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# Terrestrial Ecosystems in a Changing Environment: A Dominant Role for Water

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# Terrestrial Ecosystems in a Changing Environment: A Dominant Role for Water

## Abstract

Transpiration—the movement of water from the soil, through plants, and into the atmosphere—is the dominant water flux from the earth's terrestrial surface. The evolution of vascular plants, while increasing terrestrial primary productivity, led to higher transpiration rates and widespread alterations in the global climate system. Similarly, anthropogenic influences on transpiration rates are already influencing terrestrial hydrologic cycles, with an even greater potential for changes lying ahead. Intricate linkages among anthropogenic activities, terrestrial productivity, the hydrologic cycle, and global demand for ecosystem services will lead to increased pressures on ecosystem water demands. Here, we focus on identifying the key drivers of ecosystem water use as they relate to plant physiological function, the role of predicted global changes in ecosystem water uses, trade-offs between ecosystem water use and carbon uptake, and knowledge gaps.

## Keywords

global change, terrestrial vegetation, water use, water use efficiency

## Disciplines

Agronomy and Crop Sciences | Terrestrial and Aquatic Ecology

## Comments

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# Terrestrial Ecosystems in a Changing Environment: A Dominant Role for Water

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## Abstract

Transpiration—the movement of water from the soil, through plants, and into the atmosphere—is the dominant water flux from the earth's terrestrial surface. The evolution of vascular plants, while increasing terrestrial primary productivity, led to higher transpiration rates and widespread alterations in the global climate system. Similarly, anthropogenic influences on transpiration rates are already influencing terrestrial hydrologic cycles, with an even greater potential for changes lying ahead. Intricate linkages among anthropogenic activities, terrestrial productivity, the hydrologic cycle, and global demand for ecosystem services will lead to increased pressures on ecosystem water demands. Here, we focus on identifying the key drivers of ecosystem water use as they relate to plant physiological function, the role of predicted global changes in ecosystem water uses, trade-offs between ecosystem water use and carbon uptake, and knowledge gaps.

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## INTRODUCTION

The importance of fresh water in the terrestrial biosphere is relatively easy to conceptualize—without it, life as we know it would perish. However, this is where the simplicity ends. Too much or too little water can disrupt the functioning of an ecosystem. Even slight changes in the availability of water over time can lead to substantial ecological shifts.

Water is critical to the development of plants for multiple reasons. Water is used directly by photosynthesis—plants have evolved the capacity to absorb energy from light in order to break water molecules and harvest the energy from the protons and electrons released. Strictly speaking, this is the only component of ecosystem functioning where water is actually lost in the sense that it is being destroyed, although at the ecosystem level much of this water is again created during the process of respiration. Water remains intact for all other uses, including as the solvent within cells to carry out metabolic function, maintain turgor, and prevent desiccation of cellular tissues. It is this last use—the prevention of desiccation—that leads to the largest flux of water from a plant. This flux is frequently referred to as a water loss not because the molecular structure of water is broken but because the water is lost, at least temporarily, from being used by the plant.

Regardless of whether water is being used or borrowed, leaf net carbon assimilation in terrestrial plants is inescapably linked with a requirement for water that is orders of magnitude greater. This trade-off between carbon and water is a determining factor in many facets of terrestrial ecosystem function. Water is the most limiting resource for productivity in many areas of the planet, and the lack of it is the dominant cause for losses in agricultural yields (24, 53). Increased pressures on agriculture, including a growing population, dietary preferences for higher-trophic-level foods, and increasing cultivation of crops for an expanding bioeconomy (e.g., biofuels and industrial products) are likely to exacerbate the demand for water (37, 51, 55, 75, 107). Climate changes are driving fluctuations in both the frequency and intensity of precipitation, a factor that puts at risk both natural (145) and managed (58) ecosystems. Large swaths of forests in all regions of the planet are facing challenges that at their base stem from altered water availability (6). Although climate change is a major driver that can alter ecosystem function, ecosystems themselves can also feed back to influence climate. Further, because global changes and ecosystem responses to the

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**Leaf net carbon assimilation:** the sum of photosynthetic carbon uptake and respiratory and photorespiratory carbon loss from the leaf

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environment are complex, the rates of change observed so far are not necessarily indicative of future rates of change, and the rates of most global change factors are likely increasing (129).

## WATER AS A MAJOR DETERMINANT OF TERRESTRIAL PRODUCTIVITY

Plant productivity can be limited or colimited by a wide range of factors, including light, water, nutrients, temperature, and disturbance events, as well as edaphic factors such as the absence of adequate soil for growth. Of these factors, temperature and water are generally assumed to be the major drivers for ecosystem productivity. As such, it is temperature and water that dictate the major biomes of the globe. This does not suggest that other factors are unimportant; however, these additional limitations are generally considered to be relevant at scales much smaller than climate factors (72). In addition to the availability of water as an influence of biome distribution, drought is the largest limitation on ecosystem productivity (31, 32, 143).

Ecosystem-scale fluxes of carbon (i.e., gross primary production and, to a lesser extent, net primary production) correlate positively with both temperature and precipitation (91). Among forest ecosystems, precipitation has little influence on ecosystem carbon cycling when the mean annual temperature is below a certain threshold, and conversely, the influence of temperature is strong when precipitation is below a certain threshold (81, 91). Currently, approximately one-third of global ecosystem water use occurs in managed ecosystems (102). The water needed to sustain food production to meet population demands is presently limiting for ~25% of the global population and ~50% of global cropland, and population and climate projections indicate that these proportions are likely to increase (14, 53). Approximately one-quarter of agricultural land is irrigated, but this area produces ~34% of total agricultural output (124). Therefore, agricultural ecosystems rely heavily on the availability of precipitation or irrigation to maintain productivity (87, 116) and appear to be increasingly sensitive to changes in climate, particularly those related to warmer temperatures and dry spells (88, 89).

Despite the importance of water in determining ecosystem productivity, the direct and indirect consequences of climate change for ecosystem water use are often difficult to resolve. Many factors influence transpiration and evaporation, which together, defined as evapotranspiration (ET), determine the latent heat flux from an ecosystem. For a given terrestrial ecosystem, ET consists of up to three separate fluxes of water vapor: transpiration of water by plants, evaporation of water from plant surfaces excluding transpiration, and evaporation of water from the soil (71). The relative contributions of these three fluxes vary between ecosystems and with time within ecosystems, but transpiration is the most dominant flux when carbon uptake is strongest. In the absence of plants, a dry layer of soil near the surface decouples soil moisture from the atmosphere, so evaporation is maintained only as long as a continuum of water from the point of evaporation in the soil and the atmosphere is maintained.

The majority of a live plant's mass is water. Indeed, global estimates are that the amount of biological water is approximately double the size of the terrestrial carbon pool (102, 139); however, water taken up by plants exists within the organism for only a short time. Plants act as conduits linking soil water with the atmospheric demand for water vapor, even in the presence of a dry surface layer (18) (see sidebar Atmospheric Demand for Water Vapor). This continuum between soil moisture and the atmosphere is referred to as the soil-plant-atmosphere continuum.

