7 The Role of Biodiversity on the Evaporation of Forests

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7.1 Introduction

On visiting an arboretum or walking through a mixed-species forest, an impression one receives is that there is much diversity in the form and function of trees. The leaves of angiosperm trees can be thin or fleshy, shiny, dull, or hairy. They can be large or small. Their shape can be simple or compound, linear or lobed, cordate, deltate, ovate, or elliptical, among many examples of variation. On a stem, the leaves can be grouped in clumps, arranged in whorls or extend from individual isolated petioles. As for the regulation and transport of water, angiosperms may possess stomata on one or both sides of a leaf and have either ring porous (e.g., *Quercus* or *Ulmus* spp.) or diffuse porous (e.g., *Betula* or *Acer* spp.) xylem. Gymnosperms, by contrast, have either needles (e.g., *Pinus* spp.) or scales (*Junipers* spp.). Their phytoelements can be arranged in shoots, as with spruce (*Picea* spp.), be comprised of groups of needles on fascicles, as with pine (*Pinus* spp.). From these simple observations, one may surmise that biodiversity could affect rates of transpiration of trees and their annual water budget. But does it?

The answer to this simple question is complicated due to interactions and competition among species for light energy, water and nutrients (e.g., Allen et al. 2002), evolution (Beerling et al. 2001), and to the space and time scale at which it is asked (Waide et al. 1999). Genetic diversity, combined with biogeochemical forcings, produce plant species that differ in physiological and morphological features (Mooney 2001). A specific set of plant features contributes to a ranking of transpiration among tree species because such elements affect the energy balance of leaves and plants. For example, biodiversity, achieved through competition and evolution, is responsible for morphological differences in leaf size, thickness, shape, and reflective properties. These features are important because they affect the aerodynamic resistance and radiative balance of leaves. Species-dependent differences in physiological factors affect transpiration by altering the demand for and supply of water. For exam-

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ple, differences in surface resistance arise through species differences in photosynthetic capacity, lifespan (Reich et al. 1997), and maximum stomatal conductance (Schulze et al. 1994; Pataki et al. 2000). Species-dependent differences in the supply of water are mediated by differences rooting depth (Lewis and Burgy 1964; Ehleringer and Dawson 1992; Jackson et al. 1996), timing of physiological activity (Xu and Baldocchi 2003), and drought tolerance or avoidance (Stephenson 1998).

The second question to ask is: do all species in a mixed-species landscape make an independent and proportional contribution to canopy evaporation? The answer to this question can be debated, as there is evidence for and against. On the pro side, an analysis by Currie and Paquin (1987) shows that species richness of trees in North America increases with annual evaporation. A second line of evidence comes from grassland field studies, indicating that aboveground biomass and net primary productivity increase with species richness (Tilman et al. 1997; Hector et al. 1999; Waide et al. 1999; Roy 2001). By inference one could conclude that increasing biodiversity increases evaporation rates and amounts because evaporation of forests scales with net primary productivity (Law et al. 2002).

A contrary view can be derived on the basis of biometeorology and ecological theory. As groups of trees come together and form a closed canopy, the coupling of individual plants with the atmosphere changes (Jarvis and McNaughton 1986). Theoretical and experimental studies show that rates of evaporation, normalized by available energy and temperature, increase with leaf area up to a threshold (a leaf area index of about 3; Jarvis and McNaughton 1986; Saugier and Katerji 1991; Kelliher et al. 1995; Baldocchi and Meyers 1998; Eamus et al. 2001). On ecological grounds, the number and combination of functional factors are limited due to convergent evolution. So the total number of species across a landscape may not be as important as the different number of functional types (Hooper and Vitousek 1997; Tilman et al. 1997; Mooney 2001; Roy 2001). An intermediate view can also be drawn, based on a recent analysis of net primary productivity by Waring et al. (2002). They found that greatest species diversity, along a transect of forests in Oregon, occurs at sites of intermediate productivity.

As a micrometeorologist, I am presupposed to favor the view that the impact of biodiversity on evaporation is realized by how it alters the structural and functional properties of a plant stand, such as its aerodynamic roughness, the amount of transpiring plant material, its physiological capacity to transpire, and its ability to intercept solar radiation. However, I leave the answer to this question to be drawn at the end of this essay. To arrive at a final conclusion, I explore the question of how biodiversity may or may not affect water use of plants by examining theory and experimental data across the scales of leaf, tree, and canopy.

