

Seasonal Variation in Canopy Aerodynamics and the Sensitivity of Transpiration Estimates to Wind Velocity in Broadleaved Deciduous Species

Author(s): D. M. Barnard and W. L. Bauerle

Source: *Journal of Hydrometeorology*, Vol. 17, No. 12 (December 2016), pp. 3029-3043

Published by: American Meteorological Society

Stable URL: <https://www.jstor.org/stable/10.2307/26152584>

REFERENCES

Linked references are available on JSTOR for this article:

https://www.jstor.org/stable/10.2307/26152584?seq=1&cid=pdf-reference#references_tab_contents

You may need to log in to JSTOR to access the linked references.

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <https://about.jstor.org/terms>



American Meteorological Society is collaborating with JSTOR to digitize, preserve and extend access to *Journal of Hydrometeorology*

JSTOR

Seasonal Variation in Canopy Aerodynamics and the Sensitivity of Transpiration Estimates to Wind Velocity in Broadleaved Deciduous Species

D. M. BARNARD

Institute of Arctic and Alpine Research, University of Colorado Boulder, Boulder, Colorado

W. L. BAUERLE

Department of Horticulture and Landscape Architecture, Colorado State University, Fort Collins, Colorado

(Manuscript received 16 February 2016, in final form 6 September 2016)

ABSTRACT

Characterization of seasonal dynamics in wind speed attenuation within a plant canopy α is necessary for modeling leaf boundary layer conductance g_{bv} , canopy–atmosphere coupling Ω , and transpiration at multiple scales. The goals of this study were to characterize seasonal variation in α in four tree species with canopy wind profiles and a canopy-structure model, to quantify the impact of α on estimates of g_{bv} and Ω , and to determine the influence of variable wind speed on transpiration estimates from a biophysical model [Multi-Array Evaporation Stand Tree Radiation Assemblage (MAESTRA)]. Among species, α varied significantly with above-canopy wind speed and seasonal canopy development. At the mean above-canopy wind speed (1.5 m s^{-1}), α could be predicted using a linear model with leaf area index as the input variable (coefficient of determination $R^2 = 0.78$). However, the canopy-structure model yielded improved predictions ($R^2 = 0.92$) by including canopy height and leaf width. By midseason, increasing canopy leaf area and α resulted in lower within-canopy wind speeds, a decrease in g_{bv} by 20%–50%, and a peak in Ω . Testing a discrete increase in wind speed (0.6 – 2.4 m s^{-1} ; seasonal mean plus/minus one standard deviation) had variable influence on transpiration estimates (from -30% to $+20\%$), which correlated strongly with vapor pressure deficit ($R^2 = 0.83$). Given the importance of α in accurate representation of g_{bv} , Ω , and transpiration, it is concluded that α needs to be given special attention in plant canopies that undergo substantial seasonal changes, especially densely foliated canopies (i.e., leaf area index >1) and in areas with lower native wind speeds (i.e., $<2 \text{ m s}^{-1}$).

1. Introduction

Transpiration is often a major component of the hydrologic cycle and a mechanism for the exchange of mass and energy between vegetation and the atmosphere. Transpiration rates can be estimated by accounting for plant physiological and meteorological interactions with a linked photosynthesis and stomatal conductance g_s scheme that also estimates leaf boundary layer conductance g_{bv} (e.g., Wang and Jarvis 1990a). Accurate characterization of physiological–meteorological interactions is essential for accurate transpiration estimates given that the control of transpiration is primarily determined by g_s and g_{bv} . Of the meteorological drivers of transpiration, wind speed effects on leaf temperature T_{leaf} , air temperature T_{air} , and vapor pressure deficit (VPD)

within the canopy can be considerable (e.g., Kim et al. 2014). Given the influence of wind, it is important to account for how it varies with vertical depth into the canopy in two- and three-dimensional carbon, water, and energy flux models.

To date, there have been conflicting reports regarding the effect of wind speed on transpiration rates [for a review, see Kim et al. (2014)]. A portion of this disagreement is likely due to the variation in experimental controls among studies coupled with the complex, bidirectional, and interactive ways in which wind can influence leaf energy balance and temperature-dependent physiological processes. For example, increasing wind speed could raise the transpiration rate by increasing g_{bv} and/or by transporting drier air from aloft into the canopy that increases the leaf-to-air vapor pressure deficit D (e.g., Schuepp 1993; Martin et al. 1999; Kim et al. 2014). Conversely, the drier air can decrease g_s (Drake et al. 1970; Aphalo and Jarvis 1991; Meinzer

Corresponding author e-mail: D. M. Barnard, david.m.barnard@colorado.edu

1993; Mott and Peak 2010), which, alone or when coupled with reduced leaf temperature (and the leaf-to-air VPD), can decrease transpiration. Given that the reaction rate of each response outlined above will vary over time and among species, meteorological conditions coupled with spatially explicit physiological response functions must be considered to fully characterize wind-vegetation interactions.

Wind speed decreases with depth into the canopy as the form drag from leaves, branches, and stems within the canopy reduce bulk momentum. The decline is often characterized by an exponential coefficient α (Cionco 1965; Pereira and Shaw 1980; Cammalleri et al. 2010). Originally, α was calculated using just two wind speed measurements, one above and one within the canopy [Eq. (1); see also Inoue (1963) and Cionco (1965)]. However, subsequent studies found that the calculation of α will vary with the height of the within-canopy wind measurement, indicating that wind velocity measurements at several depths are needed to accurately characterize α (Saito 1964; Cionco 1978).

Alternatively, modeling efforts have attempted to eliminate the need for within-canopy wind speed measurements altogether. For example, Goudriaan (1977) developed a canopy-structure model (hereafter referred to as the Goudriaan model) using leaf area index (LAI), leaf width L_w , and canopy height to estimate α . Limited reports indicate the Goudriaan model exponential coefficient α_G is accurate in comparison to exponential coefficient measured from the wind profile (Goudriaan 1977; Campbell and Norman 1998). However, comparisons have been mostly limited to single time points in densely spaced agronomic crops, leaving uncertainty in the efficacy of the Goudriaan method for seasonal characterization in broadleaved tree species or how the bulk empirical wind profile fit exponential coefficient α_F may change with wind speed.

The development of leaf area and crown structure can change canopy aerodynamics, α , and g_{bv} as the season progresses. Although canopy development rates vary among plant species and biomes, α has typically been reported as a stationary parameter to represent a specific species or vegetation type (e.g., Wright 1965; Cionco 1965, 1972; Campbell and Norman 1998). To this regard, modeling investigations may be introducing substantial errors by assuming static values of canopy aerodynamics, especially in vegetation with large seasonal changes in canopy size and LAI (Westgate et al. 1997; Souch and Stephens 1998; Trout et al. 2008).

Several land surface schemes and distributed hydrologic models do not calculate g_{bv} ; instead, they assume that g_s is the primary vegetation-based control on transpiration (e.g., Ács 1994; Wigmosta et al. 1994; Sellers

et al. 1996; Tague and Band 2004; Oleson et al. 2013). However, the ratio between g_s and g_{bv} (i.e., canopy-atmosphere coupling Ω ; Jarvis and McNaughton 1986) should be considered in modeling studies as it describes how the control of transpiration is partitioned between plant physiology (i.e., g_s) and environment (i.e., g_{bv}). Furthermore, both g_s and g_{bv} are integral to predicting vegetation responses to atmospheric variability over short time scales as well as longer-term changes due to canopy-structure evolution and climate change (Schuepp 1993; Nobel 1999). Although it is recommended that Ω be characterized as a range of values per species (Meinzer 1993), it is oftentimes prescribed as a stationary parameter despite g_{bv} varying with canopy development and g_s varying in response to atmospheric conditions and physiological status (Daudet et al. 1999; Bauerle and Bowden 2011; Bauerle et al. 2014). Thus, there is a need to characterize the change in g_s and g_{bv} over the season within different canopy types to determine the influence of physiology (i.e., g_s), environment (i.e., g_{bv}), and canopy aerodynamics on Ω .

This study had four main goals: 1) to characterize the influence of seasonal leaf area development on measured values of α in four species of broadleaf deciduous trees with diverse canopy shapes and growth rates, 2) to assess the accuracy of the Goudriaan (1977) model for estimating α over an entire growing season, 3) to quantify how seasonal variation in α influences g_{bv} and how seasonal changes in α combine with seasonal changes in g_s to determine Ω , and 4) to estimate the influence of wind speed variation on transpiration with a canopy flux model [Multi-Array Evaporation Stand Tree Radiation Assemblage (MAESTRA)]. We chose MAESTRA for this study because of its physiology-environment feedback that accounts for within-canopy wind speed effects on g_{bv} .

2. Materials and methods

a. Site characteristics and plant material

This study was conducted in the summer of 2011 at a commercial nursery near Avon, Ohio (41.433°N, 82.052°W). The research site consisted of four plots, each of which contained >300 in-ground, 57-L containers (pot-in-pot production) spaced 1.5 m from center to center. Trees for each plot were grown in 57-L black plastic containers that contained a soilless substrate mixture consisting of 64% pine bark, 21% peat moss, 7% Haydite, and 7% sterilized regrid. The remaining 1% was a 12-0-42 slow-release fertilizer (Agrozz Inc., Wooster, Ohio). The species used in this study cover a range of ecological and commercial significance, growth rates, and canopy aerodynamic characteristics (*Acer rubrum* "Franksred," *Betula nigra* "Cully," *Carpinus betula* "Columnaris," and

Cercis canadensis). Trees were irrigated twice daily to container capacity with spray stakes (pressure compensating spray stakes, Netafim, Israel). A weather station (Decagon Devices, Pullman, Washington) was installed near the center of each plot at 3 m above the ground to collect measurements of wind speed U_{3m} and photosynthetically active radiation (PAR). Air temperature and relative humidity (RH) were also collected and used to calculate VPD. Seasonal variation in meteorology is shown in Fig. 1, annual mean T_{air} was 10.75°C, annual total precipitation was 99.4 cm, mean annual VPD was 0.77 kPa, and mean daily light integral (DLI) was 12.42 mol m⁻² day⁻¹.

