

Physiological Control of Evapotranspiration by Shrubs: Scaling Measurements from Leaf to Stand with the Aid of Comprehensive Models

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Abstract—Plants exert major control over the hydrologic budget—and, thus, over their own community stability—by their own transpiration and by their partial control over soil evaporation via soil shading. Furthermore, they exert a major control over atmospheric humidity and consequent radiation balance in climate. Predicting future plant status and future climate will require predicting evapotranspiration (ET) over large regions and under varied climates. Models that are useful for diverse sites and species will require understanding of ET control at the process level, physiologically and micrometeorologically. ET prediction also presents significant challenges in quantifying vegetation and its spatial and physiological heterogeneity. We review how process-level understanding can be gained and tested by scaling down from satellite data and scaling up from leaf gas exchange. We have synthesized a model of leaf conductance and fitted its parameters to data on *Larrea tridentata* and *Prosopis glandulosa*. To scale up to whole-shrub and whole-stand evapotranspiration, we must sum over all leaves, accounting for (1) their different current microclimates and (2) their physiological states of acclimation to long-term histories of temperature and irradiance. We have developed models for each of these phenomena and are fitting them to data on many individual leaves. Our model can be integrated to predict whole-plant and whole-stand ET. We outline tests that will be performed on a 1000 m x 300 m transect of mixed shrubland on the Jornada Experimental Range.

Hydrologic and Climatic Role of Plants

On a worldwide average, plants are estimated to transpire about $\frac{2}{3}$ of total evapotranspiration (ET) on land (Brutsaert 1982). Plants also intercept sunlight, affecting the soil radiative balance and thus exerting some control over soil surface evaporation, as well (Rosenberg and others 1983). In more arid areas, the proportion of ET accounted for by plants is reduced but still significant. Even in arid areas, plants have important effects on local topography generation (notably as forming "resource islands;" see Schlesinger and others 1990) and the associated hydrologic characteristics of runoff/run-off and infiltration dynamics.

In: Barrow, Jerry R.; McArthur, E. Durant; Sosebee, Ronald E.; Tausch, Robin J., comps. 1996. Proceedings: shrubland ecosystem dynamics in a changing environment; 1995 May 23-25; Las Cruces, NM. Gen. Tech. Rep. INT-GTR-338. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station.

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Atmospheric humidity is an important determinant of regional and global climate (Rind and others 1991). Plants contribute the major portion of atmospheric water balance away from continental margins (see extreme case: Salati and Vose 1984), and plants both respond to climatic change (in ET and other ways) and modify climatic change. On regional scales, alteration of vegetation density and activity does affect regional climate (Anthes 1984; Lyons and others 1993; Pielke and others 1992). On the global scale, there is a growing body of evidence that plant control of ET, as well as contribution to surface roughness for momentum exchange in wind, has modified past climatic shifts (Bonan and others 1992) and, by extension, that plants will act so in future climatic change.

It is important in climate modelling to account for plant control of ET, as argued well by Dickinson (1984) and now by many others. In general circulation models of future climate, the atmospheric water balance is one of the major uncertainties, leading to uncertainties in atmospheric radiative balance and surface temperature, in mean cloudiness, and in precipitation patterns (Slingo and Slingo 1988; Soden 1992). Given that plants respond to humidity in controlling their own ET in a regional feedback loop, will they help maintain relative humidity levels, or amplify fluctuations in humidity? In addition to climatic responses of intact vegetation, conversion of native plant communities will affect ET and water balance regionally. Crop plants on the average have more than twice the stomatal conductance of native vegetation (Schulze and others 1994).

Prospects for Predicting ET Over Large Regions

Vegetation has long been sampled for quantitative measures of cover and of physiological activity, including transpiration. It remains extremely challenging to make estimates of transpiration and carbon gain on the scale of watersheds (see Hatton and others 1993) or grid cells in general circulation models for assessing effects of climate change (for example, Hunt and others 1991). Four major problems are:

First, quantifying the vegetation, either from the ground (where the sampling problem is virtually insuperable) or from satellite imagery. While a number of vegetation indices are in use for remote sensing (Myneni and Asrar 1994), their use is compromised by atmospheric interference in the images (Kaufman 1991; Myneni and Asrar 1994), and by variation in calibration according to soil background (Myneni and others 1995).