Water movement along the soil-plant-atmosphere continuum follows the direction determined by the water potential gradient, with water flowing from higher to lower potentials (**Table 1**). The total water potential represents the sum of matric, gravitational, pressure, and osmotic potentials (80). The matric potential is the dominant water potential component that maintains soil moisture,

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**Transpiration:** the flux of water vapor that passes through the stomata of a plant

**Evaporation:** the vaporization of liquid water

**Evapotranspiration (ET):** the combination of evaporation and transpiration

**Latent heat flux:** the energy flux associated with a phase change of water

**Soil-plant-atmosphere continuum:** the pathway by which energy and mass move within an ecosystem

**Water potential:** the potential energy of water relative to a reference; it determines the movement of water from higher to lower potentials

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## ATMOSPHERIC DEMAND FOR WATER VAPOR

An atmospheric demand for water vapor exists when the actual vapor pressure of air ( $e_a$ ) is lower than the saturation vapor pressure of air ( $e_s$ ). The difference between  $e_s$  and  $e_a$  defines the vapor pressure deficit of the atmosphere. When this deficit is greater than zero, and providing moisture is available, evaporation will occur to minimize it. The unit associated with these terms is by definition pressure (kPa).

**Vapor pressure deficit (VPD):** the difference between the saturation vapor pressure of air and the actual vapor pressure of air

and the gravitational potential is the component that drives soil water drainage. The osmotic potential is the major component of the water potential that involves the movement of water into the plant. To remove water from soil, plants must maintain an osmotic potential lower than the sum of the osmotic and matric potentials of the soil, which drives the bulk flow of water into the roots; otherwise, uptake of water would cease (106).

Plants devote significant resources to acquiring water yet need to regulate transpiration to prevent unrestricted water loss. When solar radiation is sufficient to drive photosynthesis, atmospheric humidity is seldom saturating. This results in a vapor pressure deficit (VPD; see sidebar Atmospheric Demand for Water Vapor) that often corresponds with a very negative water pressure potential (**Table 1**). The water column from the soil is pulled upward through the vascular tissue by the atmospheric VPD and is facilitated by the cohesion-tension transport mechanism (125, 127, 138). The movement of water through a plant is analogous to a wick. Capillary forces, driven by a matric potential in the vascular elements, assist with the bulk flow of water through vascular tissues and the menisci, which form where water evaporates along mesophyll cell walls and assist with pulling the water toward the intercellular air spaces, where evaporation occurs (125, 127, 138). The VPD in the intercellular air spaces provides the negative water potentials needed for water to evaporate internally (see sidebar Water Flux from Leaves) and in the substomatal cavity, and a greater VPD in the atmosphere drives the diffusion of water out of the leaf (**Table 1**).

**Table 1 Major water potential values and ranges associated with the movement of water from the soil to the bulk atmosphere**

Location	Water potential (MPa)	Water potential range	Water potential component
Soil	-0.3	0 to -1.5 <sup>a</sup>	Matric, osmotic
Soil near root	-0.5	0 to -1.5 <sup>a</sup>	Matric, osmotic
Xylem in root	-0.6	-0.2 to -4 <sup>b</sup>	Hydrostatic, osmotic
Leaf water	-0.8	-0.2 to -3.5 <sup>c</sup>	Hydrostatic, osmotic, gravitational
Mesophyll surface	-0.8	-0.15 to -15 <sup>d</sup>	Hydrostatic, osmotic, gravitational
Air near mesophyll walls	-0.7	0 to -1.4 <sup>e</sup>	Air
Air near stomata	-6.9	0 to -15 <sup>e</sup>	Air
Air in canopy	-70	0 to -96 <sup>e</sup>	Air
Air above canopy	-90	0 to -320 <sup>e</sup>	Air

<sup>a</sup>Lower threshold based on water-saturated soil; higher threshold based on measurements (128).

<sup>b</sup>Range reported based on estimates from conditions when no loss of conductance was expected (137).

<sup>c</sup>Range taken from published water potential versus transpiration curves provided for various plant functional types (80).

<sup>d</sup>Range estimated from hydrostatic pressure associated with the meniscus radius at the liquid-air interface on the mesophyll surface within the leaf (80).

<sup>e</sup>Range determined based on water-vapor-saturated air and air with lower relative humidity and higher temperatures (80).

## WATER FLUX FROM LEAVES

When calculating the molar flux of water vapor from a leaf, the general assumption is that the intercellular air spaces are saturated with water vapor. This assumption has been challenged in that a gradient of water vapor concentrations from the evaporating surfaces to stomatal cavities is necessary for the net flux of water vapor from the leaf (100). This assumes that, as described by Pieruschka et al. (111), transpiration is imposed by the vapor pressure deficit (95). However, equilibrium evaporation (114) can also drive transpiration in the absence of any vapor pressure gradient within the leaf. This is done through the addition of heat into the leaf, which drives evaporation into an already saturated volume (111). Therefore, the assumption that gradients of vapor pressure are absent within the leaf is not inconsistent with the theory of evaporation, provided that leaves generally absorb significant amounts of radiant heat when transpiration is occurring.

The driving force for water movement is based on water potential. However, the flux of water is determined by the conductance (or resistance, as the inverse) of a particular component of the soil-plant-atmosphere continuum (**Table 2**). The conductance pathways associated with individual plants are generally represented by the root, stem, and leaf hydraulic conductances as well as stomatal and leaf boundary-layer conductances to water vapor (117). Although these conductances vary over time based on both physiological and environmental factors (**Table 2**), the stomatal and leaf boundary layers are the most variable, with only the stomatal conductance ( $g_s$ ) under the dynamic control of the plant. The degree to which stomata open determines the dynamic range of  $g_s$ , which in turn feeds back directly on the temperature and humidity in the intercellular air spaces, the water potential in these spaces, and the bulk flow of water from the roots.

The sum of all leaf conductances coupled with the water vapor gradient between the intercellular air spaces and the atmosphere determines leaf transpiration rates. Just as various resistances exist in the movement of water from the soil, into and through the plant, and toward air outside of the leaf, there are many components of the physical environment within plant canopies that also act as resistance pathways toward the movement of water vapor from the leaves into the bulk atmosphere. These barriers include the leaf and canopy boundary layers, over which plants have relatively little dynamic physiological control, depending instead on the physical structures of the leaves (e.g., shape, size, presence of trichomes, orientation) and canopy architecture. The release of water vapor within the plant canopy coupled with the resistance of water movement away from

**Conductance:** the ease with which a gas diffuses down a gradient; it is the inverse of resistance and is generally defined by the pathway of movement, e.g., stomata, boundary layer, etc.

**Boundary layer:** the relatively stationary layer of air in the immediate vicinity of a surface

**Table 2** Major conductance components associated with the movement of water from the soil to the bulk atmosphere

Hydraulic/diffusive conductance component	Conductance type	Factors influencing resistance
Soil	Hydraulic	Soil composition, volumetric water content
Root	Hydraulic	Apoplastic, symplastic, and transcellular movement
Stem	Hydraulic	Xylem structure, presence of embolism
Leaf	Hydraulic	Venation architecture; minor leaf vein density; apoplastic, symplastic, and transcellular movement
Stoma	Diffusive	Number of stomata, opening size
Leaf boundary layer	Diffusive	Leaf size, leaf orientation, trichomes, stomatal crypts, wind speed and direction
Canopy boundary layer	Diffusive	Wind speed, canopy roughness, canopy architecture, atmospheric stability

## EMISSIVITY

Emissivity is defined as the fraction of blackbody emittance at a given wavelength by a material. Emissivity ranges from 0, signifying a surface that emits no radiation, to 1, signifying a pure blackbody. It is equal to absorptivity, per Kirchoff's law of thermal radiation. The emissivities of most biological surfaces are close to 1 for long-wave radiation.

the plant canopy boundary layer results in a higher-humidity environment, leading to a lower VPD and less ET.