b. Canopy aerodynamic measurements

To measure α in each plot, we constructed a 3-m-tall mobile wind tower from 10-cm-diameter polyvinyl chloride (PVC) pipe. Ten-cup anemometers (Davis Instruments Corp., Hayward, California) were attached at 0.33-m intervals and connected to data collection nodes (Em50R, Decagon Devices) that recorded a 5-min average from 1-min measurement intervals. In the center of each plot, an 8-cm-diameter steel tube protruded from the ground to a height of 1 m—a plumb mount to hold the wind tower. Starting on day of year (DOY) 143, we began to rotate the wind tower among individual plots for measurement periods of >3 days (measurement periods are listed in Table 1). At the beginning of each relocation, we collected plot LAI with a handheld canopy gap-fraction analyzer (LAI-2000, LI-COR Inc., Lincoln, Nebraska). These measurements included five separate LAI readings in each plot taken 10 cm above the ground with 90° of unobstructed view facing into the plot. All measurements were taken immediately following sunset at fixed locations. On the same day that LAI was collected, we also measured canopy physical characteristics (canopy height, stem height, canopy width in the x and y axes, and L_w ; Table 1) on $n = 15$ trees per species. Leaf area density (LAD) was calculated as $(LAI \times \text{stem spacing})/\text{canopy volume}$.

c. Species-specific characterization of canopy wind speed attenuation

Wind speed within plant canopies can be approximated with an exponential equation (Campbell and Norman 1998) as

$$U_z = U_h \exp\left[\alpha\left(\frac{z}{h} - 1\right)\right], \quad (1)$$

where U_z is the wind speed at height z within the canopy and U_h is the wind speed at the top of the canopy (i.e., at height h). Equation (1) can be rearranged to solve for α using measurements of wind speed at two heights with two caveats: first, error introduced as U_h must be modeled using a logarithmic representation of above-canopy

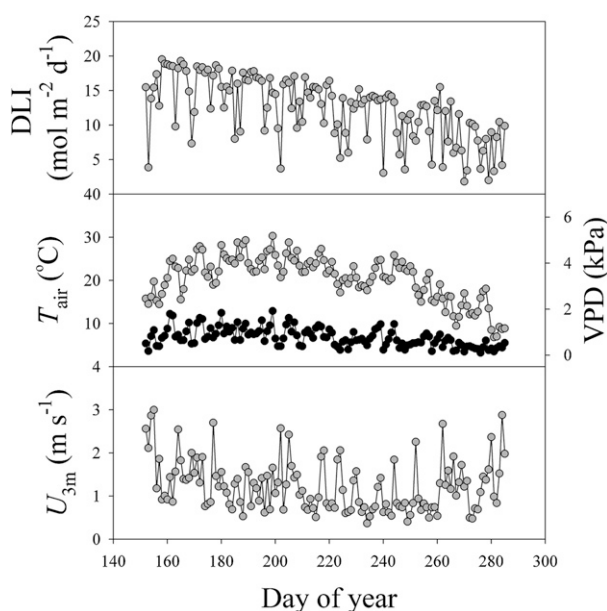


FIG. 1. (top) Seasonal DLI, (middle) mean daily T_{air} (gray points) and VPD (black points), and (bottom) U_{3m} .

wind speed that includes assumptions about the model parameters' zero plane displacement and momentum roughness (e.g., Campbell and Norman 1998), and second, α estimated by this method introduces additional error based on the height within the canopy at which the second wind speed measurement is collected (Saito 1964). Hence, we tested two different methods for determining α . First, we tested the Goudriaan (1977) model that assumes a uniform distribution of leaf area within a spherical canopy and defines α_G as

$$\alpha_G = \left(\frac{0.2LAIh}{l_m}\right)^{1/2}, \quad (2)$$

where l_m is the mixing length, describing the mean distance between leaves defined as

$$l_m = \left(\frac{6L_w^2h}{\pi LAI}\right)^{1/3}. \quad (3)$$

We calculated α_G using the canopy physical dimensions and LAI collected on the first day of each wind tower measurement period. Next, we fit the following equation to measurements of wind speed at multiple heights within the canopy to obtain the bulk empirical wind profile fit exponential coefficient α_F (Saito 1964):

$$U_z = 0.5 \exp^{\alpha_F U_{3m}}. \quad (4)$$

The exponential coefficient parameter is typically used to represent ensemble flow, but our results indicated

TABLE 1. Physical dimensions of the four study species ($n = 12$) at the beginning of the five measurement periods used to calculate the wind extinction coefficient from the Goudriaan (1977) model. LAI was estimated for each species at the plot scale. Note that period 5 LAI data were not collected for *Cercis canadensis* because of leaf senescence. Error estimates represent one standard error ($n = 15$).

Period	Period days (DOY)	Tree height (m)	Stem height (m)	Canopy width (m)	Stem caliper (mm)	LAI ($\text{m}^2 \text{m}^{-2}$)
<i>Acer rubrum</i>						
1	147–151	1.87 ± 0.15	0.74 ± 0.14	0.25 ± 0.01	22.4 ± 1.2	0.34 ± 0.04
2	166–176	2.12 ± 0.16	1.21 ± 0.09	0.43 ± 0.05	27.5 ± 1.6	0.48 ± 0.17
3	198–201	2.23 ± 0.19	1.21 ± 0.09	0.75 ± 0.05	30.2 ± 1.6	0.62 ± 0.19
4	218–222	2.34 ± 0.17	1.20 ± 0.09	0.81 ± 0.06	33.4 ± 1.7	0.65 ± 0.26
5	237–242	2.37 ± 0.18	1.20 ± 0.09	0.86 ± 0.07	34.7 ± 2.1	0.64 ± 0.29
<i>Betula nigra</i>						
1	143–147	0.61 ± 0.06	0	0.27 ± 0.06	38.4 ± 3.8	0.25 ± 0.26
2	163–166	1.14 ± 0.04	0	0.89 ± 0.09	50.3 ± 4.2	0.80 ± 0.18
3	195–198	1.71 ± 0.08	0	1.33 ± 0.06	66.8 ± 3.9	1.21 ± 0.32
4	214–218	2.19 ± 0.10	0	1.64 ± 0.14	79.0 ± 4.4	2.05 ± 0.24
5	233–237	2.25 ± 0.07	0	1.73 ± 0.09	85.5 ± 7.3	2.99 ± 0.24
<i>Carpinus betula</i>						
1	151–154	1.51 ± 0.19	0.43 ± 0.04	0.36 ± 0.05	26.1 ± 2.8	0.57 ± 0.14
2	176–180	1.82 ± 0.11	0.40 ± 0.04	0.57 ± 0.07	30.1 ± 3.1	0.65 ± 0.10
3	201–206	2.02 ± 0.21	0.39 ± 0.04	0.55 ± 0.08	32.5 ± 2.8	0.67 ± 0.33
4	222–225	2.07 ± 0.21	0.38 ± 0.05	0.56 ± 0.05	33.4 ± 3.2	0.66 ± 0.29
5	242–248	2.06 ± 0.28	0.38 ± 0.04	0.57 ± 0.07	33.6 ± 2.8	0.70 ± 0.29
<i>Cercis canadensis</i>						
1	154–157	2.12 ± 0.09	1.01 ± 0.03	0.80 ± 0.01	25.5 ± 1.8	0.49 ± 0.10
2	180–185	2.41 ± 0.23	0.98 ± 0.03	1.17 ± 0.04	28.1 ± 3.1	0.74 ± 0.12
3	206–210	2.72 ± 0.20	0.98 ± 0.02	1.41 ± 0.03	31.2 ± 3.4	1.08 ± 0.04
4	225–228	2.68 ± 0.18	0.98 ± 0.02	1.64 ± 0.05	32.4 ± 3.7	1.45 ± 0.19
5		2.68 ± 0.16	0.97 ± 0.02	1.70 ± 0.05	32.5 ± 3.9	

that α_F varies with U_{3m} (Fig. 2). Thus, to have α_F represent local equilibrium and for comparisons, we fit Eq. (4) to wind tower measurements only when U_{3m} was 1.5 m s^{-1} (i.e., seasonal mean; Fig. 1) to derive the mean fit exponential coefficient $\alpha_{F_{\text{mean}}}$.

d. Modeling the influence of wind speed on energy exchange, boundary layer conductance, and transpiration

In this study, we used the iterative approach of Leuning et al. (1995) executed in the modeling framework of MAESTRA (Wang and Jarvis 1990a) to determine the influence of changes in above-canopy wind speed (while holding α constant) on whole-canopy estimates of g_{bv} and transpiration using a precalibrated and validated set of physiological parameters for the four study species [for model validation and submodel parameter values, see Table 2 in Barnard and Bauerle (2013)]. MAESTRA divides a tree crown into individual point calculations, each with an associated leaf area volume determined by canopy leaf area distribution and shape (e.g., Wang et al. 1990; Baldwin and Peterson 1997). Radiation conductance g_{r_N} (Wang and Leuning 1998) and percentage of sunlit and shaded leaf area is calculated for each grid point (Wang and Jarvis 1990b). We assumed uniform distribution of leaf area within individual tree crowns.