Second, inadequacies in process-level understanding of transpiration. It is certainly possible to monitor ET over moderate scales (hundreds of meters) with Bowen-ratio or eddy-flux correlation systems (Dabberdt and others 1993). However, these measurements do not directly clarify the role of vegetation in determining ET. Especially, they do not indicate how vegetation, and thus ET, will behave at different sites, under new climates, or with human- or climate-induced alteration of vegetation. Predictive understanding for global change requires that the plant physiological and biophysical controls be explicitly resolved. There are simple models that treat vegetation as one or two layers of uniform leaf matter (Choudhury and others 1991). They may be reasonably accurate when calibrated for a single type of vegetation and soil, for predicting ET under different weather conditions. However, they leave the following two problems:

Third, accounting for heterogeneity of vegetation on all spatial scales. Most obviously, plants with the C_4 photosynthetic pathway differ from those with the C_3 pathway two-fold in water-use efficiency and variously in absolute water-use rates. Even within one pathway, plant species vary markedly in stomatal conductance (Schulze and others 1994). It is not yet possible to distinguish plant species or functional types simply from remote sensing of their spectral signatures, and it may never be, even with new satellite sensors that resolve very many spectral bands (Price 1994). Spectral signatures must be abetted by ground-truthing. Even then, it is not routine to estimate the spectral radiances leaving the vegetative canopy, which are diagnostic for vegetation type, from the radiances received by the satellite. The corrections for atmospheric absorption and emission can be very large (Kaufman 1991). Consider that everything looks rather blue from an airliner cruising above the troposphere, and variably so according to aerosol loads that cannot be independently estimated from satellite measurements.

And fourth, accounting for stress effects on ET, particularly water stress. Different species, especially, downregulate their stomatal conductance and ET at very different soil water status (Turner and others 1984). This amplifies the spatial heterogeneity in ET. Detection of water stress by remote sensing of spectral changes in light reflected from vegetation (the "red edge" and xanthophyll absorptions, or features sensitive to the water content of leaves) has yet to prove practical (Gamon and others 1992). There is some promise in sensing the temperature difference between air (with ground-based measurements) and the surface (vegetation plus soil) (Moran and others 1994). However, there are some important limitations on the accuracy of temperature-based inferences for ET, given that atmospheric corrections are often large (Twomey and others 1977; Price 1983). More robust inferences can be made when the atmospheric humidity content is known or estimated from ground-level measurements and standard height profiles (Price 1983). Such methods apply well over rangeland. Also limiting accuracy of ET estimates, the surface emissivity varies enough to confound the estimation of kinetic temperature from radiative or brightness temperature (Norman and others 1995). A reasonably dense sampling of emissivity on the ground is needed.

These challenges may be addressed either by scaling up ET estimates from leaf to region, or downward from region

to leaf (wherein the purpose is to verify process-level understanding). Both prospects are actively under discussion (Carlson 1991).

Scaling Down from Satellite Data

Evapotranspiration is not directly sensible by optical or microwave techniques, despite some innovative and massively data-intensive attempts to image the transport of water vapor in atmospheric eddies (Barnes and others 1990). Some empirical relations have been exploited but, in not being process-based, are not transferable between sites and climates. Most generally, remote estimation of ET must be formulated rigorously in terms of energy balance. The air carries away both the latent heat of evapotranspiration (LE below) and sensible heat (H) embodied in changed air temperature from air contacting the vegetation and soil. The source of these energy fluxes is the net input of radiation (R_n , equalling the difference between downward and upward fluxes of the sum of shortwave and thermal radiation), debited for heat flux into the soil (G):