## PLANTS AND CLIMATE

The amount of energy available to an ecosystem, referred to as net radiation, is the sum of the short-wave energy absorbed and the difference between the downwelling and upwelling long-wave radiation. The surface and atmospheric temperatures and emissivity (see sidebar Emissivity) influence the balance between downwelling and upwelling long-wave radiation, and the structure and function of terrestrial ecosystems influence the ratio of incident short-wave radiation that is absorbed to that which is reflected at the surface, defined as albedo. Many factors can influence the albedo of a terrestrial ecosystem, including plant architecture, leaf physical traits (such as trichomes), leaf orientation, and physiological and biophysical functions (such as transpiration rates, photosynthetic rates, and plant nitrogen status). The resulting net radiation drives ecosystem functioning, which includes the energy required for metabolism, latent heat fluxes, heat storage, heat transfer through the soil, and sensible heat fluxes.

**Net radiation:** the total energy available for an ecosystem to perform work

**Albedo:** the reflectivity of a surface for a given wavelength or range of wavelengths of electromagnetic radiation; it ranges from a pure blackbody at naught to a purely reflective surface at unity

**Sensible heat flux:** the energy flux associated with a plant surface or ecosystem caused by the turbulent transport of air across thermal gradients

### The Role of Energy in Ecosystem Functioning

The majority of energy is partitioned to sensible (associated with convection and conduction) and latent (associated with evaporation of water) heat fluxes. The ratio of these two fluxes is defined as the Bowen ratio (22). The Bowen ratio for a given ecosystem is highly variable across a variety of timescales and environmental conditions. Vegetation has significant control over the Bowen ratio through the stomata. When stomata are closed, a majority of the radiation incident upon the surface is absorbed by the plant canopy until its temperature exceeds that of the air, resulting in sensible heat fluxes away from the canopy. Fully open stomata result in more energy being partitioned to latent heat fluxes. In the absence of vegetation, sensible heat transfer of absorbed radiation dominates the land surface. The exception occurs during a wetting event, wherein significant amounts of energy are partitioned to latent heat fluxes from the surface of the soil. Partitioning to sensible heat fluxes drives immediate warming at the surface, whereas partitioning to latent heat fluxes moves energy away from the surface, where it is eventually released during condensation higher in the atmosphere. The importance of the heat transfer that occurs during the evaporation-condensation cycle is reflected in the role that evaporation from the surface plays in providing the energy needed to power significant local to regional meteorological events, such as convective precipitation (i.e., thunderstorms) and monsoons (21, 93).

Of the many fates of absorbed solar radiation, the small fraction of energy partitioned to metabolism drives ecosystem productivity. This energy is used to drive charge separation in the photosynthetic reaction centers to oxidize water (photosystem II) and reduce NADP



## EVAPOTRANSPIRATION AND PHOTOSYNTHESIS

As an example, a recent study conducted in the southern United States (132) calculated a mean estimate of net primary production of  $\sim 525 \text{ g C m}^{-2} \text{ year}^{-1}$  and a water use efficiency of  $0.71 \text{ g C (kg H}_2\text{O)}^{-1}$ , yielding a total evapotranspiration of  $739 \text{ kg H}_2\text{O m}^{-2}$ . The net primary production can be expressed as  $43.75 \text{ mol CO}_2 \text{ m}^{-2} \text{ year}^{-1}$ , which corresponds to an equal amount of  $\text{O}_2$  generated. Because photosynthesis requires 2 mol of  $\text{H}_2\text{O}$  to yield 1 mol of  $\text{O}_2$ , the direct requirement by photosynthesis to sustain this net primary production is  $87.5 \text{ mol H}_2\text{O m}^{-2} \text{ year}^{-1}$ . Converting the units back to mass, photosynthesis directly requires  $787.5 \text{ g H}_2\text{O m}^{-2} \text{ year}^{-1}$ , which represents approximately 0.1% of the total evapotranspiration in this region. Further, assuming 50% of a plant is water, the  $525 \text{ g C m}^{-2} \text{ year}^{-1}$  would yield a pool of stored water of  $\sim 1.05 \text{ kg H}_2\text{O m}^{-2} \text{ year}^{-1}$ , which again represents a small fraction of total evapotranspiration.

(photosystem I) for the photosynthetic carbon reduction cycle, producing oxygen as a by-product (142). Thus, the availability of water is essential for directly sustaining photosynthesis. However, despite the importance of water in maintaining photosynthesis, less than 1% of water taken up by plants is used directly by photosynthesis (see sidebar Evapotranspiration and Photosynthesis). A relatively larger fraction of water is stored within the cells of plants that includes both the water moving through vascular tissues and the intracellular water providing the medium for metabolism and maintenance of turgor. The pool of water in plants typically accounts for 40–70% of standing plant mass, yet this fraction still represents less than 1% of the total water taken up by plants over a growing season. The single largest use of water by plants is associated with the transpiration stream: water lost because of the need for  $\text{CO}_2$  from the atmosphere, which in turn leads to latent cooling. From the perspective of ecosystem water availability, however, this water loss is critically important in climate as well as the hydrologic and carbon cycles.

Evaporation of water is endothermic, and the latent heat of water vaporization is several orders of magnitude larger ( $\sim 2,000$  times) than the specific heat of air under typical atmospheric conditions; ET therefore strongly influences the surface energy balance (19, 110, 121, 147). Because of the endothermic nature of evaporation, the hydrologic cycle involves substantial cycling of energy. An estimated 50% of total annual solar radiation incident on the terrestrial surface goes directly toward ET (71). Several orders of magnitude less water is present in the atmosphere relative to that on the earth's surface (133), yet atmospheric water vapor is critical to the survival of plants. The 8–9-day residence time of water vapor in the atmosphere (134) reflects a significant flux of moisture into and out of the atmosphere driven by ET and precipitation.

### The Role of Vegetation as a Regulator of Climate

The role of plants in the regulation of climate is best understood in the context of how the evolution of higher plants transformed the atmosphere, which has been previously reviewed in depth (15). It is thought that, prior to the evolution of a vascular system, plants were physiologically active only during and immediately following wetting events, when a dry surface layer was absent (18, 62). The evolution of early land plants into vascular plants with roots, vascular tissue, cuticles, and stomata (5, 18) increased access to, and consequently transpiration of, water and broke the tight linkage between physiological activity and wetting events. By maintaining near-constant access to water in soil, plants expanded into areas previously unsuitable for survival. Through the evolution

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**Recycling ratio:**

the fraction of water evapotranspired from a given area that later precipitates in the same area

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of angiosperms, the coupling of the ability to access water and an increase in leaf venation led to a many-fold increase in rates of production (23, 26, 27, 47).