7.2 Leaf Scale

A combination of two physical laws can be used to evaluate evaporation from leaves (Jarvis and McNaughton 1986; Campbell and Norman 1998). One is an analogy to Ohm's Law (Eq. 7.1). It states that evaporation rates are proportional to the product of the leaf conductance and the potential difference in humidity between the leaf surface and the atmosphere:

$$E \sim \frac{g_s g_b}{g_s + g_b}\left(e_s\left(T_l\right) - e_a\right) \tag{7.1}$$

The other important law is the leaf energy balance relationship (Eq. 7.2). It defines how available solar and terrestrial energy is partitioned into sensible heat (*H)* and latent heat exchange (*λE)*:

$$Q = \left(1 - \varrho\right)R + \varepsilon L = \varepsilon\sigma\, T_l^4 + H + \lambda E \tag{7.2}$$

In these equations, g_s and g_b are the stomatal and boundary layer conductances, respectively, T_l is leaf temperature, e_s is the saturation vapor pressure, e_a is the atmospheric vapor pressure, ϱ is leaf reflectance, *R* and *L* are flux densities of incoming short- and long-wave energy, respectively, ε is emissivity, σ is the Stefan-Boltzmann coefficient, and λ is the latent heat of evaporation; note that Eq. (7.2) only applies to one side of a leaf.

From Eqs. (7.1) and (7.2), we can identify the plant-specific and climate factors that control leaf evaporation. The plant-specific factors that vary with plant biodiversity and alter leaf evaporation are the stomatal and boundary layer conductances and leaf reflectance. The other variables in Eqs. (7.1) and (7.2) are influenced by weather and the leaf microclimate (Campbell and Norman 1998). Since this paper is focusing on biodiversity, we will discuss the only plant-dependent variables.

On the basis of engineering theory, it can be shown that leaf boundary layer conductance (Eq. 7.3) varies with leaf size, *d*, is a function of wind speed, *u,* and is inversely related to the resistance, r_b (Campbell and Norman 1998):

$$g_b = \frac{1}{r_b} \sim const(\frac{u}{d})^{1/2} \tag{7.3}$$

By inspection of Eq. (7.3) we deduce that g_b will increase with a decrease in leaf size, thereby facilitating the transfer of vapor from the leaf to atmosphere.

To discuss and quantify the impact of biodiversity on stomatal conductance, we employ the empirical stomatal conductance model of Collatz et al. (Eq. 7.4; 1991):

$$g_s \sim m\frac{A \cdot rh}{C_s} + b_0 \tag{7.4}$$

where g_s is a function of leaf photosynthesis, A, and the relative humidity, rh, and CO_2 concentration, C_s, at the leaf's surface; m and b_0 are constants. On the basis of this equation and a survey of the ecophysiological literature one can conclude that maximum stomatal conductance for a leaf scales with leaf nitrogen, a correlate with photosynthetic capacity (Fig. 7.1; Schulze et al. 1994; Kelliher et al. 1995; Reich et al. 1997). Hence, leaves with greater amounts of nitrogen, N, attain greater rates of A and g_s. Consequently, they have the potential to transpire at greater rates than nutrient-poor leaves.

The positive relationship between g_s and N is not only a function of species, but is dependent upon climate, soil fertility, and leaf acclimation. For example, leaf thickness, which is positively correlated with photosynthesis, stomatal conductance and leaf nitrogen, increases with light exposure and climatic dryness (Niinemets 2001). At the canopy scale, leaves at the top of a plant stand are thicker and possess more N than do those near the bottom of the canopy (Reich et al. 1997).

To examine and quantify how variations in leaf boundary layer and stomatal resistances interact to alter leaf evaporation, a set of computations with a leaf energy balance model (Paw 1987; Campbell and Norman 1998) were performed. For the case of wide-open stomata (r_s equals 32 s m^{-1}), computations plotted in Fig. 7.2 show that increasing the boundary layer resistance for vapor transfer, r_v, from 2 to 1,024 s m^{-1} forces latent heat exchange, λE, to

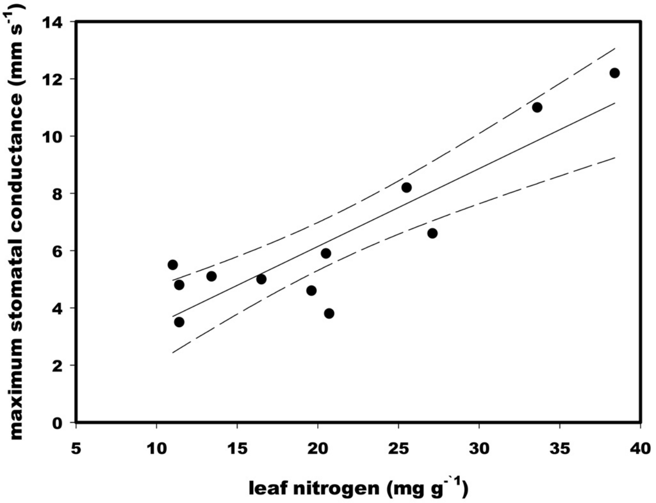

Fig. 7.1. Relationship between maximum stomatal conductance and leaf nitrogen. (Adapted from Schulze et al. 1994)