Leaf sensible and latent heat exchange are calculated in the MAESTRA model [Eqs. (5)–(8) and (10); Wang and Jarvis 1990a] to determine leaf energy balance, photosynthesis, stomatal conductance, and transpiration. Given that transpiration rates can alter the ratio of sensible to latent heat exchange, primary model iterations assume leaf conditions to be equal to ambient conditions and then the model is run iteratively until estimates converge. Sensible heat H is defined as

$$H = \rho_a C_p (T_{\text{leaf}} - T_{\text{air}}) g_{b_H}, \quad (5)$$

where ρ_a is the density of dry air and C_p is the specific heat of air. Leaf boundary layer conductance to heat g_{b_H} , which in plant canopies is defined by the sum of g_{r_N} and free $g_{b_{H_f}}$ and forced $g_{b_{H_u}}$ convection, is

$$g_{b_H} = 2(g_{b_{H_f}} + g_{b_{H_u}} + g_{r_N}), \quad (6)$$

with $g_{b_{H_f}}$ defined as

$$g_{b_{H_f}} = \frac{0.5 D_H (1.6 \times 10^8 |T_{\text{leaf}} - T_{\text{air}}| L_w^3)^{0.25}}{w} \left(\frac{P}{R T_{\text{air}}} \right), \quad (7)$$

where D_H is molecular diffusivity to heat, P is atmospheric pressure, L_w is leaf width, and R is the universal

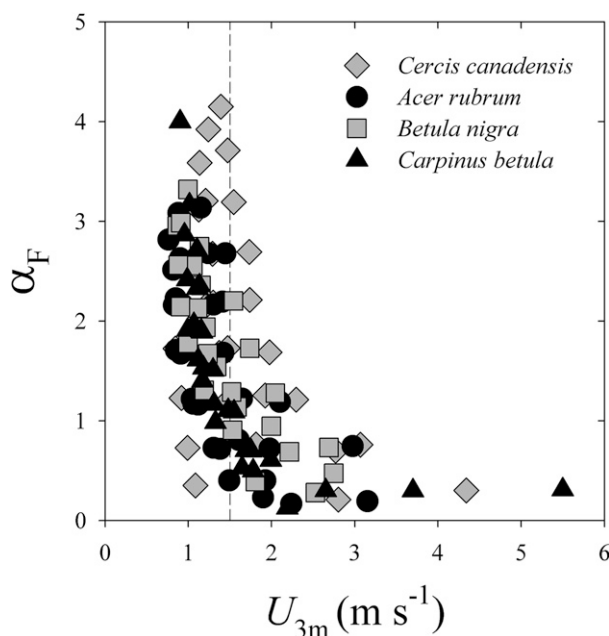


FIG. 2. Values of observed α_F are dependent on U_{3m} . Dashed vertical line represents the mean seasonal U_{3m} (1.5 m s^{-1}). Points for each species represent mean values for each of the 4–5 measurement periods (cf. Table 1) and 3–6 measurement points within the canopy (cf. Table 2).

gas constant. Boundary layer forced convection is defined as (Campbell and Norman 1998)

$$g_{b_{H_u}} = 0.003 \sqrt{\frac{U_z}{L_w}} \left(\frac{P}{RT_{\text{air}}} \right). \quad (8)$$

Latent heat flux is defined by the Penman–Monteith equation (Monteith 1965) as

$$\lambda E = \frac{sR_n + D_a g_s C_p M_a}{s + \gamma(g_{b_H}/g_v)}, \quad (9)$$

where s is the slope of the temperature–saturation vapor pressure curve, R_n is net radiation, D_a is the vapor concentration of the air, g_s is stomatal conductance, M_a is the molecular mass of air, γ is the psychrometric constant, and g_v is total leaf conductance to water vapor, which is a combination of g_s and g_{b_v} with g_{b_v} defined as

$$g_{b_v} = 1.075 \times 2(g_{b_{H_f}} + g_{b_{H_u}}), \quad (10)$$

and g_s is defined using the Leuning (1995) model as

$$g_s = g_0 + \frac{g_1 A_n}{(c_s - \Gamma)[1 + (\text{VPD}/D_0)]}, \quad (11)$$

where g_0 is minimum g_s , g_1 is the marginal cost of water per unit of carbon gain, A_n is net photosynthesis, c_s

is the CO_2 concentration, Γ is the photosynthetic CO_2 compensation point, and D_0 is an empirical coefficient. Net photosynthesis is calculated using the biochemical Farquhar–von Caemmerer model (Farquhar et al. 1980).

Finally, to describe the degree to which the canopy is aerodynamically coupled with the atmosphere, we calculated the Ω coefficient defined by Jarvis and McNaughton (1986) as

$$\Omega = \frac{(s/\gamma) + 2}{(s/\gamma) + 2 + (g_{b_v}/g_s)}. \quad (12)$$

3. Results

a. Characterization of the seasonal development of canopy aerodynamics

We observed an exponential increase (up to 6 times) in α_F with decreasing U_{3m} (Fig. 2). *Betula nigra* and *Cercis canadensis* showed the greatest variation in α_F over the season because they also exhibited the greatest seasonal variation in canopy size and LAI (Table 1). The greatest variation in α within species occurred around the mean U_{3m} (1.5 m s^{-1}).

In all four species, both LAI and $\alpha_{F_{\text{mean}}}$ increased as the season progressed (Fig. 3). The increase in $\alpha_{F_{\text{mean}}}$ was relatively consistent (i.e., plus/minus linear) over the season in all four species, with the exception of a slight decrease in $\alpha_{F_{\text{mean}}}$ for *Acer rubrum* in the final measurement period. *Betula nigra* displayed the largest change in $\alpha_{F_{\text{mean}}}$, beginning as the lowest and ending as the highest (0.3 – 2.7 ; i.e., 9 times increase in $\alpha_{F_{\text{mean}}}$). The remaining three species all showed a ~ 2 times increase in $\alpha_{F_{\text{mean}}}$ over the season, with *Carpinus betula* increasing from 0.7 to 1.53 , *Acer rubrum* from 0.45 to 1.1 , and *Cercis canadensis* from 0.95 to 1.6 . Measured LAI covaried significantly ($p < 0.05$) with $\alpha_{F_{\text{mean}}}$ in *Cercis canadensis* and not significantly in *Betula nigra* or in *Acer rubrum* ($p > 0.05$). LAI did not covary with $\alpha_{F_{\text{mean}}}$ in *Carpinus betula*. *Betula nigra* showed the greatest change in LAI from 0.3 to $2.7 \text{ m}^2 \text{ m}^{-2}$ (i.e., a 9 times increase), *Cercis Canadensis* showed the second (0.5 – $1.3 \text{ m}^2 \text{ m}^{-2}$), and *Acer rubrum* showed the third (0.3 – $0.7 \text{ m}^2 \text{ m}^{-2}$). *Carpinus betula* showed a relatively static LAI over the growing season of $\sim 0.7 \text{ m}^2 \text{ m}^{-2}$.

Initially, L_w increased in the early season in all species except for *Carpinus betula*, which had a relatively static L_w of $\sim 3 \text{ cm}$ throughout the season (Fig. 4). *Acer rubrum* and *Cercis canadensis* had L_w values that plateaued to roughly the same width at the same time (i.e., $\sim 9 \text{ cm}$). *Betula nigra* L_w also plateaued at this time, but to a narrower L_w (5.9 cm). The slopes of the initial increase in L_w were similar between *Acer rubrum* and

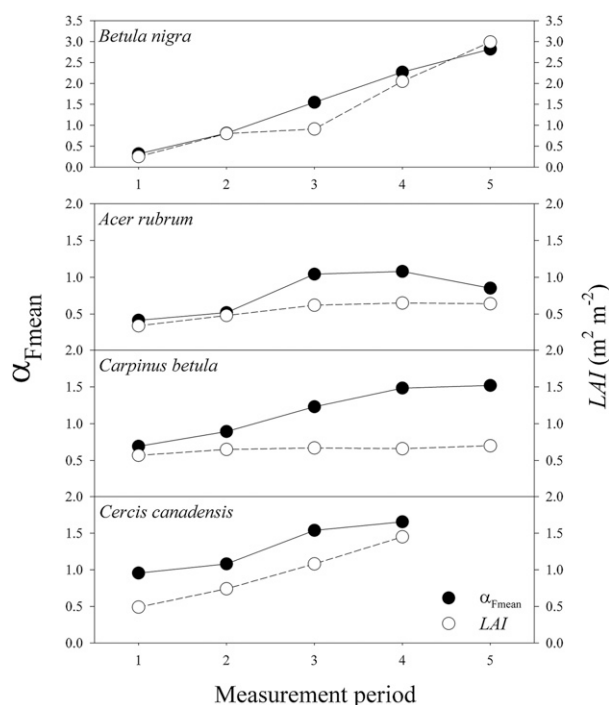


FIG. 3. Averaged canopy wind extinction coefficient values fit to within-canopy wind speed at mean seasonal daytime wind speed at 3 m above the ground (i.e., $\alpha_{F_{\text{mean}}}$) and canopy LAI over the season. Measurement periods are listed in Table 1.

Cercis canadensis. The slower rate of L_w increase in *Betula nigra* resulted in a smaller final L_w (4.7 cm) relative to the other species in the study.

b. Modeling α from LAI and canopy characteristics

The relationship between LAI and $\alpha_{F_{\text{mean}}}$ was significantly correlated in all species over the season (coefficient of determination $R^2 = 0.78$, $p < 0.01$; Fig. 5a), indicating that $\alpha_{F_{\text{mean}}}$ may be reasonably well predicted from measurements of LAI alone. The slope of the *Carpinus betula* regression fit did appear to vary from the pooled regression (i.e., a greater slope), but the other three species followed the pooled regression line closely. However, estimates of α_G were correlated more strongly with $\alpha_{F_{\text{mean}}}$ ($R^2 = 0.92$; Fig. 5b), indicating that including additional terms (i.e., L_w , canopy height, and width) substantially improves predictions of $\alpha_{F_{\text{mean}}}$.

c. Species aerodynamic characteristics affect canopy-to-atmosphere coupling

Figure 6 shows the seasonal evolution of mean daily g_s , g_{bv} , and Ω for individual canopy elements. Stomatal conductance declined linearly throughout the season with relatively constant variance in all species except for *Betula nigra*, which showed increasing variance in the second half of the season. There were also similar

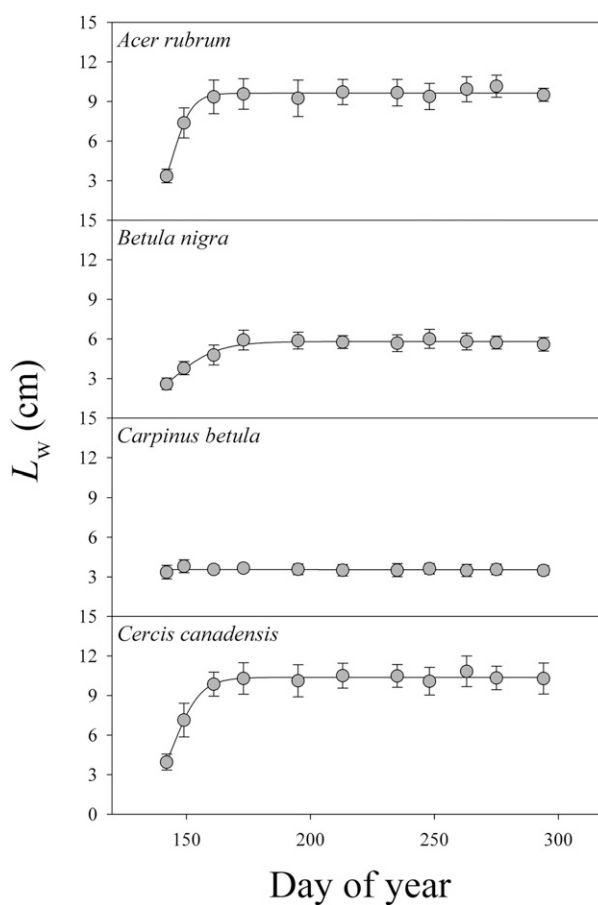


FIG. 4. Mean canopy L_w increases in the initial portion of the season before reaching a canopy maximum. Seasonal variation in L_w was not evident in *Carpinus betula*. Bars represent one std dev ($n = 14$).