There is strong evidence that the evolution of a vascular system, which allowed the atmosphere to pull water from beneath the soil surface, was environmentally transformative (18, 85, 150). The ability to access and transport water through this conduit is highly correlated with productivity, and the relationship appears to be consistent across numerous plant lineages (27). The rise of higher plants undoubtedly led to a drop in atmospheric CO<sub>2</sub> concentration ([CO<sub>2</sub>]) concomitant with a rise in oxygen concentration (28). Equally significant was the transformation of many areas of the terrestrial surface from desert-like biomes to highly productive ecosystems stemming from ET (18). Even under present-day conditions, the role of plant transpiration is an important component of the terrestrial hydrologic cycle. Terrestrial ET maintains the pool of water vapor in the atmosphere. Globally, approximately 60% of the water that falls on the terrestrial surface comes from ET, with the remaining 40% coming from ocean evaporation (120). This is a considerable amount, because the surface area and the amount of water available on the terrestrial surface are a small fraction of those found in the oceans.

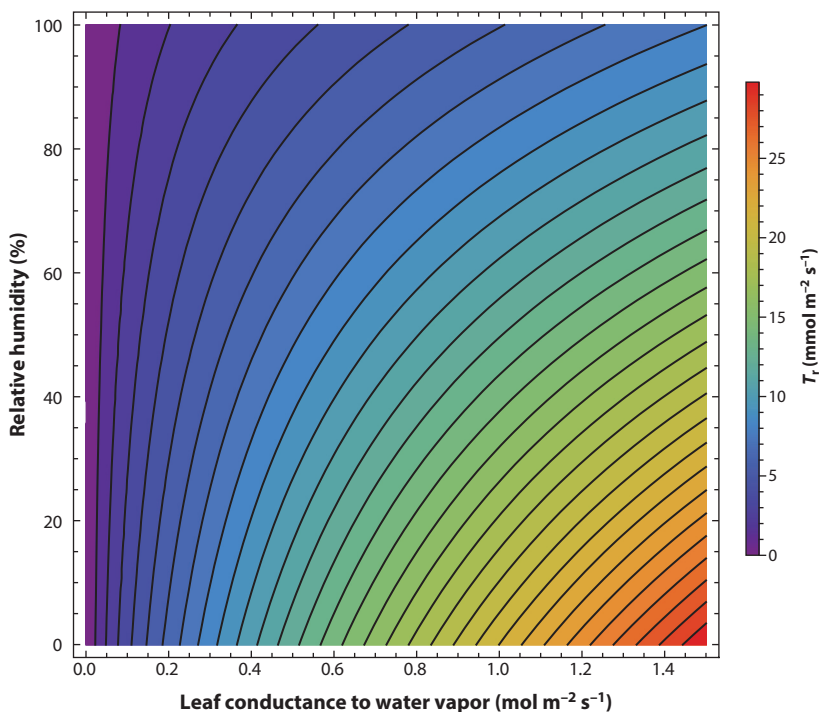
Ocean evaporation is a critical component of the terrestrial hydrologic cycle. However, the extent to which this source of water vapor contributes to terrestrial precipitation is highly variable based on time and location (40, 122). The proportion of evapotranspired water within a region that falls as precipitation in the same region is referred to as the recycling ratio; it varies from 0 (for areas where local ET does not contribute to local precipitation) to 1 (for areas where all precipitation originates from ET). These upper and lower limits are easily envisioned for extremely small spatial scales, which rely exclusively on water vapor transported horizontally by wind (i.e., advected) for precipitation and therefore have a recycling ratio of 0, and the entire globe, which has a recycling ratio of 1 because ET and ocean evaporation offset precipitation and conserve mass in an essentially closed system. The recycling ratio of a given area is critical for the movement of water vapor from a key source of moisture (e.g., the oceans) to intercontinental regions that in the absence of moisture recycling would be dominated by a dry surface layer. Recent analysis on partitioning ET into evaporation and transpiration showed that 80–90% of continental ET is transpiration (71), demonstrating the importance of plants in recycling moisture.

Precipitation recycling tends to play a larger role in supplying moisture to interior continental regions, where soil moisture and climate (i.e., land-atmosphere) coupling is strongest (38, 122), with greater recycling occurring in anomalously dry years relative to wet years (38). In other words, as moisture becomes more limiting, ecosystems may become more important in maintaining moisture availability by recycling ET, leading to increased ecosystem influence on atmospheric processes. In the absence of ET, the recycling ratio diminishes, resulting in substantial impacts on the intercontinental hydrologic cycle (38, 122). This recycling ratio does not necessarily reflect the ratio of ET to ocean evaporation, because advection can bring evapotranspired moisture into a region, but the two ratios follow a pattern similar to that described above with respect to wet and dry extremes (38). The precipitation recycling ratio for a given area is difficult to assess experimentally, although various modeling approaches suggest that changes in ET have direct effects on soil moisture, moisture recycling, and ecosystem productivity (8–10) and indirect effects on atmospheric circulation patterns (56).

Regardless of the mechanisms behind the responses, it is clear that ET is a major component of the terrestrial hydrologic cycle, influences local and regional climate patterns, and is critical to maintain the productivity of natural and managed ecosystems. Thus, with stomata serving as a valve regulating the movement of water vapor from the soil into the atmosphere, plants play a critical role in regulating both climate and energy partitioning between sensible and latent heat fluxes (121).


## GLOBAL CHANGES THAT INFLUENCE ECOSYSTEM WATER USE

Anthropogenically induced global changes, including rising temperatures, altered precipitation timing/intensity, and altered atmospheric trace gas composition, cause ecosystems to undergo key changes at a wide range of spatial and temporal scales. As outlined above, stomata are the main control point of vegetation in regulating the exchange of  $\text{CO}_2$  and  $\text{H}_2\text{O}$  and the partitioning of sensible and latent heat from the plant canopy (121) and are sensitive to many global change factors (59). Global change–induced effects on ET can have a major impact on global water resources, especially for irrigated agroecosystems, which account for  $\sim 70\%$  of global anthropogenic water use (54, 144). Although it is ecosystem-level responses that are important when considering the impacts of global change scenarios on ecosystem productivity, the key components linking global climate changes to ecosystem water use are stomata. Stomatal conductance is positively and the humidity in the air is negatively correlated with transpiration (Figure 1). Because transpiration responses to changes in the growth environment are complex, we have posted an online interactive figure to accompany Figure 1 (available at <http://demonstrations.wolfram.com/ModelingTranspirationOfLeaves>)



**Figure 1**

The two main factors that determine transpiration are the conductance of water vapor from inside the leaf to the atmosphere and the gradient of water vapor from inside to outside the leaf. It is generally assumed that the water vapor in the leaf is saturating, and thus that the gradient is determined by the leaf temperature and water vapor concentration in air. Here, relative humidity is used to determine the atmospheric water vapor, and leaf conductance to water vapor represents all diffusive conductances associated with the leaf. Leaf transpiration ( $T_r$ ) is modeled based on the leaf energy budget (29) and a Fick's law analogy (100). More details and an interactive model are available online (posted at <http://demonstrations.wolfram.com/ModelingTranspirationOfLeaves> and as a Supplemental Material download; follow the Supplemental Material link from the Annual Reviews home page at <http://www.annualreviews.org>).