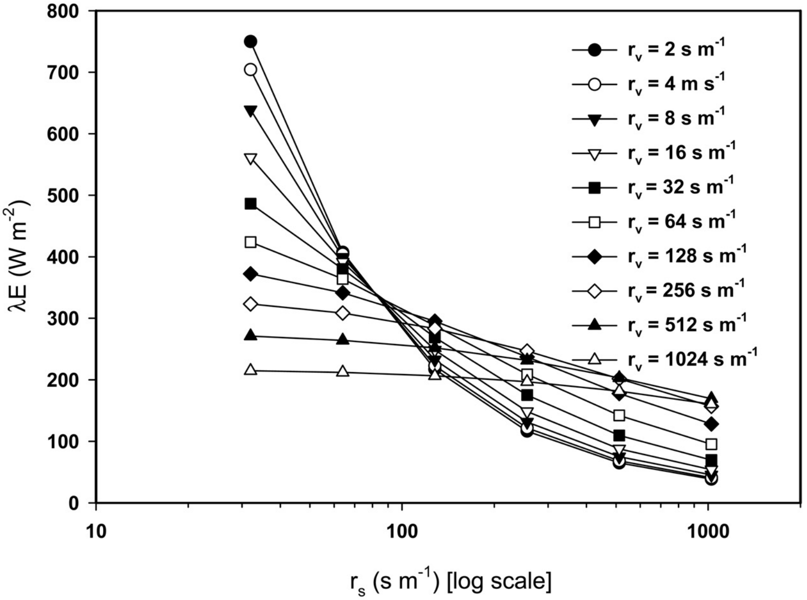

Fig. 7.2. Calculations of leaf latent heat exchange for a range of leaf size, as quantified in terms of the leaf boundary layer resistance for vapor, r_v, and stomatal resistance, r_s. These computations are for a fully sunlit leaf (incoming radiation, Q, equals 1,500 W m^{-2}, air temperature, T_a, is 25 °C and humidity, q, is 15 mg g^{-1})

decrease by 75 %. The sensitivity of λE to changes in leaf size is different when stomata are nearly closed (r_s equal 1,024 s m^{-1}). Under this situation evaporation rates – which are relatively low – increase by a factor of four as r_v increases from 2 to 1,024 s m^{-1}. Evaporation rates increase with high boundary layer resistances, when the stomata are relatively closed, because elevated leaf temperatures strengthen the vapor pressure gradient between the leaf and atmosphere and promote evaporation.

With a theoretical framework in hand, we can make additional assessments on how changes in biodiversity can influence evaporation. In Table 7.1, we catalogue the links between various species-dependent plant characteristics and the energy-balance variables they affect.

Table 7.1. A catalogue of species-dependent variables and the energy-balance variable they influence

Characteristic	Species-dependent attribute	Energy-balance variable
Photosynthetic pathway	C_3,C_4, or CAM photosynthetic pathway, maximum stomatal conductance	C_s, g_s
Leaf size/shape	Needle/planar/shoot	g_b
Stomatal distribution	Amphistomatous/hypostomatous	g_s, C_s
Leaf thickness	Photosynthetic capacity, CO_2 diffusion to chloroplast, light interception	C_s, g_s, ϱ
Leaf surface property	Waxes, pubescence	ϱ, ε, g_b

7.3 Tree Scale

At the tree scale many investigators, using sap flow measurement methods, report that trees of different species transpire at different rates (Granier et al. 1996; Pataki et al. 1998; Wullschleger et al. 1998, 2001; Catovsky et al. 2002). In Fig. 7.3, we see that transpiration rates from pine exceed those of oak (Pataki et al. 1998). In another study, Catovsky et al. (2002) report that red oak and red maple had two- and fourfold, respectively, greater annual water fluxes than eastern hemlock. In a third study, Granier et al. (1996) report a difference by a factor of 4 among transpiration rates of eight tropical tree species in French Guiana. However, is species the independent variable or are other factors such as size, microclimate, and age the cause of the differences in transpiration? In a recent review on tree transpiration, Wullschleger et al. (1998) concluded:

"The relative contribution of each species to stand transpiration was driven largely by sapwood area per unit ground area and to a lesser extent by species-specific differences in daily water use."

Their conclusion is based on the data compiled in Fig. 7.4. Across two orders of magnitude, sapwood area accounts for over 53 % of the variation in tree water use.