declines in g_{bv} among species during the first quarter of the season as mean daily U_{3m} decreased and canopy leaf area increased (Figs. 1 and 3, respectively); however, the behavior of each species differed in the second half of the season. *Acer rubrum* and *Carpinus betula* showed relatively similar behavior, with an increase in the second half of the season (Fig. 6). However, *Carpinus betula* returned to a much higher g_{bv} than did *Acer rubrum*. *Cercis canadensis* had an increase in g_{bv} in the second half of the season but to a lower level than *Carpinus betula* and *Acer rubrum*. *Betula nigra* showed almost no increase in g_{bv} in the second half of the season (except for a few isolated days), but displayed an asymptotic behavior of g_{bv} at $\sim 0.5 \text{ mol m}^{-2} \text{ s}^{-1}$ across the season. Given the linear decline in g_s and the parabolic or exponential shapes of the g_{bv} response, the resulting peaked seasonal trend of Ω also varied among species. For example, the peak of Ω for *Carpinus betula* appears to occur in the middle of the season with the rate of increase and decrease being approximately similar (i.e.,

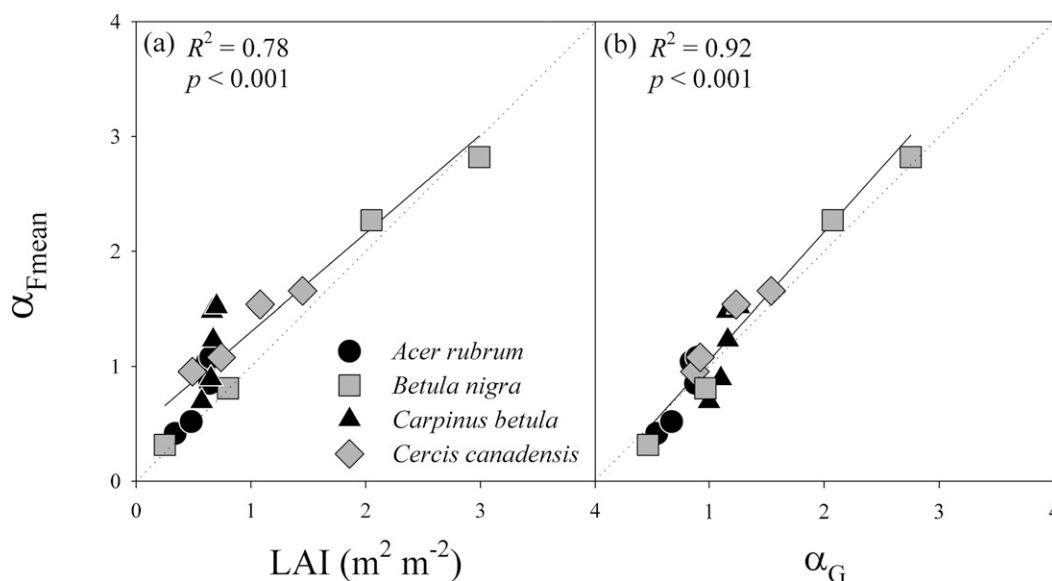


FIG. 5. LAI and Goudriaan (1977) model estimates of canopy wind extinction coefficient (i.e., α_G) regressed against mean canopy wind extinction coefficient values fit to wind tower data at mean seasonal daytime wind speed at 3 m (i.e., α_{Fmean} ; 1.5 m s^{-1}).

an inverted parabola). In the third quarter of the season, Ω peaked in both *Acer rubrum* and *Cercis canadensis* and then decreased in the fourth quarter to 75% of the peak value. *Betula nigra* showed a consistent increase in Ω until early in the fourth quarter of the season and then declined. Given that the Ω response closely mimics the inverse of g_{bv} , it would appear that in our study system g_{bv} dynamics are primarily responsible for determining Ω . There was increasing variance noted in g_{bv} toward the end of the season in all species due to increasing wind speeds (Fig. 1). We note that this heteroscedasticity was most pronounced in the species with lowest α (*Carpinus betula*) and was least pronounced in the species with the highest α (*Betula nigra*), indicating that increasing leaf area and the resulting wind attenuation buffer g_{bv} from variability in U_{3m} .

Mean daily g_{bv} for individual canopy elements was linearly correlated with daily measured U_{3m} and exponentially with daily α_{Fmean} (interpolated between measurement points; $p < 0.001$ for all regressions; Fig. 7). However, the correlation of the linear g_{bv}/U_{3m} relationships decreased with increasing LAI/α_{Fmean} , whereas the converse was true for the curvilinear g_{bv}/α_{Fmean} relationships. The nonlinear correlations were strongest in *Cercis canadensis* and *Betula nigra* ($r = 0.87$ and 0.84 , respectively). The strongest correlation between U_{3m} and g_{bv} was $r = 0.84$ in *Acer rubrum* and the weakest correlation was $r = 0.42$ in *Betula nigra*.

d. Theoretical modeling exercises

We tested 1000 random combinations of environmental conditions (VPD from 0 to 4 kPa, PAR from 0 to $2000 \mu\text{mol m}^{-2} \text{s}^{-1}$, and T_{air} from 5° to 40°C) and found that a discrete change in above-canopy wind speed, representing one standard deviation on either side of the mean (i.e., from 0.6 to 2.4 m s^{-1}), resulted in changes in crown transpiration rates ΔE_{wind} that ranged from -30% to $+20\%$ (Fig. 7). When plotted against individual environmental conditions, there was a peaked response for PAR with the most extreme ends of the range of ΔE_{wind} (i.e., from 10% to 20% and -30% to -25% ; Fig. 8a) occurring at $PAR < 200$. There was a less pronounced linear trend between ΔE_{wind} and T_{air} (Fig. 8b) but a clear logarithmic trend between ΔE_{wind} and VPD (Fig. 8c). Overall, ΔE_{wind} is negative or close to zero at VPDs below 0.2 kPa but becomes positive and asymptotic at higher VPD. Additionally, the negative end of the range generally coincides with lower T_{air} and the higher end at high T_{air} (Fig. 8c).

While the above simulations held α constant to isolate the influence of changing wind speed, we did find variation in α to have some influence on transpiration estimates. The effect was relatively small (i.e., 3% – 10%) but correlated with VPD in all four study species and reached an apex at low VPDs (Fig. 9). The maximum parameter effect of α ($\sim 11.5\%$) was observed in *Betula nigra* at VPDs between 0.1 and 0.3 kPa . The relationship was the strongest in *Carpinus betula* (i.e., $R^2 = 0.77$) and

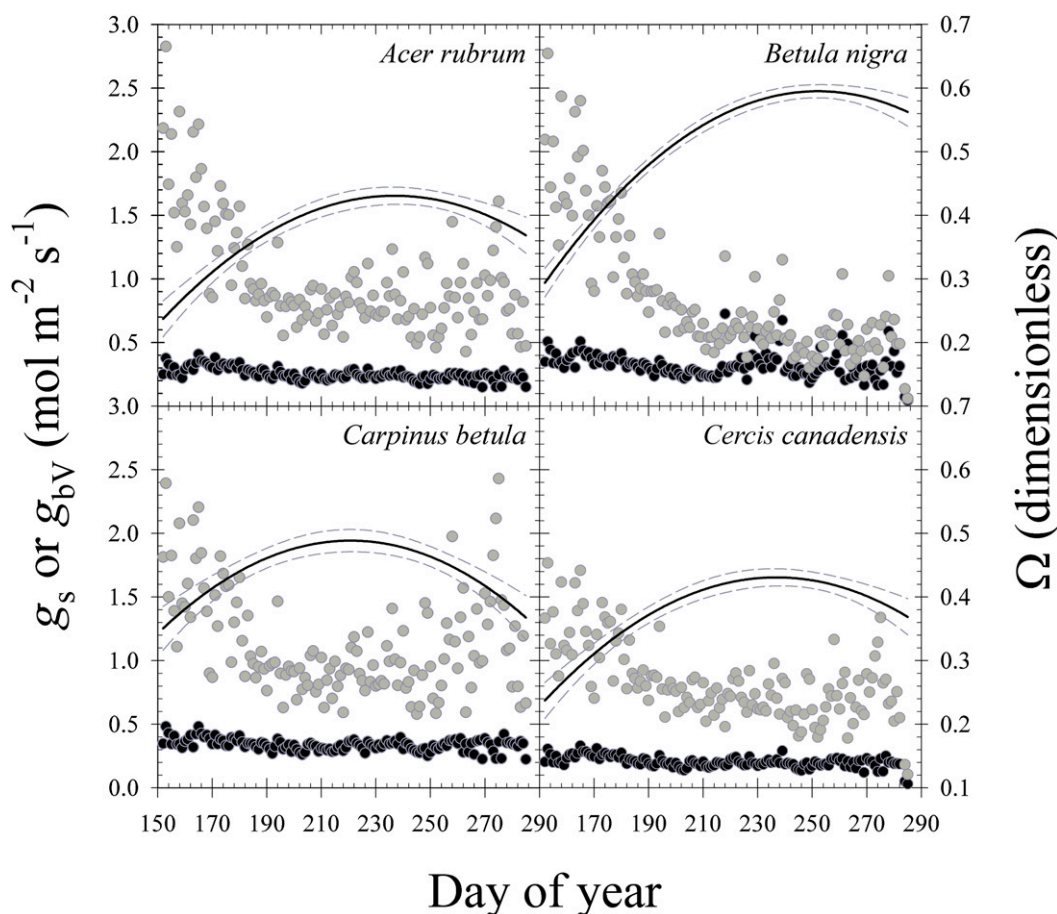


FIG. 6. Seasonal evolution of mean midday g_s (black circles), g_{bv} (gray circles), and the least squares parabolic fit of Ω (black line). Dashed gray lines represent 95% confidence interval.

weakest in *Acer rubrum* ($R^2 = 0.32$), but the exponential decay relationship was significant in all species ($p < 0.001$).