 Supplemental Material

**Feedbacks:** the influence of a flux to repress (negative feedback) or amplify (positive feedback) the flux itself

**Leaf area index (LAI):** the total plant leaf area per unit ground area

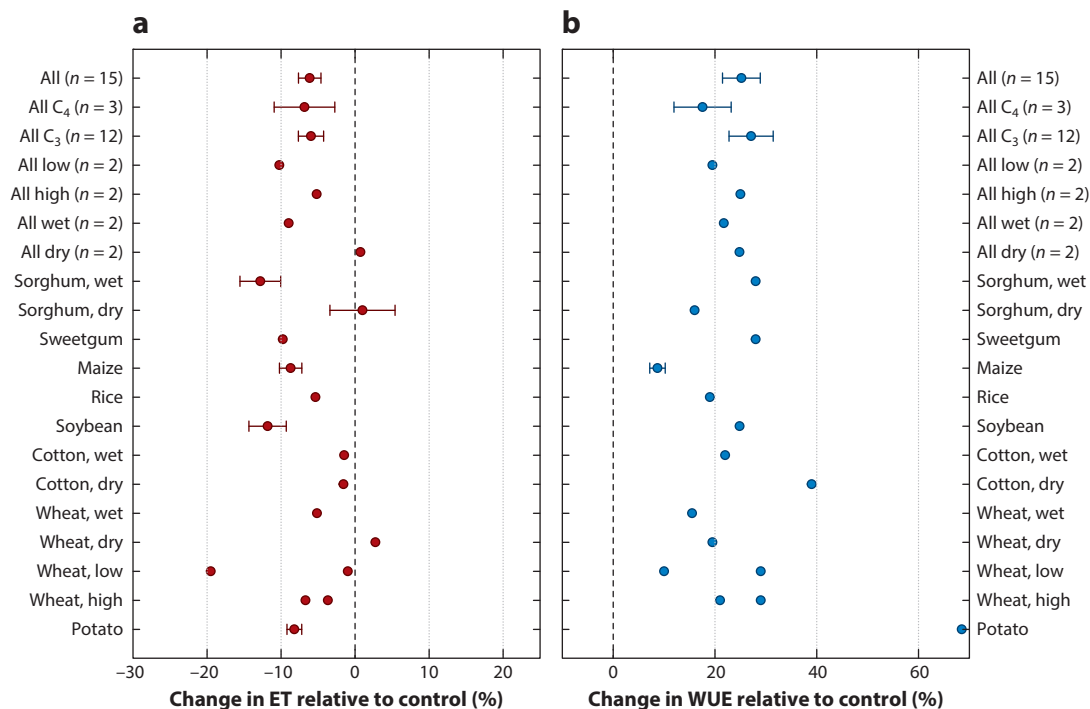
and as a **Supplemental Material** download; follow the **Supplemental Material link** from the Annual Reviews home page at <http://www.annualreviews.org> that provides modeled estimates of transpiration based on leaf energy balance (29) and a Fick's law analogy calculation for transpiration (100). In the following sections, we highlight mechanisms and feedbacks that characterize the response of ecosystem water use to the three dominant global changes: rising [CO<sub>2</sub>], warming temperatures, and increased drought frequency.

### Rising Atmospheric CO<sub>2</sub>

The response of ET to elevated [CO<sub>2</sub>] involves numerous physical and physiological processes and feedbacks, including altered physical conductances, water vapor gradients, and changes in canopy and leaf morphologies. At the leaf scale, rising atmospheric CO<sub>2</sub> generally lowers transpiration through reduced  $g_s$  (49). The sensitivity of  $g_s$ , and thus transpiration, to [CO<sub>2</sub>] has been recognized in the literature for at least a century (86). Reviews for both tree (49) and crop (1–3) species have shown consistent decreases in  $g_s$  with growth in elevated [CO<sub>2</sub>], with a potential exception of conifer species. Although the directional response of  $g_s$  to CO<sub>2</sub> is generally conserved among plant functional types, it is important to consider that a change in  $g_s$  is not perfectly coupled to an equal change in transpiration, which also depends on VPD (**Figure 1**).

In addition to  $g_s$ , numerous other conductances are involved with the movement of water from the soil to the atmosphere, leaving open the question of whether reductions in  $g_s$  associated with elevated [CO<sub>2</sub>] necessarily lead to lower ET. Multiple free-air CO<sub>2</sub> enrichment (FACE) experiments have quantified the response of ecosystem ET to elevated [CO<sub>2</sub>] under open-air field conditions (16, 64–66, 68, 76, 77, 92, 135, 146, 148). Across the various ecosystems, ET is on average ~6% lower for plants grown in elevated [CO<sub>2</sub>] relative to those grown in ambient conditions (**Figure 2**). A similar-magnitude reduction in ET with growth in elevated [CO<sub>2</sub>] is observed for both C<sub>3</sub> (5.9% ± 1.7%) and C<sub>4</sub> (6.8% ± 4.1%) species (**Figure 2**). In the two studies where drought was imposed, no elevated [CO<sub>2</sub>] effect on ET was observed (**Figure 2**), which is consistent with the trend toward a higher relative effect of elevated [CO<sub>2</sub>] on ET as moisture availability increases (**Figure 3a**).

The response of ET to elevated [CO<sub>2</sub>] is not expected to be constant across all species, as the percentage or contribution of transpiration to overall ET varies with canopy structure, roughness, and atmospheric coupling and the phenology of the species (49, 83). Through increased photosynthetic rates, elevated [CO<sub>2</sub>] stimulates growth and often leaf area index (LAI) in C<sub>3</sub> plants. A higher LAI increases the transpiration area within a plant canopy (84) and, depending on the size of the canopy, can offset the effects of lower  $g_s$  (43, 84). A stimulation in ET for dense and homogeneous canopies (e.g., soybean) is less likely to occur with further increases in LAI because much of the canopy is already buffered from the bulk atmosphere. Canopies with a relatively low LAI, where transpiration is a very small portion of the hydrologic cycle, will likely not experience much change in ET because even large changes in  $g_s$  are likely to be diluted by evaporation, which dominates ET in sparse canopies (70). However, plant canopies that have either midrange LAI values or lower leaf area densities and that experience significant increases in LAI with growth in elevated [CO<sub>2</sub>] are predicted to have increased ET with elevated [CO<sub>2</sub>] (44, 101). The global mean LAI of dominant plant functional types such as temperate broadleaf forests is ~5 m<sup>2</sup> m<sup>-2</sup>, suggesting that the effect of elevated [CO<sub>2</sub>] on  $g_s$ , and not an increase in LAI, is likely to dominate the ecosystem ET responses (7, 101). Data from FACE experiments have been used to parameterize the acclimation responses to elevated [CO<sub>2</sub>] and to validate model predictions of ET at future [CO<sub>2</sub>] levels. These studies predict that [CO<sub>2</sub>] is likely to affect ET across a wide range of environmental conditions, with some interannual and spatial variability (44, 136). However, these



**Figure 2**

A summary of published data on the effect of elevated  $[\text{CO}_2]$  on (a) growing-season evapotranspiration (ET) and (b) water use efficiency (WUE) (metrics vary by study) plotted as the percent change of elevated  $[\text{CO}_2]$  relative to control. The  $[\text{CO}_2]$  ranges from 365 to 400 ppm and from 500 to 550 ppm in control and elevated  $[\text{CO}_2]$  conditions, respectively. Error bars are plotted as  $\pm 1$  SE. Low and high refer to the amount of nitrogen treatment; wet and dry refer to ample and suboptimal irrigation levels. References for each value are as follows: sorghum wet/dry (135), sweetgum (146), maize (68), rice (148), soybean (16), cotton wet/dry (64, 77), wheat wet/dry (65), wheat low/high (66, 76), and potato (92). Figure adapted from References 57 and 84.