What other sources of variation exist with regard to the data in Fig. 7.4? In another paper, Wullschleger et al. (2001) report that there are significant differences in the sapwood area of ring-porous and diffuse-porous trees. For similarly sized individuals, species with diffuse-porous xylem had greater sapwood area, by factors of 3 to 4. So species differences still play a role on limiting transpiration.

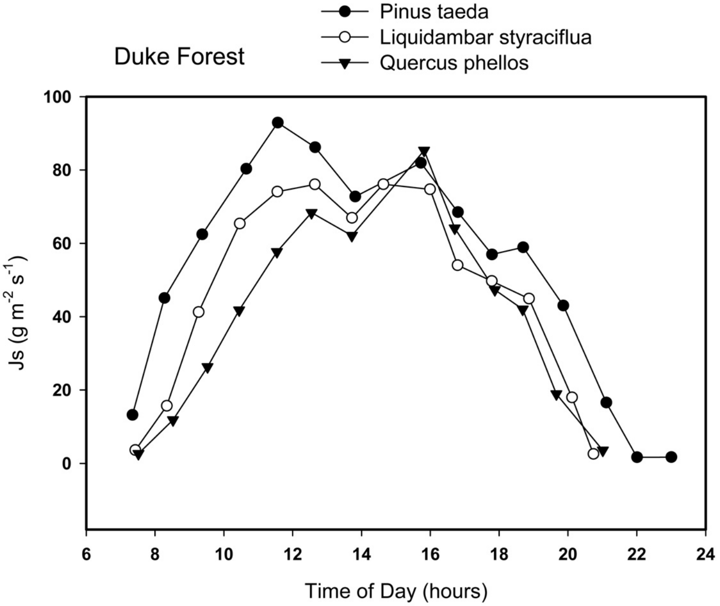

Fig. 7.3. Diurnal pattern of stem sap flow, J_s, of three species growing at Duke forest. (Adapted from Pataki et al. 1998)

On the other hand, one has to be careful about drawing broad conclusions because other groups of investigators have reported that transpiration varies with tree age and height (Vertessy et al. 1995; Ryan et al. 2000; Zimmerman et al. 2000). Acclimation can also be a source of variation, as the leaf to sapwood area ratio area within a species varies with climate factors such as maximum temperature (Mencuccini and Bonosi 2001).

The tree-based synthesis of Wullschleger et al. (1998) is supported by the scaling theory of Enquist et al. (1998). They conclude that xylem sapflow velocity (Q_{xylem}) has a squared power law dependence on diameter (D) and a 3/4 power law dependence upon mass (M), based on the following equations (Eq. 7.5a–c):

$$M_{leaf} \propto M_{stem}^{3/4}$$

$$D \propto M^{3/8}$$

$$Q_{xylem} \propto D^2 \propto M^{3/4} \qquad (7.5a, b, c)$$

An appeal of the theory of Enquist et al. (1998) revolves around its ability to successfully predict xylem sapflow rates across four orders of magnitude of tree size, five orders of magnitude in sapflow, and for 37 species (Fig. 7.5). On the other hand, one needs to carefully consider data relating transpiration

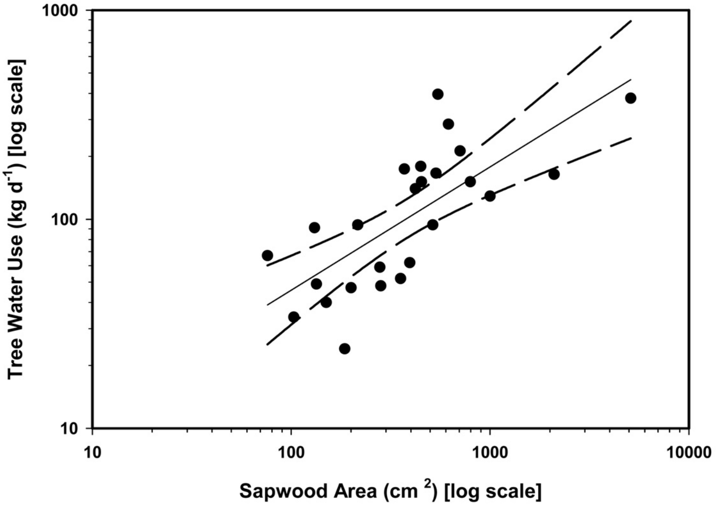

Fig. 7.4. Relation between tree water use and sapwood area (adapted from Wullschleger et al. 1998). Coefficients for the linear regression (*solid line*) are: 0.481 for the intercept, 0.589 for the slope, and 0.529 for the coefficient of determination

sums and stem size or cross section area carefully for they may suffer from autocorrelation (E. Falge, pers. comm.).

