,21], we expected the correlations between *E* and *U* to differ between coniferous and broad-leaved trees. However, the linear pattern was seen in one coniferous and two broad-leaved tree species, and the saturated pattern occurred in one coniferous and one broad-leaved tree sample.

Previously, Jones [11] calculated the relationships between *E*, g_a, and g_s using the Penman–Monteith equation and showed that *E* could increase with g_a under larger-g_s condition but not under smaller-g_s condition. When g_s is large, *E* is regulated by g_a and hence *U*, while, *E* is limited by g_s regardless of g_a when g_s is small. Therefore, a linear increase in response to *U* would occur in individuals with relatively large g_s and a saturated response to *U* would be expected in individuals with relatively small g_s. In our study, estimated g_s for *S. mahagoni*, *M. formosana,* and *A. cunninghamii* (linear trends) was larger than those of *C. obtusa* var. *formosana* and *P. acutifolia* (saturated trends), in concordance with the hypothesis. Over all, this study clarified that g_s could be an important factor determining the effects of *U* on *E* in addition to leaf shape.

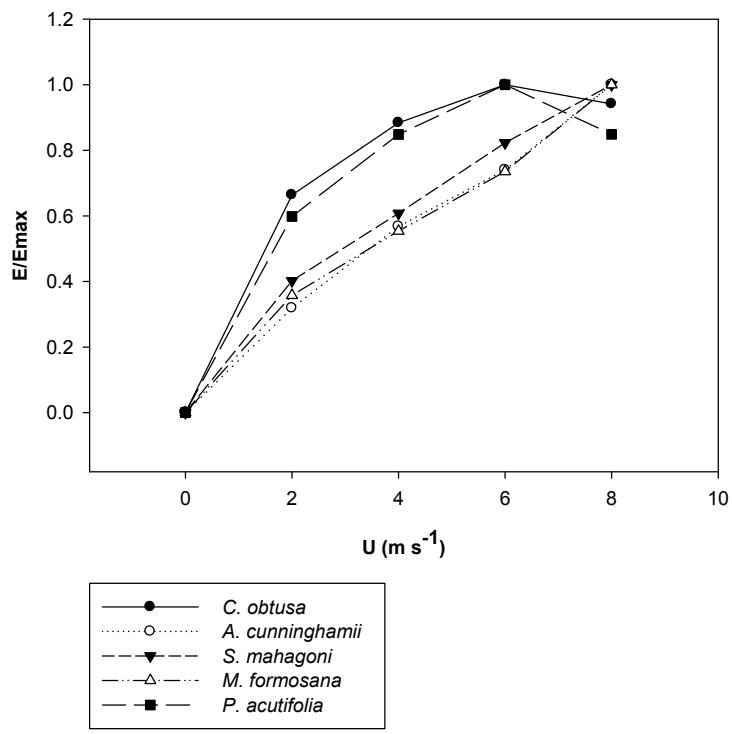

Fig. 4. Normalized transpiration rate (*E*) of five tree species based on changes in wind speed (*U*). Normalized *E* was calculated using maximum *E* in each individual during the whole experiment period

4. CONCLUSION

To clarify how steady and unsteady wind speeds affect sap flow, we investigated the *Tc* of sap flow under unsteady *U* and the relationship between *E* derived from steady sap flow, *U*, and g_s in two conifers and three broad-leaved species using a wind tunnel.

We expected to observe different patterns of water dynamics between conifers (with tracheids) and broad-leaved trees (with vessels). However, our wind tunnel experiments showed that the different xylem physiologies yielded approximately the same *Tc* values (about 10–30 min). Our samples also demonstrated two trends of *E* in response to increases

in *U*, but they were independent of leaf shape (i.e., needles vs. broad leaves). *Swietenia mahagoni*, *M. formosana,* and *A. cunninghamii*, with higher estimated g_s values, showed linear correlations between *E* and *U* and probably g_a. In contrast, the *E* values of *C. obtusa* var. *formosa* and *P. acutifolia*, with smaller g_s values, showed saturated curves, probably because *E* was limited by g_s.

We concluded that in addition to leaf shape, g_s could be a dominant factor controlling how wind speed affects *E*. However, we could not readily distinguish g_a and g_s in this experiment. Further experiments using plaster-coated branches (Landsberg and Ludlow, 1970) should enable us to separate g_a and g_s more precisely and to understand the mechanism by which wind speed impacts g_a, g_s, and *E*.

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COMPETING INTERESTS

Authors declare that no competing interests exist.

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