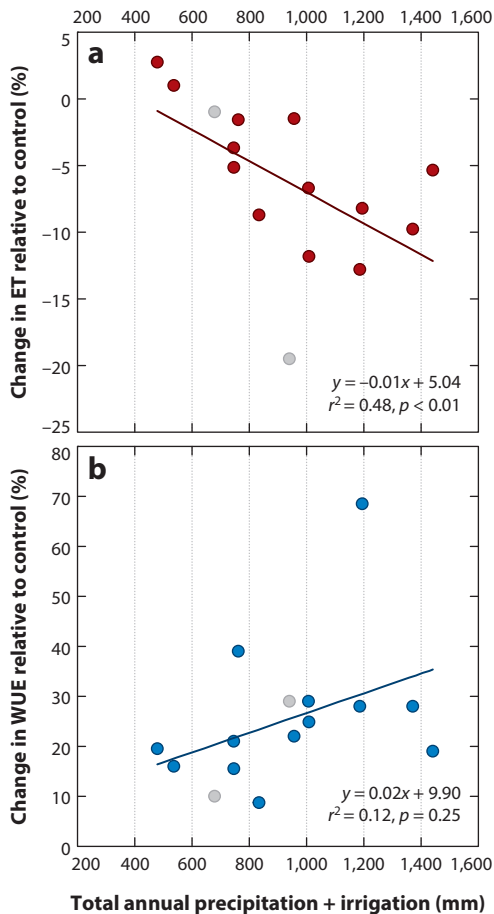
generalized responses are likely to vary based on confounding factors such as drought and warmer temperatures, as discussed below.

The consistent reduction of ET associated with plants grown at elevated  $[\text{CO}_2]$  suggests a higher amount of soil moisture availability. For example, the conservation of water by soybean grown at elevated  $[\text{CO}_2]$  maintains ET during short-term drying periods, a direct result of higher soil moisture availability (16). During longer droughts, however, the response is likely to be reversed as a direct result of higher LAI-associated growth in elevated  $[\text{CO}_2]$  (41). However, it is likely that as LAI increases above a threshold, it has a diminishing impact on ET, given the influence of the canopy boundary layer (73), consistent with diminishing improvements in water use efficiency (WUE) with increasing LAI (13). Reduced ET may also not translate into greater water availability after accounting for environmental factors, including, for example, high rates of surface or subsurface lateral flows or drainage below rooting zones.

### Increasing Global Temperatures

The most notable consequence of a higher temperature on plants relates to its link with the saturation vapor pressure of air ( $e_s$ ), which, following the Clausius-Clapeyron relation, increases exponentially with temperature. Although  $e_s$  can change many-fold over short time periods, the

**Saturation vapor pressure of air:** the maximum partial pressure of water vapor in an air mixture that can be attained while in equilibrium with a plane surface; it is highly dependent on temperature



**Figure 3**

The (a) evapotranspiration (ET) and (b) water use efficiency (WUE) data from **Figure 2** plotted versus total annual precipitation + irrigation. The gray circles are data from low nitrogen treatments, which were not included in the linear regression analysis. The precipitation data are the mean for the year(s) (January to December) when ET was reported for the respective crops. Precipitation data for Maricopa, Arizona (sorghum, cotton, wheat and potato), are from the National Weather Service (<http://www.wrh.noaa.gov/psr/climate/monthlyData.php>); for Champaign, Illinois (maize and soybean), are from the Midwestern Regional Climate Center (<http://mrcc.isws.illinois.edu>); for Oakridge, Tennessee (sweetgum), are from Reference 146; and for Shizukuishi, Iwate, Japan (rice), are from WorldClim (<http://www.worldclim.org>; 61).

actual vapor pressure of air ( $e_a$ ) is generally lower than  $e_s$  and stable over time. The difference between  $e_s$  and  $e_a$  represents the VPD of air, with higher values of VPD driving higher surface drying. Because  $e_s$  increases exponentially with temperature, so too does VPD when  $e_a$  remains constant. Although  $e_a$  is predicted to rise with increasing global mean temperatures, it is unlikely that increases in  $e_a$  will be matched with the exponential rise in  $e_s$  (33). Global warming has already resulted in an increase in VPD in many areas, as has been shown for the growing-season months in the midwestern United States (89). This increase in VPD is the major factor explaining the increased sensitivity of maize to drought, and if this pattern holds, the predicted increase in VPD by 2050 is likely to reduce maize yields, barring crop improvements, by  $\sim 15$ – $20\%$  (104). Although

**Vapor pressure of air:** the partial pressure of water in gaseous form within air

these analyses were conducted on major crops (89, 104), the underlying principles suggest that similar impacts of rising temperatures on water use can impact most terrestrial ecosystems.

Temperature plays a key role in regulating plant development (i.e., phenology), which can be a critical component determining ET. Warmer temperatures are likely to lead to longer growing seasons, which require more water. Some of the more notable consequences of warmer, prolonged growing seasons relate to increased ET, which can affect the frequency of drought owing to less water infiltration and soil moisture recharge/storage during a shorter dormancy (67). In managed ecosystems, temperature shifts resulting from global change can alter the timing of planting and other important management factors, which in turn impact the growing-season length and ET. This is already apparent in some heavily managed regions where changes in management and crop phenology are driving shifts in ET and the surface energy balance (118). Longer growing seasons associated with natural ecosystems have myriad effects. When Law et al. (81) summarized eddy covariance ET data across multiple years and locations, they found a relationship of  $\sim 20$  mm per degree Celsius of warming during the growing season. Another factor is a trend toward more precipitation falling as rain rather than snow, which can influence soil water infiltration rates, and earlier spring snowmelt runoff may also alter the availability of water to ecosystems (67).

Rising  $[\text{CO}_2]$  affects  $g_s$ , leaf temperature, and consequently VPD, all of which are critical in determining transpiration fluxes. Studying the combined effects of elevated  $[\text{CO}_2]$  and increased temperatures on ET is very difficult to achieve empirically because artificial means of heating canopies alter ecosystem temperature and VPD. Model analyses parameterized with data from in-field FACE experiments provide an alternative means to quantify the effects of rising temperatures on ET (e.g., 43, 44, 82). However, the net effect of increased  $[\text{CO}_2]$  and temperature will depend on the overall sensitivity of various species to  $\text{CO}_2$  and temperature. Model predictions for temperate crops suggest that the reduction in ET at elevated  $[\text{CO}_2]$  will be largely offset by a  $1^\circ\text{C}$  increase in global mean temperature (30, 82), whereas most global circulation models predict warming beyond  $2^\circ\text{C}$ . Historical observations indicate an overall intensification of the hydrologic cycle, including increased precipitation, ET, and runoff and decreased residence times of water in the biosphere, a pattern that has been attributed to warming temperatures (67). The water savings of elevated  $[\text{CO}_2]$  being smaller than the effect of temperature on ET is anticipated to be a global phenomenon, contributing to an overall drying of land surfaces (36, 69, 123).