7.4 Canopy Scale

While sap flow on a tree basis scales with size and sapwood cross section, which is linked to species differences, what happens when you add up all the evaporation from trees on a landscape?

As noted earlier, Currie and Paquin (1987) reported that annual evaporation of eastern US forests increases with species richness. However, their finding was drawn by taking data from a north-south gradient of forests, which also differed in available energy, temperature, and rainfall. Furthermore, their estimates of evaporation were inferred from the temperature-dependent Thornthwaite equation, as noted in the cited *Climate Atlas of North America*. If one could normalize these data for climate differences, and if one used measured rates of evaporation, would one arrive at the same answer?

New theory on scaling tree information to the landscape scale suggests that species may have little or no effect on transpiration. Enquist (2002) shows that xylem flow on the land surface basis, Q_{land}, is scale invariant. The result occurs because self-thinning and competition for limited resources causes the maximum number of trees, $N_{\max}$, to scale with the –3/4 power of plant mass, M, and

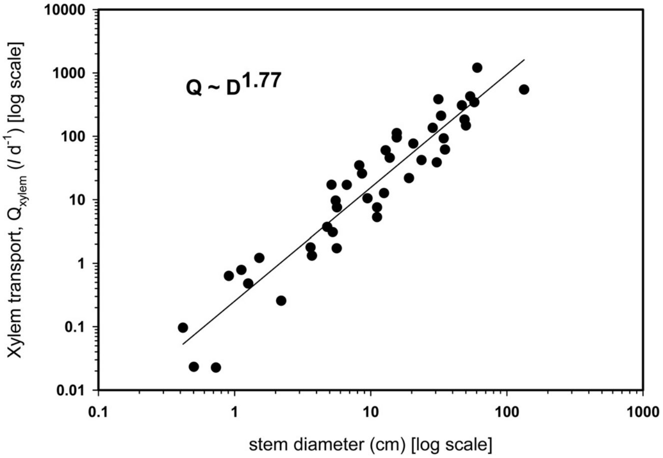

Fig. 7.5. Relationship between the rate of xylem transport of water, Q_{xylem}, and stem diameter, D. Data are from 37 species. (Adapted from Enquist et al. 1998)

sap-flow rates of individual trees scale with the 3/4 power of plant mass (Eq. 7.6):

$$
\begin{aligned}
&N_{\max} \propto M^{-3/4}\\
&Q_{\mathrm{xylem}} \propto M^{3/4} \therefore\\
&Q_{\mathrm{land}} \propto N_{\max} \cdot Q_{\mathrm{xylem}} \propto M^{0}
\end{aligned}
\tag{7.6}
$$

Enquist and coworkers (Enquist et al. 1998; Enquist 2002) have validated this theory using data across 12 orders of magnitude of plant size (Fig. 7.6). However, close inspection of Fig. 7.6 shows that for a given size class the range of data on xylem flux ranges across two orders of magnitude. So the explanation for these sources of variation remains unsolved by scaling theory. There is also a need to normalize transpiration data for temperature and available energy.

To address the source of variation in transpiration within the class of a landscape, we draw on canopy evaporation data from micrometeorological field studies and models. Working with colleagues in the boreal forest of Canada during the BOREAS experiment, we reported that dissimilar rates of evaporation occurred from aspen/hazel, black spruce, and jack pine forest stands when they were exposed to the same weather (the forest stands were located within 50 km of each other; Baldocchi et al. 2000). The greatest evaporation rates emanated from the broadleaved aspen/hazel stand, due to its greater leaf area index. Next in rank was evaporation from a black spruce stand growing on a water-logged habitat, followed by evaporation from a jack

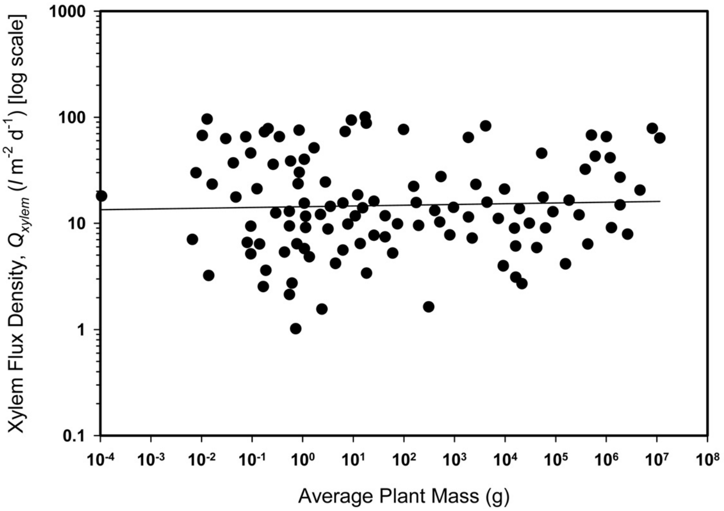

Fig. 7.6. The relationship between landscape scale xylem flux and plant size. (Adapted from Enquist et al. 1998)

