

## Ecohydrology Bearings—Invited Commentary

# Proposed principles governing how vegetation changes affect transpiration

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### ABSTRACT

Understanding global variation in evapotranspiration (ET) is critical for accuracy of climate models, predictions used in water resources management, and assessment of land use change impacts on the water balance of ecosystems—yet we lack unifying principles to predict when transpiration (T) varies with land use. Plant T is a dynamic and often dominant component of ET, and is affected by a variety of processes controlled by land use changes superimposed onto edaphic conditions. We propose the following three principles that determine whether T will vary with changes in vegetation: variation will result if energy balance partitioning has been altered, if deeper or shallower active rooting depth has changed the amount of soil moisture accessible to plants, or if temporary changes in water use add up over longer time scales. Clearly these concepts are not new; however, they are often overlooked in favor of blanket assumptions that large changes in vegetation inevitably alter T. Not so. Our suggested framework incorporates both edaphic and plant traits that determine whether T will vary or not in response to altered land cover conditions. We suggest that this simple set of principles unifies results of wide-ranging studies of T following land use change and can explain underlying causes of T variation. These principles are illustrated through case studies from four different environments: Pacific Northwest forest, Texas mesquite brushland, Texas savanna and woodland, and Middle Rio Grande riparian forest. The proposed principles seem broadly applicable, should be further evaluated, and are directly relevant for land management. Copyright © 2011 John Wiley & Sons, Ltd.

**KEY WORDS** energy balance; root depth; soil water storage; vegetation characteristics

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### INTRODUCTION

Understanding of spatial variation in evapotranspiration (ET), which has now been predicted at the global scale (Zhang *et al.*, 2010), is important for several reasons. The inability of climate change models to adequately account for changes in land use limits their applicability (Pitman, 2003). An improved understanding of how land use changes alter latent heat flux, a major climate driver, will enhance our ability to predict future climate scenarios (Mahmood *et al.*, 2006; Niyogi *et al.*, 2009; Dirmeyer *et al.*, 2010; Mahmood *et al.*, 2010). And detailed predictions of ET are critical for water resources management in regions where water is limited (Jackson *et al.*, 2001; Newman *et al.*, 2006). Without reliable estimates of ET at the appropriate scale (Bosch and Hewlett, 1982; Jackson, 1985; Zhang *et al.*, 2001), we cannot predict impacts of land use changes on the water

balance of ecosystems. Furthermore, an improved process-based understanding of ET across scales is needed so that hydrologic models use only the most relevant parameters (McDonnell *et al.*, 2007).

Using data from flux networks and satellite-derived Normalized Difference Vegetation Index values, Zhang *et al.* (2010) predicted annual ET across the globe. They predicted that mean annual ET varied from 202 mm in arid shrublands to 1138 mm in evergreen broadleaf forests. However, uncertainties in modeled ET, especially in tropical regions, resulted in rather large errors, up to 100 mm per year. Large-scale, generally climatic drivers of variation have not yet been reconciled with local drivers such as vegetation type and abundance (Sivapalan, 2003). To incorporate local variation, models often employ vegetation indices to estimate ET as a function of potential ET under wide-ranging vegetation conditions (Mata-Gonzalez *et al.*, 2005; Wang *et al.*, 2007). For these reasons among others, uncertainty in model predictions of ET remains high. Zhang *et al.* (2010) reported up to 20% uncertainty in their model based on the relative difference

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between modeled ET and inferred ET from basin-scale water balance. We propose that these knowledge gaps could largely be filled using existing concepts reorganized into a set of basic principles.

Typically, land conversions from tall canopies (e.g. natural forest) to short canopies (e.g. agricultural crops) alter radiation balance, aerodynamic roughness, and maximum rooting depth, which often alters ET. Recognizing this, previous authors have developed a simplified scheme for estimating water use based on such fundamental differences between tall and short canopies (Calder, 1998). Cultivated crops vary in vegetation amount and structure, soil disturbance (which can impact infiltration), growth rates, irrigation or water requirements, and time spent fallow. Our framework complements previous efforts to explore underlying principles governing changes in ET using examples from forest, range, and riparian settings; however, the same can be applied to any land use comparison.