## Drought and Moisture Availability Responses

Many factors can lead to an increased frequency of drought as global change progresses. The combined effects of elevated  $[\text{CO}_2]$  and temperature are predicted to result in an overall increase in ET and decrease in soil water availability, which together will lead to potential decreases in productivity in key agricultural regions (82). The higher rates of ET with warming are likely to further augment drought frequency around the globe (36, 113). Analysis of historical records over the last century has shown that warming-induced drying has occurred to such an extent that the land area in the band between  $60^\circ\text{S}$  and  $75^\circ\text{N}$  designated as “dry” nearly doubled from 1950 to 2008 (35, 36). This band is where most land mass is, and the drying is consistent with predictions that land surfaces will warm more than oceans (123).

As stated above, warmer temperatures increase  $e_s$ . Climate models predict that relative humidity will remain approximately at present levels, but the average VPD is likely to increase globally (33). This leads to an increase in surface potential evaporation, which determines the maximum rate of evaporation from the surface under a given set of environmental conditions. With a higher  $e_s$  and increased potential evaporation, rates of potential ET will likely exceed precipitation in many areas (35), which is sustainable only on short timescales. Thus, once soil moisture reserves

in the rooting zone are exhausted, ET is necessarily reduced. This scenario, although only one of many factors influencing precipitation, can potentially lead to increased drought frequency and intensity.

Alternatively, a higher  $e_a$  could lead to increased precipitation rates, although predictions support the idea that this scenario could lead to increased rates of precipitation per event but fewer events (67). The future rate of ecosystem water use will depend on the balance of water availability and on the combined effects of reduced water loss under elevated  $[\text{CO}_2]$  and increased water loss at elevated temperatures and VPDs. Under drought conditions, the water-saving effects of elevated  $[\text{CO}_2]$  dissipate (**Figure 3**), as all available water is likely used regardless of stomatal responses to  $[\text{CO}_2]$  (30). Although elevated  $[\text{CO}_2]$ -induced reductions in water use are smallest under drought conditions, the effects of reduced water use leading up to drought conditions significantly alter photosynthesis and yield (20, 84, 94). Ultimately, this outcome is attributable largely to increases in WUE.

## WATER USE EFFICIENCY

The WUE metric has long been used to quantify the trade-off between water loss and carbon uptake. The term itself has been criticized in that efficiency, as defined from an engineering perspective, must have a theoretical maximum (i.e., unity), and any loss in efficiency must be the product of system processes that are less than or equal to unity (97, 98, 126). Despite this criticism, WUE has proven to be a useful metric that quantifies the fact that water loss is required for productivity at any scale. The methods and descriptions of the underlying processes associated with WUE have diversified over time to increase the utility of the metric over different scales (13, 25, 39, 96–98, 131), ranging from instantaneous measurements of carbon fluxes to seasonal or entire ecosystem life cycles (**Table 3**).

### Definitions of Water Use Efficiency

The term instantaneous or integrated often precedes WUE to differentiate among the different scales. Despite the use of the term instantaneous to represent flux measurements of carbon uptake, the actual timescale can range from seconds (for direct chamber-based measurements of WUE) to half an hour or longer (when utilizing micrometeorological measurements of carbon fluxes, such as the use of eddy covariance). Similarly, integrated measures of WUE do not necessarily require

**Table 3** Water use efficiency (WUE) metrics scaled from the leaf to the ecosystem

Scale	Instantaneous WUE	Integrated WUE	Intrinsic WUE
Leaf	$A/T_r$ (13, 46, 50)	$\Sigma A/\Sigma T_r$	$A/g_s$ (45)
Canopy	$GPP/T_{r(\text{can})}$	$NPP/\Sigma ET$ (25, 126)	$GPP/g_c$ (13)
Ecosystem	$NEE/ET$ (11)	$NEP/\Sigma ET$ (81, 149)	$NEE/g_{\text{surf}}$
Harvest	—	$\text{Yield}/\Sigma ET$ (34, 131, 151)	—
Biome	—	$NBP/\Sigma ET$ (141)	—

Abbreviations:  $A$ , leaf net carbon assimilation ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ );  $ET$ , evapotranspiration ( $\text{mm H}_2\text{O}$ );  $g_c$ , canopy conductance ( $\text{mol m}^{-2} \text{s}^{-1}$ );  $GPP$ , gross primary production ( $\text{g m}^{-2} \text{s}^{-1}$ );  $g_s$ , stomatal conductance ( $\text{mol m}^{-2} \text{s}^{-1}$ );  $g_{\text{surf}}$ , surface conductance ( $\text{mol m}^{-2} \text{s}^{-1}$ );  $NBP$ , net biome productivity ( $\text{g C m}^{-2}$ );  $NEE$ , net ecosystem exchange ( $\text{g C m}^{-2} \text{s}^{-1}$ );  $NEP$ , net ecosystem productivity ( $\text{g C m}^{-2} \text{s}^{-1}$ );  $NPP$ , net primary production ( $\text{g C m}^{-2} \text{s}^{-1}$ );  $T_r$ , leaf transpiration ( $\text{mmol m}^{-2} \text{s}^{-1}$ );  $T_{r(\text{can})}$ , canopy transpiration ( $\text{g m}^{-2} \text{s}^{-1}$ ); yield, harvested biomass ( $\text{g dry matter m}^{-2}$ );  $\Sigma$ , time integrated. Dashes indicate metrics that are not applicable. *Note:* 1 mm  $\text{H}_2\text{O}$  over 1  $\text{m}^2$  area = 1 L  $\text{H}_2\text{O}$  = 1 kg  $\text{H}_2\text{O}$ .



seasonal or longer timescales and can represent discrete shifts in stored carbon pools over time, for example, the amount of water evapotranspired over an incremental biomass increase (60).

The versatility of the WUE metric also extends beyond instantaneous and integrated measures of carbon uptake to include different carbon pools within an ecosystem. For example, ecosystem-scale WUE focuses, in the numerator, on carbon exchange between the atmosphere and an ecosystem and can be expressed as instantaneous fluxes or by accumulating the fluxes to represent a carbon pool (11). An agronomic measure of WUE is based on the amount of harvested biomass, termed harvest WUE, and the cumulative ET over the growing season is typically expressed as the denominator (130, 141). The amount of carbon left in an ecosystem after all disturbance-related carbon losses, which can include harvests, fires, or a range of other carbon-releasing processes, has been termed biome WUE (130, 141). Despite these different WUE metrics, they can be considered in parallel to assess the water costs of ecosystem services as a whole. For example, in assessing the conversion of land use from annual row crops to perennial grasses, increases in harvest WUE and biome WUE (both considered positive ecosystem services) have been observed (141, 149).