pine forest, which grew on a dry, sandy upland habitat. Drawing on evaporation data from the Siberian boreal forest produces a similar conclusion. Kelliher et al. (2001) reported that differences in tree life form and nitrogen contributed to differences in evaporation. They report that greatest evaporation rates were associated with deciduous broadleaved trees, followed in sequence by deciduous needle-leaved and evergreen needle-leaved trees.

At the canopy scale, the Penman-Monteith Equation can be used to identify and quantify the factors governing rates of evaporation to the atmosphere (Jarvis and McNaughton 1986). Consequently, it (Eq. 7.7) can be used as a tool to inquire how biodiversity may or may not affect stand evaporation rates.

$$\lambda E = \frac{s(R_n - S) + \rho \cdot C_p \cdot G_H \cdot D}{s + \gamma + \gamma \frac{G_H}{G_s}} \tag{7.7}$$

In this equation, R_n is net-radiation flux density, S is the soil-heat flux density, G_h and G_s are the canopy-scale conductances for boundary layer and surface, D is vapor pressure deficit, s is the slope of the saturation vapor pressure–temperature curve, and γ is the psychrometric constant. The Penman-Monteith equation can also be inverted to compute the canopy surface conductance (Kelliher et al. 1995; Baldocchi and Meyers 1998).

By comparing measured evaporation rates, normalized by the rate of equilibrium evaporation (Eq. 7.8),

$$\lambda E_{eq} = \frac{s}{s+\gamma}(R_n - S), \tag{7}$$

against estimates of surface resistance ($R_c = 1/G_c$) one can investigate and quantify how biodiversity affects evaporation rates, at the functional level. Figure 7.7 shows that normalized forest evaporation rates vary markedly among forest stands. In general, normalized evaporation rates decrease with increasing surface resistance. Alternatively, we observe that $\lambda E/\lambda E_{eq}$ approaches the value of the Priestly-Taylor coefficient (1.26) as surface resistance drops below 40 s m^{-1}, a value representative of the evaporation ratio for extended, healthy, and well-watered crop surfaces. It is also an observation that is consistent with the theoretical predictions of McNaughton and Spriggs (1986).

Variations in the surface resistance of forest canopies are due to variations in leaf area index, maximum stomatal conductance, and drought (Kelliher et

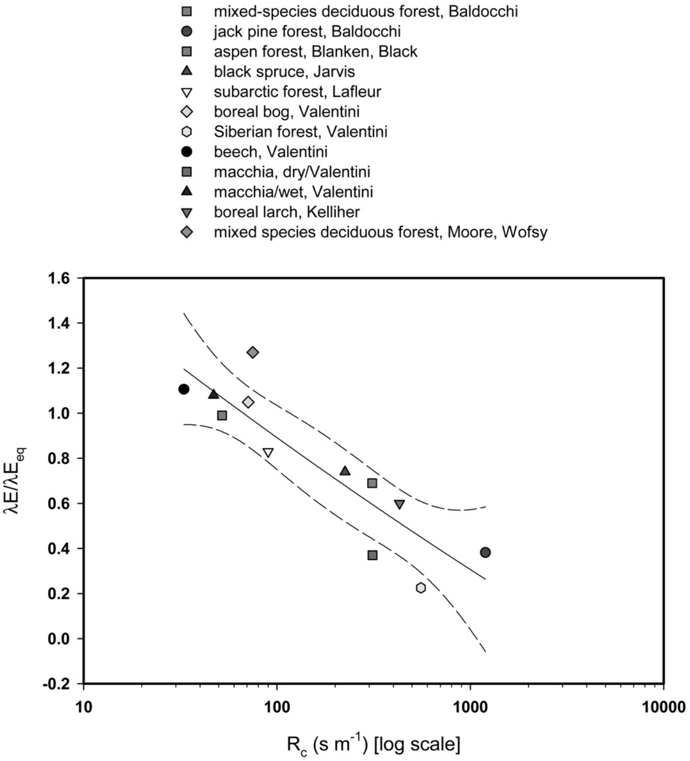

Fig. 7.7. Relationship between latent heat exchange rates of forests, λE, (normalized by the equilibrium rate, λE_{eq}) and their canopy surface resistance, R_c. This figure is adapted from Valentini et al. (1999) and Baldocchi et al. (2000). Listed with each forest stand is the principal investigator of that site. Other sources of data and relevant literature citations are listed in Table 7.2