Ecosystems can be energy-limited or water-limited. In ecosystems where water is plentiful, ET will be limited by available energy. However, in ecosystems where water is scarce, or intermittently available, ET will be limited by water availability. Calder (1998) presents a framework for how ET varies between temperate and tropical regions and between wet and dry climates. We agree with Calder that the key to robust estimates of ET is to identify the principle controls for a particular vegetation and climate. However, changes in vegetation may cause an energy-limited system to switch to water-limited, or vice versa. For example, changes in vegetation may result in increased rooting depth and access to deep soil moisture, provided that local edaphic and environmental conditions are right for rooting depth to increase. Roots tend to grow only as deep as necessary to meet evaporative demands (Schenk, 2008).

Transpiration (T) is a dynamic and often dominant component of ET (Moreira *et al.*, 1997; Williams *et al.*, 2004). In arid systems, reduced vegetation density may reduce T on a stand basis, but increased soil evaporation below the more open canopy may compensate; however, if T is not reduced, ET is likely the same or higher (but most certainly not lower) than in more dense vegetation (Simonin *et al.*, 2007). In humid systems, reduced vegetation density may, again, reduce T on a stand basis, but in this case evaporation via canopy interception may be an important component of ET and site water balance (Whitehead and Kelliher, 1991; Link *et al.*, 2004; Pypker *et al.*, 2005). The partitioning between evaporation and T is thus dependent on the regional climate and vegetation (Calder, 1998). The focus of this paper is on T because physical and physiological responses of T to altered vegetation are more complex and challenging to predict than drivers of soil and canopy evaporation.

T is constrained by radiant energy, temperature, humidity, wind, and soil water availability (Jones, 1992). Soil water availability, in turn, is mediated by edaphic factors such as soil depth, soil water holding capacity, and soil hydraulic conductivity. Those abiotic factors also affect T by changing the vegetation structure and composition, for

example, leaf area and biomass (Palmer *et al.*, 2010), plant structural traits above and below ground (Nepstad *et al.*, 1994; Dodd *et al.*, 1998; Jackson *et al.*, 2000b; Breshears, 2006; Xu and Li, 2006; Heilman *et al.*, 2009), and phenology (Phillips and Oren, 2001). Therefore changes in land use due to such things as natural disturbance, exotic plant invasions, or crop or timber production may change T. In the global ET model of Zhang *et al.* (2010), eddy flux data were used from a global network of sites located in signature ecosystems characteristic of each ecoregion. Extrapolating those measurements to a highly heterogeneous landscape required modifications to account for the wider range of regional land cover types associated with such changes in vegetation structure and composition.

We assert that the high level of heterogeneity of land cover types creates a mosaic across the landscape that may or may not translate into equally dynamic patchworks of T. Researchers have investigated potential changes in T in managed forests (Vertessy *et al.*, 2001), land conversions from forest to crop (Leblanc *et al.*, 2008; Radford *et al.*, 2009), and in grasslands that are transforming to shrublands (Huxman *et al.*, 2005). Results from wide-ranging studies have been summarized in review papers (Bosch and Hewlett, 1982; Eshleman, 2004; Brown *et al.*, 2005; Llorens and Domingo, 2007). In some cases drastic changes in vegetation have led to drastic changes in water balance (Jobbágy and Jackson, 2004), while in other cases they have not (Nagler *et al.*, 2009). A potential weakness in many studies is the underlying assumption that potential changes in T are driven solely by changes in vegetation structure and composition.

## A FRAMEWORK FOR UNDERSTANDING TRANSPIRATION CHANGES

The potential for T to vary is constrained by physical factors (soil and climate) and land use changes (Figure 1). These factors together alter the type, amount, and spatial organization of vegetation. In a given localized area, T will vary between contrasting vegetation patches if (1) more energy is partitioned into latent heat in one patch than the other, (2) one patch has access to more available water than the other, or (3) available water is depleted faster in one patch than the other, provided such differences in water use are maintained over long time scales.