4. Discussion

a. Characterizing canopy growth and aerodynamics

We found α_F to vary substantially with above-canopy wind speed. The dependence of α_F on wind velocity above the canopy has not been reported before as it is assumed to be an ensemble representation of average conditions (Cionco 1965; Campbell and Norman 1998; Cammalleri et al. 2010). We note that cup anemometers have a high energy of activation that can increase with sensor age, and thus the α values at very low U_{3m} values (i.e., $<0.5 \text{ m s}^{-1}$; as per Davis manufacturer specifications) may be subject to instrumentation error. For example, cup anemometers within the canopy could be regularly subject to wind speeds lower than the 0.5 m s^{-1} threshold, and results should be considered with this limitation in mind. Nevertheless, given that canopy characteristics change continually over a growing season

and wind speed varies among locations and over time, static α parameterization has the potential to introduce substantial error in turbulent flux calculations of surface energy balance (e.g., Cammalleri et al. 2010). The change in canopy leaf area is of particular importance in short-rotation agricultural crops (e.g., maize), rapidly growing biofuel and pulp crops (e.g., hybrid *Populus* and *Eucalyptus*), and seasonally deciduous ecosystems. It is important for future studies to account for the effect of local wind speed on α_F when comparing values collected at different time periods or from locations with different wind speeds (e.g., Campbell and Norman 1998). As a benchmark, our results indicate that α should be characterized precisely in areas with lower mean U_{3m} (i.e., $<4 \text{ m s}^{-1}$).

The variation of α as wind speed reaches a lower asymptote suggests that the form drag from leaves and branches can saturate, or that increasing wind speed forces individual leaves to orient parallel with the wind. Therefore, the lower range of α likely depends on how flexible a species' branches and petioles are, whereas the

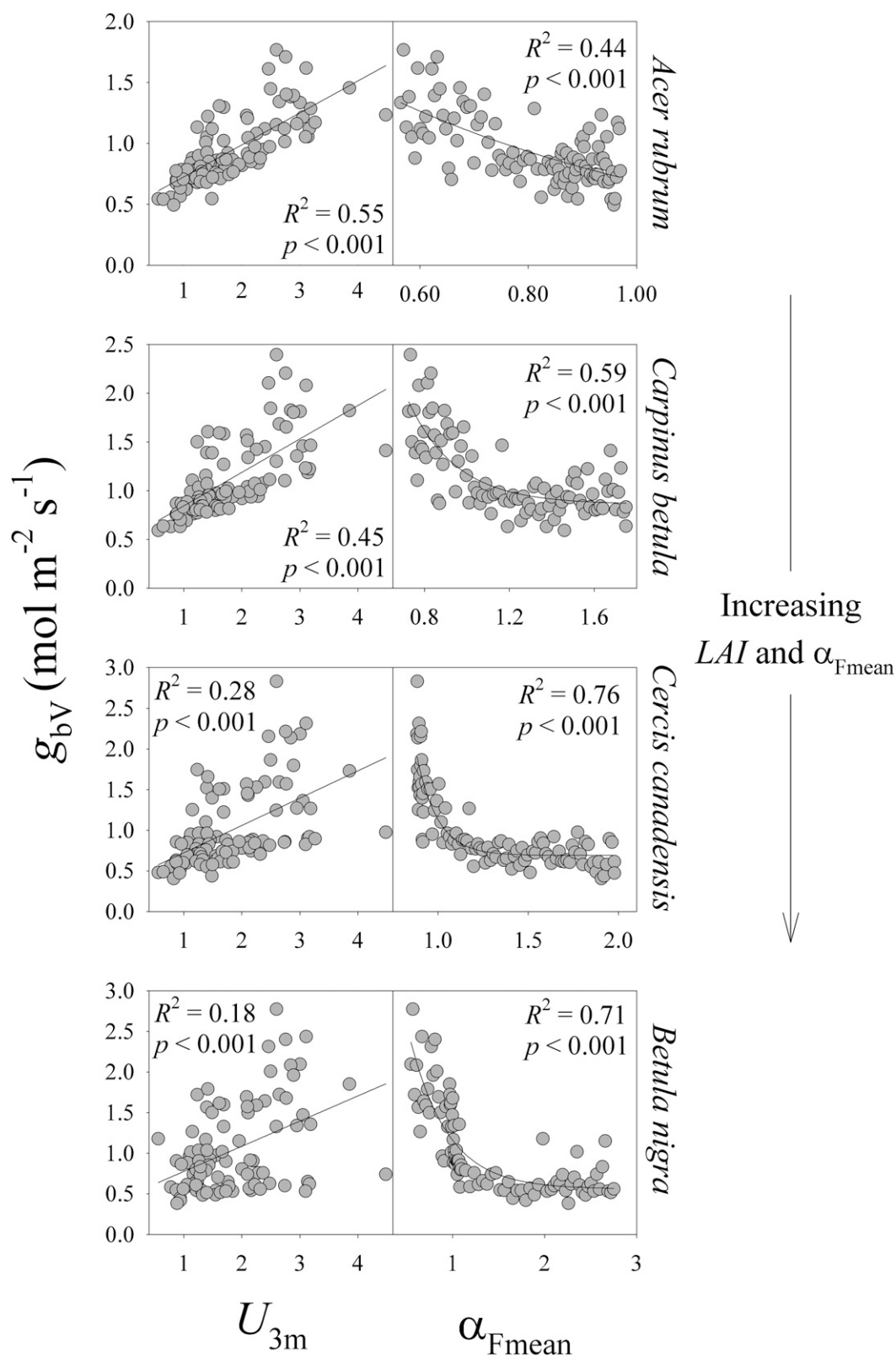


FIG. 7. The correlation between g_{bv} and U_{3m} or $\alpha_{Fseason}$ for (from top to bottom) increasing order of measured α (cf. Fig. 2). The correlation between g_{bv} and α_{Fmean} increases as mean seasonal α_{Fmean} and LAI increase. Note that y-axis scales differ among the four species.

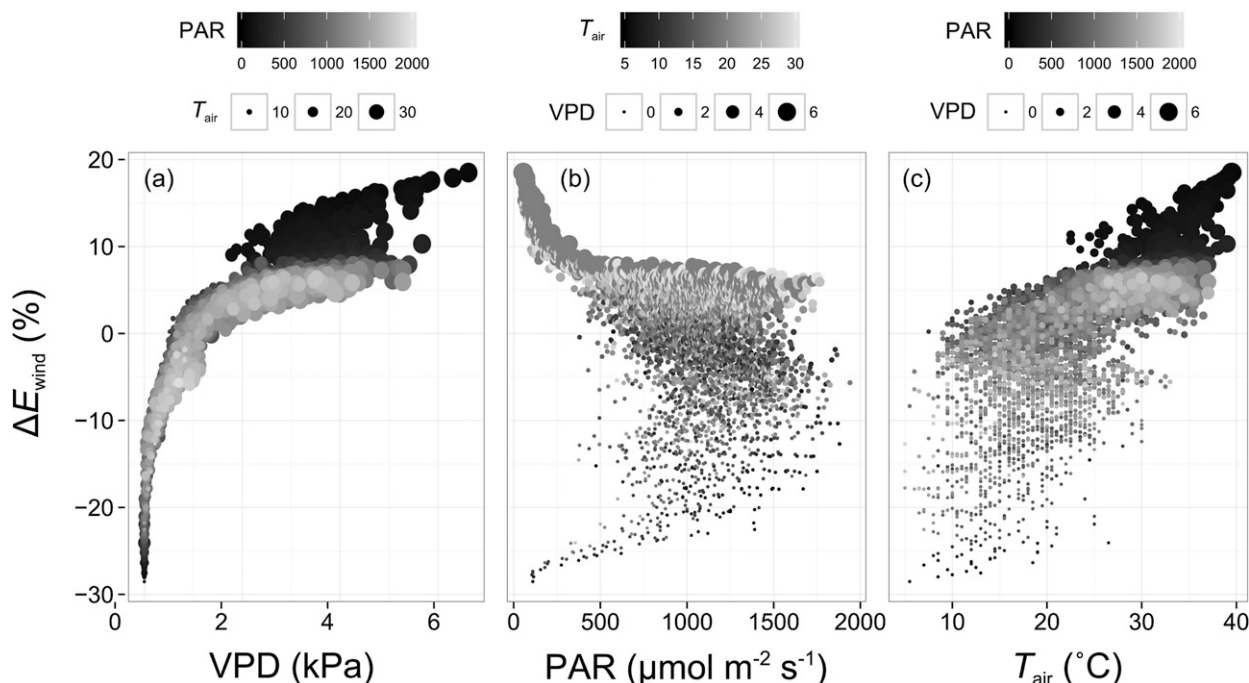


FIG. 8. The influence of a discrete increase in wind speed ($0.6\text{--}2.4\text{ m s}^{-1}$; Table 1) on ΔE_{wind} at 1000 random combinations of T_{air} , PAR, and VPD. Each panel represents the 1000 random combinations sorted by individual meteorological condition, with circle shading indicating (a),(c) PAR level and (b) T_{air} and circle size representing (a) T_{air} and (b),(c) VPD.

upper range likely depends on L_w and LAI. The Cionco (1972, 1978) studies describe α_F as proportional to canopy characteristics, whereby a term was included for element flexibility (leaf, branch, and stem element absorption of wind momentum transfer), but α_F was not thought to change with wind speed. We note that it is possible that the tree species used in this study may ultimately converge at a lower asymptote value of α_F at higher wind speeds (i.e., $>5\text{ m s}^{-1}$). Future studies would benefit from including areas with higher native wind speeds to define this lower asymptote with greater resolution. Future studies should also include greater resolution in areas with low wind speed, as we found α to be a more significant parameter at wind speeds $<2\text{ m s}^{-1}$. Nevertheless, given the wind speed influences on α , we normalized α_F to the mean wind speed at our measurement site for further comparisons and model validation.