Table 7.2. List of field sites, species, and citations of data used in Figs. 7.8 and 7.9

Site	Key species, >5 % of number or area	Reference
Prince Albert, Sask.	*Populus tremuloides*, *Corylus cornuta*	Blanken et al. (2001)
Borden, Ont.	*Populus grandidentata, Acer rubrum, Populus tremuloides, Fraxinus Americana, Pinus strobus*	Lee et al. (1999); Staebler et al. (2000); AmeriFlux data of Lee and Fuentes
Petersham, MA	*Quercus rubra*, *Acer rubrum*, *Tsuga canadensis*, *Pinus strobes*, *Pinus resinosa*	Moore et al. (1996); Barford et al. (2001); Ameriflux data of Wofsy and Munger
Hesse, France	*Fagus sylvatica, Betula pendula, Quercus petraea, Larix deciduas, Prunus avium, Fraxinus excelsior, Carpinus betulus*	Granier et al. (2000)
Oak Ridge, TN	*Quercus alba, Q. prinus, Q. rubra, Q. velutina, Acer Rubrum, Liriodendron tulipera, Pinus echinata*	Hutchison et al. (1986); Wilson and Baldocchi (2000); Falge and Schindler (unpubl.)
	P. strobes	
	P. Virginia, Carya, Fagus, Juglans, Cornus, Fraxinus	
Pellston	*Populus grandidentata, Pinus strobus, Quercus rubra, Acer rubrum, Betula papyrifera*	Curtis et al. (2002); AmeriFlux data of Curtis et al.

al. 1995; Baldocchi and Meyers 1998). Since these factors are modulated by species (but can also be influenced by ecological and biogeochemical factors), the begging question is whether or not forest evaporation correlates with species diversity?

We address this question next by using the FLUXNET database (http://www-eosdis.ornl.gov/FLUXNET/; Baldocchi et al. 2001) and data published in the literature (Table 7.2). We narrow the scope of this analysis and its susceptibility to confounding factors by focusing only on data from broadleaved deciduous forests. In addition, we confine the analysis to the summer growing season, when the forests have adequate soil moisture and form closed canopies.

We submit a priori that all species do not contribute equally to canopy evaporation. Instead we intend to count the number of species that affect ecosystem functioning most, through their ability to capture and use soil resources (Chapin et al. 1997; Roy 2001). As a first guess, we consider the number of species that make up more the 5 % of the stand on a stem- or leaf-area basis. Using this metric, we observe that normalized evaporation rates decrease as the number of species increase. We also observe that 93 % of the variance in the dependent variable is explained with this independent variable (Fig. 7.8).

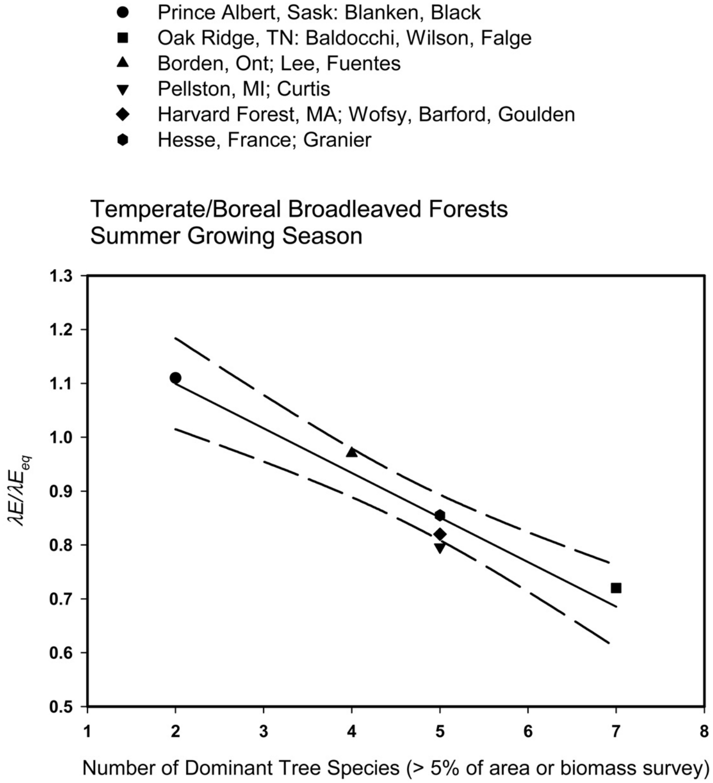

Fig. 7.8. The relationship between normalized evaporation and dominant species number of temperate and boreal deciduous broadleaved forest stands. The coefficients of the linear regression are: 1.26 for the intercept, –0.082 for the slope, and 0.932 for the coefficient of determination. Sources of data are listed in Table 7.2