The first principle is that variation will result if energy balance partitioning has been altered. T is controlled by the amount of energy that is available to change the phase of water from liquid to vapor in the interior of leaves. Changes in plant species composition or vegetation amount can increase or decrease available energy (Kessler and Jaeger, 1999; Kurc and Small, 2004; Oliphant *et al.*, 2004; Rost and Mayer, 2006), depending upon how species composition affects shortwave and longwave radiation balances, and heat storage in the canopy and in the soil. The amount of available energy partitioned into T is constrained by rainfall, water retention in the root zone,

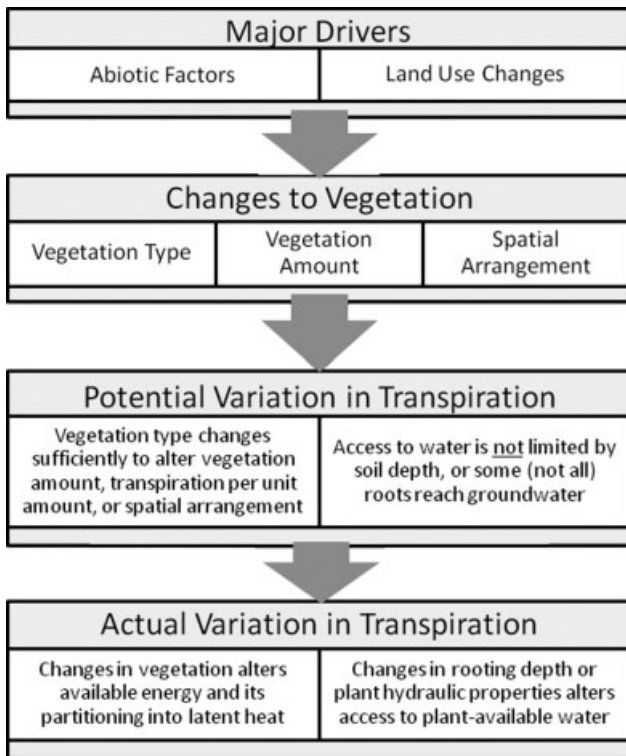


Figure 1. Framework for understanding whether vegetation change will alter transpiration. Climate and edaphic factors constrain how land use will alter vegetation condition. The next step is to inquire: Does the new type of vegetation transpire at a different rate? Did the vegetation amount increase or decrease? Did the spatial arrangement of vegetation change? If so, then there is a potential for transpiration to be different. However, for transpiration to actually vary there must have been either a change in the available energy or a change in access to plant-available water.

and plant hydraulic properties (Rost and Mayer, 2006). If changes in vegetation amount and structure result in increased available energy, increased T per unit amount of biomass, or enhanced turbulent transport of water vapor, then T may increase. It is also possible that changes in one factor (e.g. available energy) may be offset by changes in another factor (e.g. canopy conductance), leaving T relatively unchanged.

The second principle is that variation will result if changes in rooting depth change the amount of water accessible by plants. Woody vegetation usually has deeper roots than grasses (Schenk and Jackson, 2002), which may allow access to more water from deep soil layers (Jackson *et al.*, 2000a; Casper *et al.*, 2003) or water stored in bedrock (Schwinning, 2010). Root systems are generally deeper in dry regions than in wet regions, and are deeper in coarse-textured soils (Schenk and Jackson, 2002; Collins and Bras, 2007). In climates where water is limiting, edaphic factors are the major driver in T variation (Scanlon, 1994; Newman *et al.*, 2006) because limited water increases the partitioning of available energy into sensible heat at the expense of latent heat. In dry environments where access to water is constrained by soil depth, T will likely be similar among patches despite differences in vegetation, because each will consume all available water in the root zone (Porporato *et al.*, 2002;

Querejeta *et al.*, 2007; Schwinning, 2010). Where water is not limiting, a higher percentage of available energy will be partitioned into latent heat, provided there is adequate water storage capacity in the root zone. The same is true in patches where all roots can reach the groundwater because T is no longer constrained by available water, but by available energy.