$$LE - H = R_n - G.$$

Volumes have been written about various ways to estimate each term (see, for example, Rosenberg and others 1983; Brutsaert 1982; Asrar 1991; and many journal articles). The most general and reliable methods require that satellite measurements of radiative fluxes (down and up), vegetative cover (and type, if possible), and surface temperature be augmented by ground-based measurements at least of windspeed, air humidity, and air temperature at several heights. The radiative measurements yield estimates of R_n , though ground-based measurements to augment satellite measurements are widely gaining favor (Sellers and others 1995). If G is not measured on the ground, then it may be estimated in long-term average as a fraction of R_n (Clothier and others 1986; Daughtry and others 1990).

Several methods exist to partition the net energy flow between LE and H. One way is to estimate H from the surface-air temperature difference and the eddy diffusivity of the air, K, in turn estimated from the ground-measured profile of windspeed versus height. In sparse canopies such as in shrubland, estimation of K requires careful consideration of how plants and soil combine to set atmospheric drag and transfer characteristics (Kustas and others 1992).

For process understanding, it is required to relate estimated LE or ET to vegetation amount, type, and physiological status (developmental stage and stress degree). Vegetation amount is typically quantified by spectral indices, such as the normalized difference of infrared and red radiances, $NDVI = (IR - R) / (IR + R)$. Without local calibration of this index to biomass or leaf area index, its quantitative meaning is somewhat weak (Myneni and others 1994). This is particularly true in sparse canopies such as of shrubs, where spectral noise or soil color differences are equivalent to large relative changes in vegetative cover fraction (Price 1995). An alternative to simple indices is interpretation of radiances in as a mixture of spectra of pure components or "end members" (soil, vegetation, and sunlit and shaded portions of both); see Huete (1988). This method requires local calibration for soil

and vegetation color, as well as for the angles of solar illumination and of view, which affect shadow fractions.

Overall, then, scaling down from remote sensing to plant processes offers the ability to consider large scales, up to global. However, it runs into some significant challenges that can be met as yet only by: (1) Extensive use of ground-based measurements. This is not to be regretted, in that it assures contact with reality. The expense of ground work, while high, should be compared with the expense of satellite imagery. With proper design of protocols to measure ET with mixed satellite and ground information, the types of information multiply each other's value considerably and minimize the total cost. (2) Extensive local calibration of methods. We lack the power to generalize most things, such as how fractional cover by vegetation relates to ET. Escaping this limitation as much as possible is our research focus.

Scaling Up from Leaf and Plant Scales

Leaf conductance (g_s) and transpiration must be predicted under arbitrary conditions. Then, conditions on each leaf (or class of leaf) must be estimated from a knowledge of plant and community structure, including soil water status. Our knowledge of physiological control of g_s and leaf transpiration, $E_{L,a}$, is well advanced (Carlson 1991). Among a variety of formulations, we employ in our research an effective and

concise one based on the empirical Ball-Berry relationship (Ball and others 1987):

$$g_s = mA_h_s/C_s + b.$$

This expresses the close scaling of g_s to CO_2 assimilation rate, A , in a very specific way. It also embodies the scaling of g_s to humidity, specifically to the relative humidity at the leaf surface, h_s , below the leaf boundary layer. Finally, it incorporates short-term responses to varying leaf-surface CO_2 concentration, C_s . The factors m (slope) and b are constants, presumably permanent developmental characteristics of a leaf. Remarkably, well-watered plants from almost any habitat show very similar values of m , close to 10.0 (Gutschick and others, in preparation, studies of xeric shrubs, mesic crops, Eastern trees; fig. 1).

To complete the description of how leaf microenvironment determines $E_{L,a}$, we need process equations for (1) how A responds to light level (PAR irradiance), leaf temperature (TL), and CO_2 concentration as provided by the models of Farquhar and others (1980), and (2) how leaf temperature is determined by the balance between radiative gain, radiative loss, and cooling by transpiration and convective-conductive transfer (for example, Nobel 1992). When scattered radiation is prevalent, as within a canopy, the radiative transfers are tedious, if straightforward, to calculate (Gutschick and Wiegand 1984 and many others).

