Sensitivity of stand transpiration to wind velocity in a mixed broadleaved deciduous forest

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ABSTRACT

Wind velocity (U) within and above forest canopies can alter the coupling between the vapor-saturated sub-stomatal airspace and the drier atmosphere aloft, thereby influencing transpiration rates. In practice, however, the actual increase in transpiration with increasing U depends on the aerodynamic resistance (R_A) to vapor transfer compared to canopy resistance to water vapor flux out of leaves (R_C, dominated by stomatal resistance, R_{stom}), and the rate at which R_A decreases with increasing U. We investigated the effect of U on transpiration at the canopy scale using filtered meteorological data and sap flux measurements gathered from six diverse species of a mature broadleaved deciduous forest. Only under high light conditions, stand transpiration (E_C) increased slightly (6.5%) with increasing U ranging from ~0.7 to ~4.7 m s^{-1}. Under other conditions, sap flux density (J_s) and E_C responded weakly or did not change with U. R_A, estimated from Monin–Obukhov similarity theory, decreased with increasing U, but this decline was offset by increasing R_C, estimated from a rearranged Penman–Monteith equation, due to a concurrent increase in vapor pressure deficit (D). The increase of R_C with D over the observed range of U was consistent with increased R_{stom} by ~40% based on hydraulic theory. Except for very rare half-hourly values, the proportion of R_A to total resistance (R_T) remained <15% over the observed range of conditions. These results suggest that in similar forests and conditions, the direct effect of U reducing R_A and thus increasing transpiration is negligible. However, the observed U–D relationship and its effect on R_{stom} must be considered when modeling canopy photosynthesis.

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1. Introduction

Because of their expanse, forests greatly impact the exchange of mass and energy between the biosphere and atmosphere with consequences ranging from effects on local weather conditions (Juang et al., 2007; Konings et al., 2011) to influences on global atmospheric circulation (Avissar and Werth, 2005; Bauerle and Bowden, 2011). Forests also play an important role in the provision of ecosystem services, including water yield, biomass production and carbon sequestration. Improved understanding of these exchanges and benefits involves a combination of observations and models. Estimates of mass (including carbon and water) and energy exchange between the biosphere and atmosphere commonly rely on modeled

and measurement-based estimates of a series of resistances to these exchanges, each affected by biological and physical factors.

The flux of water vapor through stomata (i.e. transpiration) is an important flux since it represents the major component of water returned to the atmosphere from forests. Transpiration is also tightly coupled to CO_2 exchange (i.e. canopy photosynthesis or gross primary production) because stomata serve as the common port for the fluxes of these gases. Thus, tree and ecosystem physiologists often investigate the sources of variation of resistances to water vapor flux in lieu of the variation of resistances to CO_2 flux (Kim et al., 2008; Schäfer et al., 2003), and models often computationally link canopy CO_2 uptake to transpiration via the carbon-based water-use efficiency (Running and Hunt, 1993). Transpiration is convenient flux to use in such analysis because, unlike CO_2 flux, the dynamics of its exchange is straightforward to measure (Granier, 1987; Oishi et al., 2008; Oren et al., 1998; Schäfer et al., 2000).

Table 1
Field studies that have investigated relationships between transpiration (or sap flux) and wind velocity.

Correlation	Site description (species)	Wind velocity (m s^{-1})	Tree stage(age in years)	LAI[a]	SLA[b] (cm^2 g^{-1})	Source
Positive	Hardwood, South Australia (*Eucalyptus globulus*)	–	Young (7)	–	62–192[d]	Taylor et al. (2001)
	Boreal mixedwood, Alberta, Canada (*Picea glauca, P. balsamifera, Betula papyrifera*)	0–2	Mature (45–50)	–	–	Bladon et al. (2006)
	Shrub, Tengger desert, China (*Artemisia ordosica*)	–	(10)	0.5–0.9	–	Lei et al. (2010)
	Temperate hardwood, Estonia (*B. pendula, P. tremula + P. tremuloides*[c])	0–4	Seedling (1)	–	–	Kupper et al. (2011)
	Temperate hardwood, China (*Populus alba*)	0–0.6	Young (7–10)	0–2	100–120[d]	Xu et al. (2006)
Negative	Shrub, island of Kauai, USA (*Coffea arabica* L.)	1–3	(1–5.3)	0.7–6.7	–	Gutiérrez et al. (1994)
	Hardwood, Wisconsin, USA (*P. nigra + P. maximowiczii*[c])	0–4.5	Young	–	–	Zalesny et al. (2006)
Weak or none	Hardwood, Plauzat, France (*Juglans regia*)	0–4	Mature (20)	9	82–398[d]	Daudet et al. (1999)
	Softwood, Chiba, Japan (*Cryptomeria japonica*)	0–1.5	Young (8)	3.7	–	Komatsu et al. (2006)
	Crop, Nebraska, USA (*Zea mays* L.)	0–7	–	1–5	–	Irmak and Mutiibwa (2010)
	Temperate hardwood, Durham, USA (*Liriodendron tulipifera, Liquidambar styraciflua, Carya tomentosa, Quercus alba, Q. michauxii, Q. phellos*)	0.8–4.7	Mature (80–100)	7.03	102–174	This study