The third principle is that variation in T will result if temporary changes in water use add up over long time periods. For example, one patch of vegetation may extract soil moisture more rapidly than another due to differences in available energy or stomatal conductance. However, over time, both species may use all of the available water in the root zone, resulting in little difference in long-term sums. On the other hand, some species are able to maintain T at lower soil water potentials than other species (Schwinning, 2008), which over time may allow them to extract more soil water. A key factor is water storage capacity of the root zone. If storage capacity is restricted, less water is stored during periods of high rainfall for later use by plants during dry periods (Milly and Dunne, 1994). Regions with low water storage capacity are likely to experience higher runoff and deep drainage. If water storage is adequate, then soil moisture can diverge between two vegetation patches; a patch with low rates of root water uptake is more likely to reach saturation after rainfall than a patch where rates of root water uptake are high.

The following four case studies, which have been published in detail elsewhere, illustrate some of the complex interaction of factors that influence T: a juniper-oak woodland and savanna in central Texas (Litvak *et al.*, 2010), a mesquite brushland in southern Texas (Moore *et al.*, 2010; Moore *et al.*, in review), a Middle Rio Grande riparian forest (Moore and Owens, in press), and a Pacific Northwest forest ecosystem (Moore *et al.*, 2004). We have applied our simple framework to each of these studies.

## CASE STUDIES

### Central Texas juniper savanna and oak-juniper woodland

These ecosystems are located on the karst Edwards Plateau in south-central Texas. Soils are generally shallow and rocky. Summers are generally warm and dry with sporadic rainfall, while winters are cool with frequent rainfall. The savanna consists of clusters of Ashe juniper (*Juniperus ashei* Buckholtz) and a few honey mesquite trees (*Prosopis glandulosa* Torr.) interspersed among intermittently grazed, mixed C<sub>3</sub>/C<sub>4</sub> grassland. Soil depth is approximately 1.6 m, and root excavations showed that 80% of all tree roots are in the upper 60 cm of the soil profile. The woodland is dominated by juniper and live oak (*Quercus virginiana* Miller) in a continuous interlocking canopy. The soil, about 20 cm deep, overlies fractured indurated limestone. Both oak and juniper form dense root mats at the soil–rock interface.

Eddy covariance measurements over a 2-year period showed that ET at the savanna was higher than at the

woodland, by an average of 21 mm year<sup>-1</sup>. Although available energy in the woodland was 8% higher than at the savanna, much less water was stored in the woodland soil because it was very shallow. As a result, a smaller fraction of available energy was partitioned into latent heat flux than at the savanna. The woodland did extract some water from the bedrock, but water uptake from the bedrock was insufficient to meet the evaporative demand as soil water was depleted.

These results suggest that ET in karst ecosystems of the Edwards Plateau is storage limited. Woody cover does increase available energy, but the degree to which higher available energy results in higher ET depends on the amount of water retained and stored in the root zone. Thus, the impact of land use change on ET is highly dependent on edaphic factors. Over time, rain-limited Plateau ecosystems will most likely consume all of the available water in their root zones, regardless of plant species composition.

### South Texas mesquite brushland

The hydrology in this mesquite brushland ecosystem is similar to that in the central Texas oak-juniper savanna described above, except this area in south Texas has generally deep, fine sandy soil (Moore *et al.*, 2010). Management, specifically root plowing, drove the spatial vegetation pattern. After plowing, the system was only temporarily transformed to open grassland and recovered quickly within 15 years to closed canopy mesquite shrubland if plowing was not repeated.

It was expected that clearing of brush would decrease T because grasses typically root more shallowly than shrubs and because the brush has a greater total leaf area than grasses. Indeed, shallower root depths persisted for 5 years after plowing, but root depths had recovered by 15 years to values equal to mature brushland that had never been cleared. Chloride mass balance measurements showed that chloride concentration, which increases in the root zone if root water uptake exceeds downward flushing of solutes, was greatest in untreated plots. In plots that were root plowed, chloride concentration had decreased by 75% 5 years after plowing, then increased only slightly after 15 years as shrub growth recovered. In a series of 12 paired plots (plowed and unplowed), in all but one case deep drainage was greater in treated plots than in adjacent untreated plots that had never been plowed. Differences were small; averaging only 1.9 mm year<sup>-1</sup> compared with the average annual rainfall of about 600 mm, and after treatment began to converge over time. This suggests that differences in T between shrublands and grasslands were real, but temporary, as after about 5–15 years shrubs grew back to densities nearly as high as those observed in sites with mature mesquite shrubland.