Thermal radiative transfers are likewise rather involved (Kimes and others 1981; Paw U and others 1989; Huband

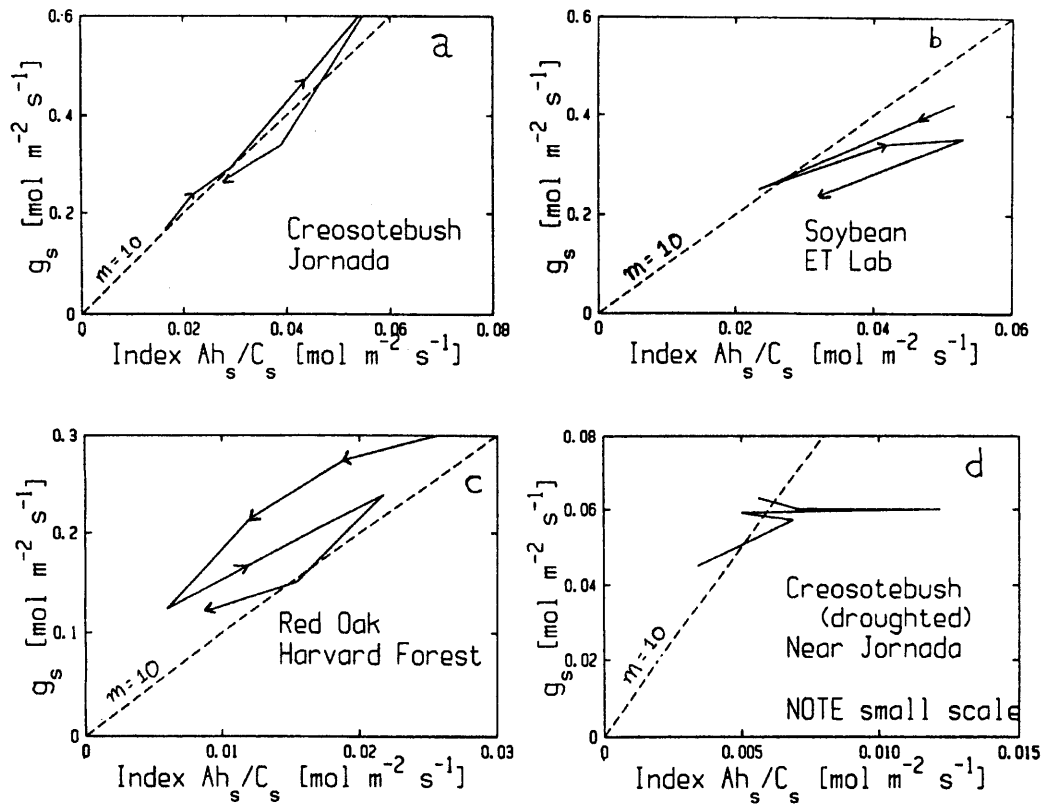


Figure 1—Similarity of Ball-Berry slope, m_{BB} , for several plant species when well-watered (a-c), and divergence from common slope for stressed plant (d). Measurements were made with open-mode gas-exchange system by the author's research group as noted in Acknowledgments.

and Monteith 1986). In any event, simultaneous solution of all three major equations for single leaves is possible (Collatz and others 1991). Computationally efficient solutions (Gutschick, in preparation, and fig. 2) are demanded to describe whole plant canopies with reasonable effort.