Measured values of $\alpha_{F_{\text{mean}}}$ increased among all species over the season as canopy leaf area developed. The upper value of $\alpha_{F_{\text{mean}}}$ in *Betula nigra* ($2.7\text{ m}^2\text{ m}^{-2}$) is particularly noteworthy because a value of 3 was hypothesized as an upper limit, described in Cionco (1978). The seasonal variation we observed warrants attention given the assumption that α represents bulk conditions and is constant per vegetation type (Cionco 1972; Goudriaan 1977; Inoue and Uchijima 1979; Sauer et al.

1995; Daudet et al. 1999; Kim et al. 2014), except for Cionco (1978), who reported a decrease in α as the canopy developed in maize. Among species, we found $\alpha_{F_{\text{mean}}}$ to increase over the season at variable rates that were presumably in response to the development of LAI and L_w . For example, *Cercis canadensis* and *Betula nigra* had $\alpha_{F_{\text{mean}}}$ values that tracked LAI closely, whereas the rate of increase of $\alpha_{F_{\text{mean}}}$ outpaced LAI in *Carpinus betula*. Also, in *Acer rubrum*, we observed an increase in $\alpha_{F_{\text{mean}}}$ early in the season and a decrease later in the season, neither of which correlate with changes in LAI. Two potential sources of error may explain this divergence: 1) seasonal variation in branch, stem, and/or petiole flexibility due to secondary growth was not captured by our measurements (Cionco 1978) or 2) a possible error in gap-fraction LAI estimates due to small canopies with high LAD. In the latter scenario, portions of the crown leaf area may be obscured in the image because of leaf overlap, resulting in an underestimation of LAI (e.g., Weiss et al. 2004). Partitioning these two potential error sources within the context of seasonal evolution of element flexibility would allow future studies to separate their influence on canopy aerodynamics.

Although we found the simple relationship between LAI and $\alpha_{F_{\text{mean}}}$ to be relatively accurate at predicting canopy $\alpha_{F_{\text{mean}}}$, the Goudriaan model yielded greater

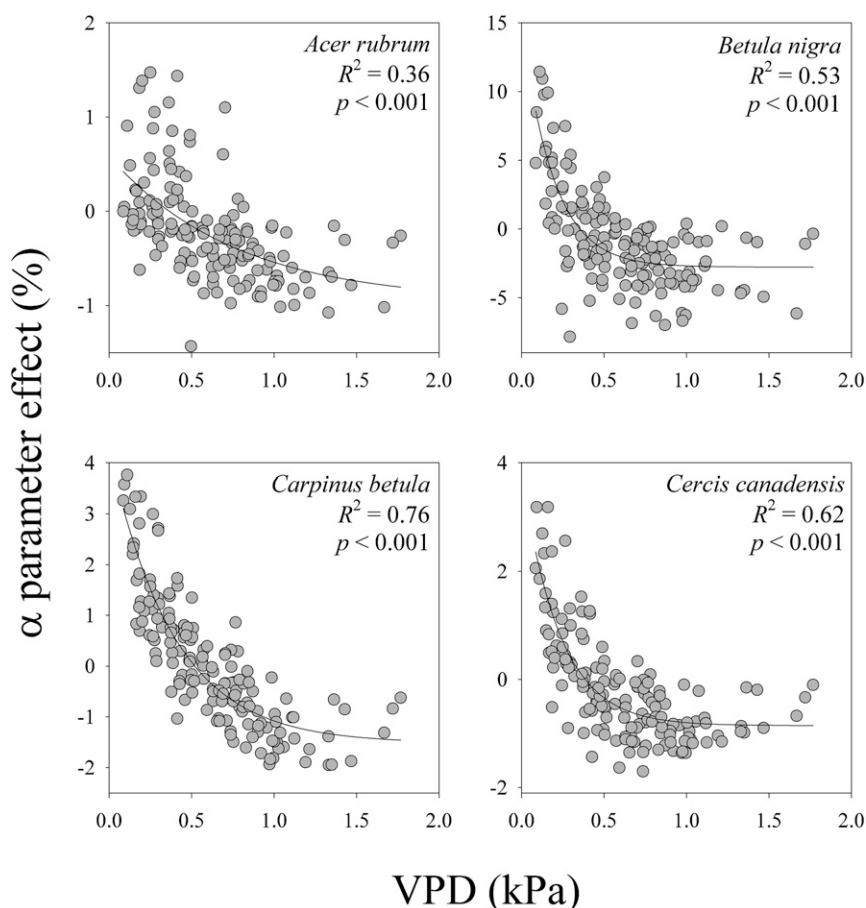


FIG. 9. The parameter effect of α on transpiration estimates is correlated with atmospheric VPD. Note that y-axis scales differ among the four species.

predictive accuracy by including two additional parameters (i.e., L_w and tree height). The lower R^2 of the LAI- $\alpha_{F_{\text{mean}}}$ model may be due to the individual slopes of *Acer rubrum* and *Carpinus betula* being higher than the pooled regression. These differences may, again, be due to the influence of LAD on LAI estimates (e.g., Weiss et al. 2004). However, if we assume that there is no error in the gap-fraction LAI data, the improved relationship of species-specific $\alpha_{F_{\text{mean}}}$ with α_G would support LAD as a source of error because the Goudriaan model indirectly accounts for canopy density by distributing LAI over a discrete canopy volume. Nevertheless, previous studies have reported a general agreement between the Goudriaan model and α_F (e.g., Cionco 1978; Campbell and Norman 1998). Additionally, Cammalleri et al. (2010) found strong agreement between measured and modeled fluxes of sensible heat when α was characterized using the Goudriaan model. An alternate benefit of using the Goudriaan model to calculate α is that the equation may be rearranged to solve for LAI if $\alpha_{F_{\text{mean}}}$, canopy height, and L_w are known. This could offer a

straightforward, real-time method for determining LAI, which could be particularly beneficial in vegetation that experiences large changes in LAI over a growing season (e.g., agronomic or biomass crops). A similar result could be accomplished from the LAI- $\alpha_{F_{\text{mean}}}$ model but with less accuracy.

b. Canopy aerodynamics determine variable canopy-to-atmosphere coupling

The Ω coefficient is important for quantifying how the control of transpiration is partitioned between leaf-level physiology and the environment, ranging from 0 (total physiological control) to 1 (total environmental control). Increases in Ω will occur as g_{bv} decreases or as g_s increases. While changes in g_s can be due to a combination of physiological and environmental responses, g_{bv} is generally dependent on how L_w and wind velocity influence forced convection and how the T_{leaf} to T_{air} differences influence free convection [i.e., Eqs. (8) and (10)]. In this study, modeled mean g_s declined throughout the season, likely due to net photosynthesis

TABLE 2. Seasonal mean crown LAD, mean maximum L_w , $g_{s_{\max}}$, and photosynthesis A_{\max} at 400 ppm CO_2 . Error estimates represent one standard error: $n = 15$ for LAD and L_w and $n = 5$ for $g_{s_{\max}}$ and A_{\max} .

	LAD ($\text{m}^2 \text{m}^{-3}$)	L_w (cm)	$g_{s_{\max}}$ ($\text{mol m}^{-2} \text{s}^{-1}$)	A_{\max} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)
<i>Acer rubrum</i>	0.33 ± 0.01	8.9 ± 0.21	0.489 ± 0.03	10.38 ± 1.05
<i>Betula nigra</i>	0.12 ± 0.01	4.7 ± 0.13	0.801 ± 0.07	13.72 ± 0.65
<i>Carpinus betula</i>	0.46 ± 0.01	3.3 ± 0.09	0.601 ± 0.04	10.81 ± 0.77
<i>Cercis canadensis</i>	0.08 ± 0.01	9.6 ± 0.25	0.443 ± 0.02	9.44 ± 0.92

declining as the shaded fraction of leaf area increased (Bauerle et al. 2004; Campoe et al. 2013). Increasing leaf age has also been shown to result in decreased g_s in trees (Field 1987); however, the biochemical dynamics of this response are not characterized in the MAESTRA model formulation and thus do not describe this decline. Full descriptions of the physiological submodels and parameterization can be found in Barnard and Bauerle (2013). Despite variable rates of canopy development among species, the rates of seasonal g_s decline were similar, suggesting a potential meteorological driver. Individual species each displayed different mean daily g_s early in the season that corresponded to species-specific $g_{s_{\max}}$ (Table 2). Regardless, the daily variation in g_{bv} (and corresponding variation in Ω) suggests that wind velocity and canopy aerodynamics are the predominant influences on canopy-to-atmosphere coupling. For example, *Acer rubrum* and *Cercis canadensis* had relatively similar seasonal evolution of Ω despite divergent physiology and $\alpha_{F_{\text{mean}}}$ values. The reason being that *Cercis canadensis* had lower mean g_{bv} in the early and midseason because of lower within-canopy wind velocities (Fig. 2). Reduced within-canopy wind velocity was a result of both decreasing above-canopy bulk wind speed (Fig. 1) and increasing canopy leaf area (Fig. 3). However, lower $\alpha_{F_{\text{mean}}}$ yielded higher g_{bv} in *Acer rubrum*, which was counterbalanced by higher mean canopy g_s , resulting in similar Ω values to *Cercis canadensis*. Regardless, our findings clearly point to g_{bv} as the main driver of canopy Ω , a finding that is contrary to a study that found spatial variability in leaf g_s to dictate variation in Ω (Daudet et al. 1999). The Daudet et al. (1999) study investigated a single species (and thus a single L_w), but it is unlikely that the greater representation of a range of L_w in this study is responsible for the disparity given the strong relationship between g_{bv} and Ω .