ET was higher by modest amounts in the shrubland than in the plowed grassland. Given that this site was water-limited, edaphic factors were the major driver. (In other words, soils were sufficiently deep for roots to differentiate between land use types.) Shrub roots could access more

deep soil moisture than shallower roots of grasses and small shrubs, resulting in increased partitioning of available energy into latent heat. Soil moisture measurements taken 2 m belowground in plowed plots increased by as much as 17% during a year with twice the annual precipitation, increasing the likelihood (or frequency) soil water reached saturation and drained below the root zone. During that same wet year, no such increase in soil moisture was observed in the shrubland plots.

### Middle Rio Grande riparian forest

This riparian forest located in central New Mexico also has a semiarid climate, but has shallow groundwater accessible to roots. The dominant vegetation is composed of either native or exotic phreatophytes. Invasive species removal drove spatial vegetation patterns. Native cottonwood forests (*Populus fremontii* S. Watson) commonly had a dense understory of exotic saltcedar (*Tamarix* sp.) trees. For the purpose of fire prevention, managers cut and mulched all understory trees and left only the mature cottonwood overstory.

Common phreatophytes in the western United States [cottonwood, willow (*Salix gooddingii* C.R. Ball), and saltcedar] use similar amounts of water per unit leaf area (Sala *et al.*, 1996). It was expected that removal of the saltcedar understory would decrease T because an entire layer of dense vegetation would be removed, thus altering the amount of vegetation available to capture energy. However, the cottonwood trees compensated for reduced stand density by increasing their water use per unit of sapwood (Moore and Owens, in press). Further, removal of the understory altered vegetation amounts only slightly. Although the exotic species represented about 90% of the total stems in the invaded stands, it amounted to only 4% of the total sapwood area, contributing proportionately less to T compared with cottonwood. Therefore, there were no changes in T at the stand scale; cottonwoods were such a large component of the stand that removal of saltcedar was inconsequential. Because all roots could reach the groundwater, ET was not constrained by available water, but by available energy which was mostly partitioned into the cottonwood overstory.

### Pacific Northwest forests

This site is located in the H.J. Andrews Forest in central Oregon's western Cascade Mountains. The environment features wet winters, dry summers, steep terrain and roots primarily in the upper 2 m. Silviculture drove the spatial vegetation pattern; Pacific Northwest forests consist of a patchwork of regenerating stands of different ages and species composition. This research focused on Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), red alder (*Alnus rubra* Bong.), and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.). A stand-age comparison of T was done to evaluate factors controlling T (age, species composition, and sapwood area), and rank these factors according to their relative impact.

Age comparison results revealed that young Douglas-fir (about 40 years since harvest) used 2.3 times more

water than old-growth Douglas-fir (about 450 years since last disturbed) on a per unit sapwood basis (Moore *et al.*, 2004). In the young stand, red alder used more water than Douglas-fir, especially in the late season. In the old stand, Douglas-fir used more water than western hemlock, especially in the early season. On the basis of these results, and observations that young stands had 21% greater total sapwood area than old stands, young forests had 29% more hardwoods like red alder which use more water, and old forests had more hemlocks which use less water, young forests were estimated to use 3.3 times more water than old-growth forests. Surprisingly, the old and young forests had very similar leaf areas. These results indicate that T can differ greatly between two forests with similar leaf area, because shifts in species composition affect the total conducting sapwood area per unit basal area and the sapflow velocity per unit sapwood. At this site, young forests had greater T per unit amount of vegetation.