[a] Leaf area index.
[b] Specific leaf area.
[c] Hybrid between the two species.
[d] General values from various studies.

Resistance to transpiration (R_T) can be partitioned into two serial components, bulk surface resistance (R_{sur}) and aerodynamic resistance (R_A),

$$R_T = R_{sur} + R_A \qquad (1)$$

both of which depend on leaf physiology, canopy architecture and the atmospheric conditions above and within the canopy (Jones, 1992; Kumagai et al., 2004). R_{sur} is generally attributed to canopy resistance (R_C) and soil (or forest floor) resistance (R_{soil}) acting in parallel (Allen, 2005).

$$R_{sur} = \frac{R_C R_{soil}}{R_C + R_{soil}} \qquad (2)$$

Soil evaporation is minor under high canopy leaf area, making R_C effectively equivalent to R_{sur} when leaf area index (LAI) is greater than 3 (Kelliher et al., 1995; Waring, 2007). R_C can be expressed as a combination of stomatal resistance (R_{stom}) and leaf boundary layer resistance (R_{bl}) in series (Aphalo and Jarvis, 1993):

$$R_C = R_{stom} + R_{bl} \qquad (3)$$

R_{stom} reflects complex physiological responses of stomata to variation in atmospheric conditions, such as light availability, air temperature (T_a), humidity, CO_2 concentration (Jarvis, 1976). R_{bl} is the resistance to vapor transfer within the air layer near leaf surface, and can be affected by wind velocity (U), leaf shape, leaf size, edge characteristics, and surface structure (Schuepp, 1993; Stokes et al., 2006). R_{bl} is generally much smaller than R_{stom} unless leaf size is large or U is low (Aphalo and Jarvis, 1993; Schuepp, 1993).

Over time scales in which soil moisture and plant hydraulic properties (e.g. soil-to-leaf path-length, sapwood-to-leaf area ratio, hydraulic conductivity) can be considered invariable, R_C is largely determined by R_{stom}. Jarvis (1976) described stomatal conductance (the inverse of R_{stom}) as a form of multiplicative function with

photon flux density, vapor pressure deficit (D), T_a, ambient CO_2 concentration, and leaf water potential. Many formulations for R_{stom}, ranging from empirical to theoretically-based functions have been proposed and used (Holmgren et al., 1996; Jonard et al., 2011; Launiainen et al., 2011; Pataki and Oren, 2003; Stewart, 1988), but except for allowing interactions among the controlling variables (Ward et al., 2008), this approach remained fundamentally unaltered. The other primary component of R_T, R_A, is determined by the physical conditions above and within the canopy, such as U, atmospheric stability, and canopy structure (Kumagai et al., 2004; Lindroth, 1993; Morris et al., 1998). Although estimates of R_A in forests are usually small relative to R_C, reflected in that R_A is neglected in some biosphere–atmosphere exchange models (Granier et al., 2000; Kelliher et al., 1993; Köstner et al., 1992), few studies have actually quantified the effect of U on R_A and, in-turn, on transpiration (Table 1). The results of these studies are inconclusive: some studies observed increased transpiration with U (Chu et al., 2009; Grace and Russel, 1982; Kitaya et al., 2004); others observed a decline (Caldwell, 1970; Campbell-Clause, 1998; Dixon and Grace, 1984; Gutiérrez et al., 1994), or found transpiration to be insensitive to U (Komatsu et al., 2006).

Here we analyze the effect of U on transpiration through measurements and by quantifying the response to U of estimated resistances in the water vapor pathway, focusing on the reduced expression:

$$R_T = R_A + R_{bl} + R_{stom} \qquad (4)$$

Many of the studies on transpiration response to U were performed in wind tunnels (Caldwell, 1970; Chu et al., 2009; Dixon and Grace, 1984; Grace and Russell, 1982; Kitaya et al., 2004). However, results of wind tunnel experiments may differ from those of field experiments because they do not account for the effect of neighboring crowns (shelter effect) on the coupling between stomata