Mean canopy g_{bv} was variably correlated with U_{3m} and LAI among species. Along a gradient of increasing LAI and $\alpha_{F_{\text{mean}}}$, there was a decrease in the correlation between U_{3m} and g_{bv} and an increase in the correlation between daily interpolated values of $\alpha_{F_{\text{mean}}}$ and g_{bv} . Hence, increasing canopy leaf area deemphasizes the effect of above-canopy wind speed in determining mean canopy g_{bv} . Instead, in more densely foliated canopies

(i.e., $\text{LAI} > 1.25 \text{m}^2 \text{m}^{-2}$), accurate g_{bv} estimates require both U_{3m} and $\alpha_{F_{\text{mean}}}$ because of the decoupling of above- and within-canopy wind fields as increased leaf area increases form drag and reduces bulk wind momentum in the canopy. More sparsely foliated canopies (e.g., *Acer rubrum* and *Carpinus betula*) do not appear to impact the wind field as much, and thus U_{3m} can predict mean g_{bv} relatively well. It is important to note that although $\alpha_{F_{\text{mean}}}$ is a parameter of increasing importance in densely foliated canopies, it still explains 66% of the variation in g_{bv} in sparsely foliated canopies. Moreover, Fig. 9 shows that the parameter effect of α increases with increasing VPD, suggesting that accurate characterization of α is very important in well foliated canopies in drier conditions.

c. Wind speed influences on transpiration are dependent on climate variables

The modeling framework we used provides a foundation to examine the theoretical influence of above-canopy wind speed on transpiration over a wide range of concomitant environmental conditions that need to be considered together (Hobbins et al. 2012). In our 1000 simulations, we observed above-canopy wind speed influences on transpiration ranging from -30% to $+20\%$, corresponding with the range reported from several studies previously (Kim et al. 2014). We acknowledge that the extreme ends of these meteorological combinations may appear to be outside the range of what could be realistically expected, but we chose to include them to represent extreme environments such as hot and dry climates like the southwestern United States. Nevertheless, two important conclusions can be drawn from these modeling exercises that have not been previously discussed. First, in low-light conditions (i.e., $\text{PAR} < 250 \mu\text{mol m}^{-2} \text{s}^{-1}$), ΔE_{wind} is at the extreme upper and lower ends of the effect range. This suggests that the greatest possible wind speed influence may occur in the early morning, late evening, and at nighttime, during which the variability will be dependent on other environmental conditions (e.g., T_{air} and VPD). Given that nighttime transpiration can account for $>20\%$ of total daily transpiration (Benyon 1999; Dawson et al. 2007), the VPD–wind speed interactions during this period

warrant future work and attention given the potential impact on daily transpiration estimates. Second, the strong observed relationship between ΔE_{wind} and VPD (Fig. 8c) may identify a primary mechanism by which wind speed can influence transpiration. For example, there have been numerous studies with contradictory results regarding the influence of wind speed on transpiration. In moderately humid areas, Kim et al. (2014) and Daudet et al. (1999) showed only a marginal influence of wind on transpiration, whereas Taylor et al. (2001) found a significant positive effect at forest edges in an arid zone and Gutiérrez et al. (1994) found a negative influence in coffee hedgerows in a humid tropical zone. Hence, there is an apparent relationship between the directional influence of wind speed and native VPD. Building off of this potential relationship, our simulations suggest that VPD influences transpiration by altering the partitioning of turbulent fluxes.

Kim et al. (2014) provided an alternate explanation for why the wind speed effect on transpiration is variable, finding that the reduced canopy resistance from increased wind speed is negligible but that the relationship between wind speed and mixing effects on within-canopy VPD may interact with physiology to influence transpiration in either direction. However, their analysis was from one-dimensional simulations of aerodynamic and physiological resistances and did not take into account leaf energy balance. Moreover, they filtered the data to remove the influence of light and VPD, thereby eliminating the potential to evaluate such influences.

5. Conclusions

In this study, we describe the influence of seasonal development of canopy aerodynamics on α in four broadleaf tree species. We found α to vary substantially with changes in above-canopy wind speed as well as with canopy development, two sources of variation that may not be well represented in land surface or hydrologic modeling schemes if α is held constant spatially and/or temporally. The influence of increasing leaf area on α is of particular importance in plant systems that experience large seasonal changes in canopy leaf area such as agronomic and biofuel crops and deciduous ecosystems. The change in α with wind speed did appear to reach a uniform lower asymptote across species regardless of canopy structure or development stage, but at an above-canopy wind speed that was more than two standard deviations above the site mean. Nevertheless, α measured at the mean above-canopy wind speed for our research plot (1.5 m s^{-1}) could be predicted by LAI alone, but more accurately with the Goudriaan (1977) model that includes a term for canopy height and L_w .

Using either method to predict α has the potential to minimize the need for intensive field-based sampling.

We found variation in g_{bv} from bulk wind velocity and from changes to the canopy over the growing season to have a greater influence on daily Ω than stomatal dynamics. We also found mean daily g_{bv} to be well correlated with above-canopy wind speed in less densely foliated canopies, but as canopy LAI approached $1 \text{ m}^2 \text{ m}^{-2}$, α became increasingly important for accurate g_{bv} estimates.

Vapor pressure deficit interacts with wind speed to affect transpiration and the magnitude of influence that errors in α have on transpiration estimates. The α parameter is an important parameter for modeling g_{bv} and is thus important for understanding how the control of transpiration is partitioned between leaf-level physiology and the environment. Hence, the importance of the α parameter is most essential at scales that consider a stratified canopy with distinct leaf sizes and distribution, for which g_{bv} needs to be calculated. We conclude that accurate characterizations of the components constraining the flux of water and energy are essential at scales ranging from the leaf to the ecosystem.

Acknowledgments. We thank T. Demaline and Willoway Nursery staff for donating plant material and site maintenance. This project was funded by the USDA National Institute of Food and Agriculture, Specialty Crops Research Initiative (Award 2009-51181-05768), and Cooperative Agreement (Award 58-6618-2-0209). Decagon Devices Inc. subsidized equipment costs in Award 2009-51181-05768.

REFERENCES

- Åcs, F., 1994: A coupled soil–vegetation scheme: Description, parameters, validation, and sensitivity studies. *J. Appl. Meteor.*, **33**, 268–284, doi:[10.1175/1520-0450\(1994\)033<0268:ACSVSD>2.0.CO;2](https://doi.org/10.1175/1520-0450(1994)033<0268:ACSVSD>2.0.CO;2).
- Aphalo, P., and P. Jarvis, 1991: Do stomata respond to relative humidity? *Plant Cell Environ.*, **14**, 127–132, doi:[10.1111/j.1365-3040.1991.tb01379.x](https://doi.org/10.1111/j.1365-3040.1991.tb01379.x).
- Baldwin, V. C., Jr., and K. D. Peterson, 1997: Predicting the crown shape of loblolly pine trees. *Can. J. For. Res.*, **27**, 102–107, doi:[10.1139/x96-100](https://doi.org/10.1139/x96-100).
- Barnard, D., and W. Bauerle, 2013: The implications of minimum stomatal conductance on modeling water flux in forest canopies. *J. Geophys. Res. Biogeosci.*, **118**, 1322–1333, doi:[10.1002/jgrg.20112](https://doi.org/10.1002/jgrg.20112).
- Bauerle, W. L., and J. D. Bowden, 2011: Separating foliar physiology from morphology reveals the relative roles of vertically structured transpiration factors within red maple crowns and limitations of larger scale models. *J. Exp. Bot.*, **62**, 4295–4307, doi:[10.1093/jxb/err156](https://doi.org/10.1093/jxb/err156).
- , —, M. F. McLeod, and J. E. Toler, 2004: Modeling intra-crown and intra-canopy interactions in red maple: Assessment of light transfer on carbon dioxide and water vapor exchange. *Tree Physiol.*, **24**, 589–597, doi:[10.1093/treephys/24.5.589](https://doi.org/10.1093/treephys/24.5.589).
- , A. B. Daniels, and D. M. Barnard, 2014: Carbon and water flux responses to physiology by environment interactions: A