### CONCLUSIONS AND PRIORITIES FOR FUTURE RESEARCH

Do changes in land use inevitably lead to changes in T? Our answer is no, guided by a set of three principles that explain the complex interplay between physical and biological factors that control T. First, land use change will alter T if it changes available energy and its partitioning between latent and sensible heat. Changes in available energy can be compensated for by changes in how that energy is partitioned. Second, land use change will alter T if it leads to changes in rooting depth and access to available water. Soil depth and water storage capacity are constraints on this occurrence. Third, land use change will alter T if it leads to changes in the rate of water use that are sustainable over the long term. Change in land use may alter the rate of water withdrawal by plants, but if water is limiting, all of the available water will be used, regardless of plant species composition.

Practically speaking, the best way to know if a particular site comparison is likely to exhibit differences in T is to evaluate whether it complies with our guiding principles (Figure 1). In conducting comparative studies, we believe it is critical to assess site conditions and describe heterogeneity in the terms we have outlined. Field measurements should be designed to quantify spatial variation in the energy balance, especially available energy (net radiation minus storage heat flux). Improved methods are needed so that point-scale measurements can better translate to robust estimates of energy balance and plant-available water at the landscape-scale.

Sometimes the greatest driving factor for T variation may be below ground. To determine whether plant-available water differs with land use change, we simply need better tools to map spatial variation in root zone soil moisture and rooting distribution at the landscape-scale. In rocky soils, water storage capacity may be constrained not only by depth and texture, but also by the volume fraction of rock in the soil matrix (Schwinning, 2010). Surprisingly,

effects of soil depth have not been systematically explored *except in models*, and there solely from the perspective of limited water storage capacity (e.g. Milly, 1994; Milly and Dunne, 1994; Kleidon and Heimann, 1999). Field methods for quantifying soil depth, soil water content, and rooting depth (e.g. soil coring, ground-penetrating radar, electromagnetic induction, time-domain reflectometry, neutron scattering) are difficult to implement in heterogeneous terrain at the spatial density necessary to capture the full range of site variability. Microwave remote sensing of soil moisture from aircraft and satellite is limited to soil surface layers and very large spatial footprints. Research priorities should be aimed at detecting and modeling how plant-available moisture is distributed throughout the root zone (Mahfouf *et al.*, 1996) across heterogeneous terrain, and how it is partitioned to overstory and understory species.

Determination of temporal dynamics in dry down cycles between precipitation events will also provide new insights for predicting whether land use will alter T. In ecosystems with deep soils (e.g. south Texas mesquite brushland), soil storage absorbs any imbalance between water inputs and outputs, so that excess precipitation can be stored locally and used later for T. However, in ecosystems with shallow soils (e.g. central Texas oak-juniper woodland), a greater proportion of annual precipitation is expected to run off with negative consequences for rain use efficiency (Huxman *et al.*, 2004b). Thus for storage-limited ecosystems, not only is the amount of precipitation critical, but also the *timing of events*. Noy-Meir's pulse-reserve paradigm for water-limited systems (Noy-Meir, 1973; Schwinning and Sala, 2004; Schwinning *et al.*, 2004) has been used to great effect in decomposing ecosystem fluxes of water, carbon, and nitrogen (e.g. Huxman *et al.*, 2004a; Fernandez, 2007; Sponseller, 2007; Collins *et al.*, 2008; Heisler-White *et al.*, 2008). This 'event-based' approach to ecosystem ecology provides a powerful basis for evaluating effects of precipitation change, particularly changes in precipitation event sizes and the length of drought periods separating them that are predicted to accompany global warming (Groisman *et al.*, 2005; Easterling *et al.*, 2007).

At even longer time scales (annual to decadal), differences in T between contrasting ecosystems may diminish despite measurable differences spanning shorter time spans. This relates to the third principle. For example, conversion from evergreen to deciduous vegetation would alter seasonal dynamics, but not necessarily annual water balance. As shown in the mesquite brushland example, modest reductions in T scarcely accumulated over many years because excess soil water was soon consumed by vigorous regrowth. By contrast, forests that have been converted to agriculture and maintained in a cultivated state for many years, as is the case in Australia, have led to dramatic cumulative impacts on regional water balance (Petheram *et al.*, 2002).

In conclusion, the three principles we propose for determining whether T will vary with changes in vegetation are arguably broadly applicable, should be further evaluated by the ecohydrology community, and

have direct relevance for numerous ecohydrological land management challenges.

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