The choice of 5% of the total stem or leaf area, as the cutoff value for counting the number of key species, is arbitrary and merits further inquiry. If we consider the total number of species in a stand instead, we find that the coefficient of determination of the linear regression with the dependent variable ($\lambda E/\lambda E_{eq}$) is reduced markedly, decreasing from 0.93 to 0.53 (Fig. 7.9). In future, using more sophisticated analyses, one will need to consider wind direction and the composition of vegetation within the defined flux footprint.

Why does normalized evaporation decrease with species diversity? One can hypothesize that deciduous broadleaved stands, composed of greater species diversity, have a greater mix of ring-porous and diffuse-porous trees that possess different abilities to transfer water and transpire (Wullschleger et al. 2001). There may also be an effect of the nitrogen economy of the stand on the surface conductance, as a limited pool of nitrogen must be distributed

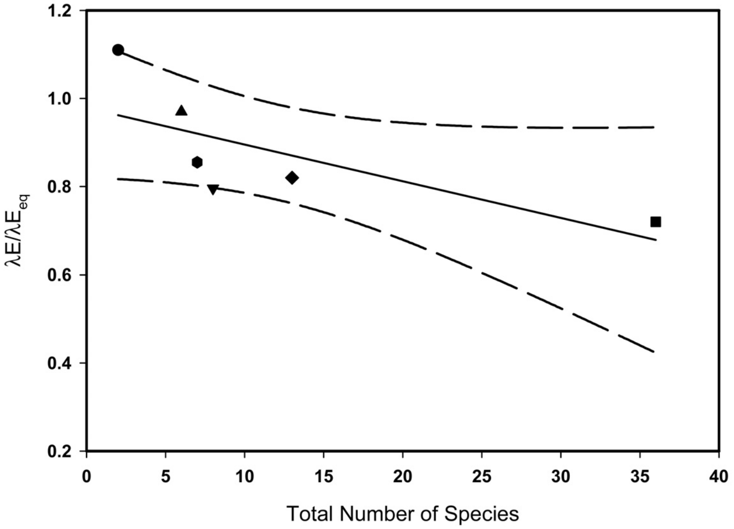

Fig. 7.9. Relationship between normalized latent heat exchange and total number of species in temperate broadleaved forests. Coefficient of variation, r^2, is 0.53. The evaporation data come from summer periods and are averaged over the course of days

among more species and functional types, thereby reducing g_s and G_c. This second hypothesis is proffered on the basis of work by Hooper and Vitousek (1997). They reported that a prevailing functional type or species may dominate the pools of available N and lower the amount available to other species. If this effect occurs in forests, stomatal conductance, and leaf area index will be lower for the canopies with higher numbers of species, and so will their canopy conductance.

It is doubtful that the results shown in Fig. 7.8 are an artifact of different leaf area, since all the stands are closed, and it is known that normalized evaporation rates become saturated at high leaf-area indices. Weather effects, radiation, humidity, and temperature, are discounted by the normalization with λE_{eq} and by considering ecosystems in relatively temperate and humid climates. In any event, these results are preliminary and merit further scrutiny as more data are entered into the FLUXNET database.

7.5 Conclusions

In this paper we have discussed the impact of biodiversity on forest evaporation at three scales: leaf, tree, and canopy. Whether or not biodiversity affects evaporation may come down to an argument on semantics. By applying biophysical theory, we show that it is the functional plant variables, e.g., stomatal and boundary layer conductance, hydraulic conductivity, rooting depth, leaf reflectivity, that affect evaporation. So in this context one may argue that functional diversity affects evaporation more than species diversity. On the other hand, evolutionary pressures have forced different species to adopt different functional features. While many different species may transpire at different rates, issues relating to functional convergence can cause many different species to transpire at the same rate, given similar environmental forcings.

At the landscape scale, an evaluation of eddy flux data suggests that increasing biodiversity may result in lower rates of normalized evaporation, but the pool size of the data is small and this hypothesis needs revisiting as more data become available. It also is in contrast with the scale invariant hypothesis of Enquist et al. (1998) and a correlative analysis by Currie and Paquin (1987). However, the variance of information shown at particular class sizes by Enquist et al. (1998) is huge, ranging two orders of magnitude, and the analysis of Currie and Paquin (1987) may be an artifact of using indirect estimates of evaporation, leaving plenty of room for observations reported here.

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