- sensitivity analysis of variation in climate on photosynthetic and stomatal parameters. *Climate Dyn.*, **42**, 2539–2554, doi:[10.1007/s00382-013-1894-6](https://doi.org/10.1007/s00382-013-1894-6).
- Benyon, R. G., 1999: Nighttime water use in an irrigated *Eucalyptus grandis* plantation. *Tree Physiol.*, **19**, 853–859, doi:[10.1093/treephys/19.13.853](https://doi.org/10.1093/treephys/19.13.853).
- Cammalleri, C., M. C. Anderson, G. Ciraolo, G. D'Urso, W. P. Kustas, G. La Loggia, and M. Minacapilli, 2010: The impact of in-canopy wind profile formulations on heat flux estimation in an open orchard using the remote sensing-based two-source model. *Hydrol. Earth Syst. Sci.*, **14**, 2643–2659, doi:[10.5194/hess-14-2643-2010](https://doi.org/10.5194/hess-14-2643-2010).
- Campbell, G. S., and J. M. Norman, 1998: *An Introduction to Environmental Biophysics*. Springer, 286 pp.
- Campoe, O. C., J. L. Stape, Y. Nouvellon, J.-P. Laclau, W. L. Bauerle, D. Binkley, and G. Le Maire, 2013: Stem production, light absorption and light use efficiency between dominant and non-dominant trees of *Eucalyptus grandis* across a productivity gradient in Brazil. *For. Ecol. Manage.*, **288**, 14–20, doi:[10.1016/j.foreco.2012.07.035](https://doi.org/10.1016/j.foreco.2012.07.035).
- Cionco, R. M., 1965: A mathematical model for air flow in a vegetative canopy. *J. Appl. Meteor.*, **4**, 517–522, doi:[10.1175/1520-0450\(1965\)004<0517:AMMFAF>2.0.CO;2](https://doi.org/10.1175/1520-0450(1965)004<0517:AMMFAF>2.0.CO;2).
- , 1972: A wind-profile index for canopy flow. *Bound.-Layer Meteor.*, **3**, 255–263, doi:[10.1007/BF02033923](https://doi.org/10.1007/BF02033923).
- , 1978: Analysis of canopy index values for various canopy densities. *Bound.-Layer Meteor.*, **15**, 81–93, doi:[10.1007/BF00165507](https://doi.org/10.1007/BF00165507).
- Daudet, F., X. Le Roux, H. Sinoquet, and B. Adam, 1999: Wind speed and leaf boundary layer conductance variation within tree crown: Consequences on leaf-to-atmosphere coupling and tree functions. *Agric. For. Meteorol.*, **97**, 171–185, doi:[10.1016/S0168-1923\(99\)00079-9](https://doi.org/10.1016/S0168-1923(99)00079-9).
- Dawson, T. E., S. S. O. Burgess, K. P. Tu, R. S. Oliveira, L. S. Santiago, J. B. Fisher, K. A. Simonin, and A. R. Ambrose, 2007: Nighttime transpiration in woody plants from contrasting ecosystems. *Tree Physiol.*, **27**, 561–575, doi:[10.1093/treephys/27.4.561](https://doi.org/10.1093/treephys/27.4.561).
- Drake, B., K. Raschke, and F. Salisbury, 1970: Temperature and transpiration resistances of *Xanthium* leaves as affected by air temperature, humidity, and wind speed. *Plant Physiol.*, **46**, 324–330, doi:[10.1104/pp.46.2.324](https://doi.org/10.1104/pp.46.2.324).
- Farquhar, G. D., S. Caemmerer, and J. Berry, 1980: A biochemical model of photosynthetic CO₂ assimilation in leaves of C₃ species. *Planta*, **149**, 78–90, doi:[10.1007/BF00386231](https://doi.org/10.1007/BF00386231).
- Field, C. B., 1987: Leaf-age effects on stomatal conductance. *Stomatal Function*, E. Zeiger, G. D. Farquhar, and J. R. Cowan, Eds., Stanford University Press, 367–382.
- Goudriaan, J., 1977: *Crop Micrometeorology: A Simulation Study*. Pudoc, Center for Agricultural Publishing and Documentation, 249 pp.
- Gutiérrez, M., F. C. Meinzer, and D. Grantz, 1994: Regulation of transpiration in coffee hedgerows: Covariation of environmental variables and apparent responses of stomata to wind and humidity. *Plant Cell Environ.*, **17**, 1305–1313, doi:[10.1111/j.1365-3040.1994.tb00532.x](https://doi.org/10.1111/j.1365-3040.1994.tb00532.x).
- Hobbins, M., A. Wood, D. Strubel, and K. Werner, 2012: What drives the variability of evaporative demand across the conterminous United States? *J. Hydrometeorol.*, **13**, 1195–1214, doi:[10.1175/JHM-D-11-0101.1](https://doi.org/10.1175/JHM-D-11-0101.1).
- Inoue, E., 1963: On the turbulent structure of airflow within crop canopies. *J. Meteor. Soc. Japan*, **41**, 317–326.
- Inoue, K., and Z. Uchijima, 1979: Experimental study of micro-structure of wind turbulence in rice and maize canopies. *Bull. Natl. Inst. Agric. Sci., Ser. A*, **26**, 1–88.
- Jarvis, P. G., and K. McNaughton, 1986: Stomatal control of transpiration: Scaling up from leaf to region. *Adv. Ecol. Res.*, **15**, 1–49, doi:[10.1016/S0065-2504\(08\)60119-1](https://doi.org/10.1016/S0065-2504(08)60119-1).
- Kim, D., R. Oren, A. C. Oishi, C. Hsieh, N. Phillips, K. A. Novick, and P. C. Stoy, 2014: Sensitivity of stand transpiration to wind velocity in a mixed broadleaved deciduous forest. *Agric. For. Meteorol.*, **187**, 62–71, doi:[10.1016/j.agrformet.2013.11.013](https://doi.org/10.1016/j.agrformet.2013.11.013).
- Leuning, R., 1995: A critical appraisal of a combined stomatal–photosynthesis model for C₃ plants. *Plant Cell Environ.*, **18**, 339–355, doi:[10.1111/j.1365-3040.1995.tb00370.x](https://doi.org/10.1111/j.1365-3040.1995.tb00370.x).
- , F. Kelliher, D. D. Pury, and E. D. Schulze, 1995: Leaf nitrogen, photosynthesis, conductance and transpiration: Scaling from leaves to canopies. *Plant Cell Environ.*, **18**, 1183–1200, doi:[10.1111/j.1365-3040.1995.tb00628.x](https://doi.org/10.1111/j.1365-3040.1995.tb00628.x).
- Martin, T. A., T. M. Hinckley, F. C. Meinzer, and D. G. Sprugel, 1999: Boundary layer conductance, leaf temperature and transpiration of *Abies amabilis* branches. *Tree Physiol.*, **19**, 435–443, doi:[10.1093/treephys/19.7.435](https://doi.org/10.1093/treephys/19.7.435).
- Meinzer, F. C., 1993: Stomatal control of transpiration. *Trends Ecol. Evol.*, **8**, 289–294, doi:[10.1016/0169-5347\(93\)90257-P](https://doi.org/10.1016/0169-5347(93)90257-P).
- Monteith, J., 1965: Evaporation and environment. *Symp. Soc. Exp. Biol.*, **19**, 205–234.
- Mott, K. A., and D. Peak, 2010: Stomatal responses to humidity and temperature in darkness. *Plant Cell Environ.*, **33**, 1084–1090, doi:[10.1111/j.1365-3040.2010.02129.x](https://doi.org/10.1111/j.1365-3040.2010.02129.x).
- Nobel, P. S., 1999: *Physicochemical and Environmental Plant Physiology*. Academic Press, 474 pp.
- Oleson, K., and Coauthors, 2013: Technical description of version 4.5 of the Community Land Model (CLM). NCAR Tech. Note NCAR/TN-503+STR, 420 pp., doi:[10.5065/D6RR1W7M](https://doi.org/10.5065/D6RR1W7M).
- Pereira, A. R., and R. H. Shaw, 1980: A numerical experiment on the mean wind structure inside canopies of vegetation. *Agric. Meteorol.*, **22**, 303–318, doi:[10.1016/0002-1571\(80\)90009-6](https://doi.org/10.1016/0002-1571(80)90009-6).
- Saito, T., 1964: On the wind profile within plant communities. *Bull. Natl. Inst. Agric. Sci., Ser. A*, **11**, 67–74.
- Sauer, T., J. Norman, C. Tanner, and T. Wilson, 1995: Measurement of heat and vapor transfer coefficients at the soil surface beneath a maize canopy using source plates. *Agric. For. Meteorol.*, **75**, 161–189, doi:[10.1016/0168-1923\(94\)02209-3](https://doi.org/10.1016/0168-1923(94)02209-3).
- Schuepp, P., 1993: Tansley review No. 59. Leaf boundary layers. *New Phytol.*, **125**, 477–507, doi:[10.1111/j.1469-8137.1993.tb03898.x](https://doi.org/10.1111/j.1469-8137.1993.tb03898.x).
- Sellers, P., and Coauthors, 1996: A revised land surface parameterization (SiB2) for atmospheric GCMs. Part I: Model formulation. *J. Climate*, **9**, 676–705, doi:[10.1175/1520-0442\(1996\)009<0676:ARLSPF>2.0.CO;2](https://doi.org/10.1175/1520-0442(1996)009<0676:ARLSPF>2.0.CO;2).
- Souch, C., and W. Stephens, 1998: Growth, productivity and water use in three hybrid poplar clones. *Tree Physiol.*, **18**, 829–835, doi:[10.1093/treephys/18.12.829](https://doi.org/10.1093/treephys/18.12.829).
- Tague, C., and L. Band, 2004: RHESSys: Regional hydro-ecological simulation system: An object-oriented approach to spatially distributed modeling of carbon, water and nutrient cycling. *Earth Interact.*, **8**, doi:[10.1175/1087-3562\(2004\)8<1:RRHSSO>2.0.CO;2](https://doi.org/10.1175/1087-3562(2004)8<1:RRHSSO>2.0.CO;2).
- Taylor, P. J., I. K. Nuberg, and T. Hutton, 2001: Enhanced transpiration in response to wind effects at the edge of a blue gum (*Eucalyptus globulus*) plantation. *Tree Physiol.*, **21**, 403–408, doi:[10.1093/treephys/21.6.403](https://doi.org/10.1093/treephys/21.6.403).
- Trout, T. J., L. F. Johnson, and J. Gartung, 2008: Remote sensing of canopy cover in horticultural crops. *HortScience*, **43** (2), 333–337.
- Wang, Y.-P., and P. Jarvis, 1990a: Description and validation of an array model—MAESTRO. *Agric. For. Meteorol.*, **51**, 257–280, doi:[10.1016/0168-1923\(90\)90112-J](https://doi.org/10.1016/0168-1923(90)90112-J).
- , and —, 1990b: Influence of crown structural properties on PAR absorption, photosynthesis, and transpiration in Sitka

- spruce: Application of a model (MAESTRO). *Tree Physiol.*, **7**, 297–316, doi:[10.1093/treephys/7.1-2-3-4.297](https://doi.org/10.1093/treephys/7.1-2-3-4.297).
- , and R. Leuning, 1998: A two-leaf model for canopy conductance, photosynthesis and partitioning of available energy. I: Model description and comparison with a multi-layered model. *Agric. For. Meteorol.*, **91**, 89–111, doi:[10.1016/S0168-1923\(98\)00061-6](https://doi.org/10.1016/S0168-1923(98)00061-6).
- , P. Jarvis, and M. Benson, 1990: Two-dimensional needle-area density distribution within the crowns of *Pinus radiata*. *For. Ecol. Manage.*, **32**, 217–237, doi:[10.1016/0378-1127\(90\)90172-8](https://doi.org/10.1016/0378-1127(90)90172-8).
- Weiss, M., F. Baret, G. Smith, I. Jonckheere, and P. Coppin, 2004: Review of methods for in situ leaf area index (LAI) determination: Part II. Estimation of LAI, errors and sampling. *Agric. For. Meteorol.*, **121**, 37–53, doi:[10.1016/j.agrformet.2003.08.001](https://doi.org/10.1016/j.agrformet.2003.08.001).
- Westgate, M., F. Forcella, D. Reicosky, and J. Somsen, 1997: Rapid canopy closure for maize production in the northern US corn belt: Radiation-use efficiency and grain yield. *Field Crops Res.*, **49**, 249–258, doi:[10.1016/S0378-4290\(96\)01055-6](https://doi.org/10.1016/S0378-4290(96)01055-6).
- Wigmosta, M. S., L. Vail, and D. P. Lettenmaier, 1994: A distributed hydrology–vegetation model for complex terrain. *Water Resour. Res.*, **30**, 1665–1679, doi:[10.1029/94WR00436](https://doi.org/10.1029/94WR00436).
- Wright, J. L., 1965: *Evaluating Turbulent Transfer Aerodynamically within the Microclimate of a Cornfield*. Cornell University, 174 pp.