The microenvironment on each leaf is determined by the interplay of the microenvironment at the canopy boundary (PAR flux density, windspeed, temperature, and humidity at the top of the canopy) and the canopy structure. Once we know the light flux, windspeed, temperature, and such at a

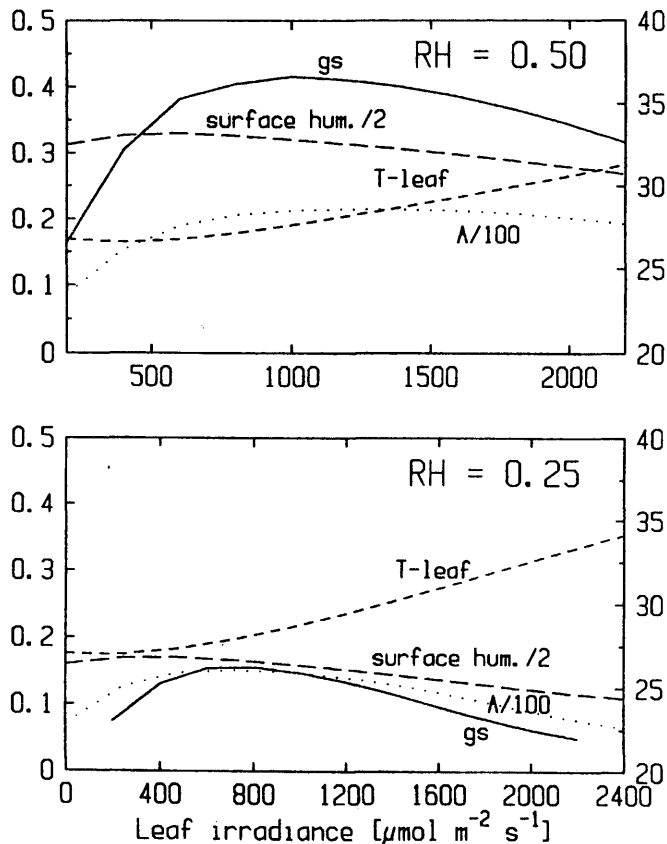


Figure 2—Model calculations of gas-exchange performance of single leaves in a cluster, operating at various leaf irradiances because they have various leaf angles. Results are presented for two different relative humidities (RH) in free air. Curves are given for stomatal conductance (g_s ; as $\text{mol m}^{-2}\text{s}^{-1}$), CO_2 assimilation rate (A ; as $\mu\text{mol m}^{-2}\text{s}^{-1}$, divided by 100), leaf surface humidity (h_s ; divided by 2), and leaf temperature (T -leaf; degrees C, read on right-hand axis scale). Note the predicted falloff of performance at high irradiance, resulting from leaf heating and consequent drop in surface humidity. The drop is relatively much less significant at high RH. Leaves share the same Ball-Berry parameters (slope $m = 10$, intercept $b = 0.008 \text{ mol m}^{-2}\text{s}^{-1}$) and maximal carboxylation capacity ($81 \mu\text{mol m}^{-2}\text{s}^{-1}$ at 25°C). They share the same microenvironment of air temperature (30°C), sky radiative temperature (0°C), ambient CO_2 partial pressure (35 Pa), and windspeed and hence boundary-layer conductance ($2 \text{ mol m}^{-2}\text{s}^{-1}$). Calculations were made with the authors model described in text.

leaf location within the canopy, the leaf's temperature, too, is determined. The profile of humidity is affected rather little by the vegetation itself, especially in sparse shrubs. However, the profile of air temperature is notably affected by vegetation; the solution must be determined interactively (Gutschick 1988, 1994, and many others).

The structure of the vegetation community is very complex but can often be approximated very well by simple functions to describe leaf positions and orientations (Campbell and Norman 1989). Sparse, irregular canopies, as in shrub land, are quite challenging to describe. The penetration of light into canopies is a very well developed topic. It remains more challenging to describe wind penetration into arbitrary structures (Raupach 1988), though some relatively simple ideas may apply (Goudriaan 1989; Massman 1987). By simple, I mean not computationally simple, but having a small demand for descriptors of the canopy structure. Computing power is easy to get; data on field vegetation never is. For any canopy, after its geometric arrangement is described, it is necessary to describe how leaf maximal g_s or, equivalently, maximal A , varies with position. Fortunately, canopy development is under genetic control, closely maximizing net assimilation (Sellers and others 1992; Myneni and others 1992). Thus, we can estimate maximal A of each leaf from the local microenvironment (seasonally averaged irradiance, temperature).

Water stress reduces g_s and E and introduces considerable diversity in plant control of g_s (Turner and others 1984). Using the Ball-Berry description, we may ask if stress alters slope m , assimilation capacity A , or both. We find that the answer is "both," and the stress level at which changes occur varies markedly with species. Acting to reduce the diversity is the generalization that g_s responds to soil water status primarily, not to more derived leaf water status (Tardieu and others 1993 and refs. therein), and in particular to soil mechanical strength (Masle and Passioura 1987). We seek to reduce the complication of diversity further. We postulate that stress responses diverge about a mean that is conservative among different communities in the same climatic zone. We are testing this empirically.

We are also attempting to explain such patterns with models of plant coexistence with competitive resource use (see Tilman 1994 and refs. therein; Maynard and others 1973). There are two additional stresses that alter A and thus g_s : thermal stress (Björkman and others 1980) and photoinhibition (Baker and Bowyer 1994; Ball and others 1991). These too, are potentially predictable from the leaf's microenvironmental history (Ögren and Sjöström 1990); we are developing general models in collaboration with M. Ball of the Australian National University (see Ball and others 1991).

Transect Study

ET has been measured on shrubland in the past. On the Jornada, W. A. Dugas, H. Mayeux, R. E. Gibbens, and their associates performed long-term monitoring of 4 different communities in 1991-1992, using the Bowen ratio method. We are constructing estimates of ET scaled up from our leaf-level gas exchange, to compare with these data. We further propose an intensive, one-day field campaign, tentatively set for September 1995, for two purposes:

The first is to test our ability to predict ET from microenvironment and vegetation structure in diverse plant communities. We will sample areas (covered by Landsat TM pixels) variously dominated by different, single shrub species and also intermixed. A 1000 m x 300 m transect in pasture 15 has been selected and given preliminary characterization for soils and vegetation. We will use our body of data on physiological control of g_s and $E_{L,a}$ in the plant species on this transect.

We will scale up from leaf gas exchange done on the campaign data, to whole branch or plant E as measured with novel sapflow gauges (Senock and Ham 1993). We will also scale down from Landsat TM data reduced to (a) estimates of vegetation leaf area, compared with aerial photos reduced by our methods of digital image analysis and (b) predictions of E as described earlier. We will measure vegetation water-stress level with time-domain reflectometry. If we find systematic discrepancies between the scaled-up and scaled-down estimates of ET, we will seek to assign them quantitatively to description approximations both in measurements and in usage of simple models, both in canopy structure and in physiological models of g_s control.

The second purpose is to test our ability to measure and use compact descriptions of vegetation, including its diversity in stomatal control. We have been developing image-analysis techniques for quantifying leaf area and angle distribution on a number of spatial scales, from branch to plant to community. In addition to testing the compact description of vegetation per se, we will test the use of simple transport models to predict irradiance and temperature on leaves. We will compare these to irradiance measurements made with compact, leaf-mounted light sensors (Gutschick and others 1985) and to leaf temperatures measured by contact and by imaging thermal infrared.

Acknowledgments

The experimental work was designed and carried out with extensive help from Connie Maxwell, Erik Jackson, Felicia Najera, Nancy Stotz, Andy Browman, Cesar Rivera-Figuera, and Robber Core. Bhaskar Choudhury helped with valuable discussions on remote sensing and modelling. Jay Ham helped with valuable discussions on energy balance and sapflow measurement. We gratefully acknowledge funding from the National Oceanic and Atmospheric Administration Office of Global Programs (award NA16RC0435), the Department of Energy's National Institute for Global Environmental Change, South-Central Regional Center (award TUL-022-94/95), and the National Science Foundation's Long-Term Ecological Research Program (award DEB-94111971).

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