In addition to the role of stomata in influencing WUE is the water vapor gradient from inside to outside the leaf. All else being equal, changes in the vapor pressure within a plant canopy can induce significant variation in WUE. Modifying WUE by expressing it as a function of conductance (e.g.,  $A/g_s$  rather than  $A/T_r$ , where  $A$  is leaf net carbon assimilation and  $T_r$  is leaf transpiration) rather than a flux of water vapor removes much of the variability caused by the vapor gradient (115). This expression of WUE is generally termed intrinsic WUE (Table 3). Although intrinsic WUE removes some variation in cross-site measurements, significant variation still exists based on species, location, and growing-season conditions at the leaf (115) and ecosystem (13) scales.

As with other WUE metrics, the conductance value used will vary based on the scale of the carbon fluxes or pools being considered. Leaf-scale measurements of intrinsic WUE are relatively straightforward measurements that rely on infrared gas exchange measuring systems to provide the rate of both net carbon assimilation and water loss (Table 3); however, determining canopy or surface conductances at larger scales is subject to significant assumptions and potential errors. Therefore, normalizing instantaneous or integrated WUE by VPD (WUE/VPD) is a close approximation for intrinsic WUE. This approximation is based on the use of a Fick's law analogy in calculating fluxes, which in the case of leaf transpiration, for example, yields  $T_r = g_s[e_{a(\text{leaf})} - e_{a(\text{air})}]$ . Because VPD in the leaf is approximately zero, this equation correlates with  $T_r = g_s(\text{VPD}_{\text{air}})$ . Therefore, either presenting intrinsic WUE using conductance or normalizing WUE using VPD could be an effective strategy. However, VPD has a strong influence on  $g_s$ , so caution is needed when applying the technique to measurements made under conditions with varying VPD (52).

## Water Use Efficiency and Global Change

That rising  $\text{CO}_2$  improves WUE directly has been demonstrated over many spatial and temporal scales. Stable isotope techniques allow for an assessment of leaf-level WUE that represents an integration of the undisturbed physiological and environmental conditions that influenced carbon and water exchange over the lifetime of the plant (46). Because all plant carbon is assimilated via photosynthesis, using the stable carbon isotope composition of biomass as a means to assess WUE is limited to intrinsic WUE integrated over the growth of the plant. An estimate of instantaneous WUE can be derived from intrinsic WUE when VPD data are available. In the case of trees, each growth ring represents an incremental growing period for the growing season (or shorter timescales). Thus, analyzing the stable carbon isotope composition in tree rings provides estimated changes in WUE over multiple decades and centuries (48, 74, 119). Similarly, archival plant tissues from long-running agronomic experiments have provided assessments of the changes in WUE on

seminatural grasslands over approximately 150 years (78). For natural alpine grasslands, Barbosa et al. (12) derived changes in WUE over 69 years using stable carbon isotopes in animal tissues (horns of *Capra ibex*) as a proxy for the carbon isotope composition of their diet, as isotopic signals are propagated along trophic levels. The results from these temporally and spatially integrated isotopic analyses of grassland vegetation suggest that intrinsic WUE has been increasing over time. However, the increase in intrinsic WUE translated into an increase of instantaneous WUE only when VPD did not change (in the spring) (78), whereas the offsetting influence of increasing  $[\text{CO}_2]$  on  $g_s$  and of increasing VPD on the water vapor gradient between the leaf and atmosphere yielded no change in instantaneous WUE at the alpine site (12) or in summer and fall (78).

Increases in the terrestrial carbon pool have been reported from models, satellite observations, terrestrial flux measurements, and distributed sampling (63, 105). Measuring changes in ET over the terrestrial surface, however, is more challenging because, unlike carbon, the fluxes do not accumulate into long-lived pools. Despite these challenges, historical records indicate that river discharge to oceans has been steadily increasing over time (67, 79), consistent with a reduction in ET driven by higher  $[\text{CO}_2]$ . However, assumptions that river discharge has been increasing and that the rise in river discharge is due to increases in  $[\text{CO}_2]$  are debated largely because of the high degree of variability associated with measuring various components of the hydrologic cycle (109). As mentioned above, a near-universal decrease in ET has been observed in FACE studies specifically looking at the effect of growth in elevated  $[\text{CO}_2]$  conditions (**Figure 2a**). This is consistent with reduced terrestrial ET, although these elevated  $[\text{CO}_2]$  studies do not simulate the increase in atmospheric VPD predicted with global warming. However, unlike ET, the effect of  $\text{CO}_2$  on WUE appears to have little dependence on water availability (**Figure 3b**). Further evidence using ecosystem flux measurements over long time periods supports the conclusion that WUE is increasing with  $[\text{CO}_2]$  (42, 74, 99); however, initial reports of ~80% increases in WUE at the leaf level (112) are significantly greater than those reported at the canopy or ecosystem scale (108) (**Figure 2b**).

## KNOWLEDGE GAPS

The impacts of independent global change factors on ET and WUE will not occur in isolation, as increases in  $[\text{CO}_2]$  will inevitably result in warmer mean temperatures and complex interactions in hydrology. VPD will likely increase with  $[\text{CO}_2]$  driving global mean temperature higher. Therefore, the influences of higher VPD coupled with rising  $[\text{CO}_2]$  and increased plant biomass create a complex interaction that challenges current predictions of WUE changes with increasingly rapid global changes. The effect of global change on WUE may also vary significantly among the various WUE metrics used (**Table 3**). This can be attributed to differences in how photosynthesis, yield, and/or respiration respond to environmental change (20).

The responses of ET and WUE to global change are complex. Therefore, it is critical to understand how individual treatment studies can be used to understand key interacting effects on ecosystem water use (103). For example, the uncertainties in the projections of tropospheric ozone concentrations ( $[\text{O}_3]$ ) are higher than those for  $[\text{CO}_2]$ , and there is considerable uncertainty about the responses of various species and plant functional types to  $\text{O}_3$  (4, 17, 90). Although some species show a consistent reduction in  $g_s$  with increasing  $[\text{O}_3]$ , this response is not universal (90).  $\text{O}_3$  decreases WUE in soybean despite significant reductions in  $g_s$  because the damaging effects on photosynthesis are greater than the observed decrease in  $g_s$  (140). Thus, it can be expected that species that experience reduced photosynthesis and not reduced  $g_s$  with high  $[\text{O}_3]$  will experience even greater losses in WUE. Whether these responses are consistent with increased  $[\text{O}_3]$  combined with increased  $[\text{CO}_2]$  and/or warmer temperatures is less certain. Similarly, the influence of  $\text{CO}_2$ ,

temperature, VPD, and  $O_3$  on ET and WUE will vary with species, adding further complexity and uncertainty to future water-related issues associated with ecosystem function and climate feedbacks. Experiments combining global change factors or imposing treatments across a broad range of potential global change scenarios, particularly through direct manipulation of VPD in the growth environment coupled with other key climate change factors, will help to significantly reduce these layers of uncertainty.

As discussed above, plants play a major role in shaping climate, so changing the surface energy balance and ecosystem water use will add even more complexity to resolving the impacts of anthropogenic emissions on climate. The evolution of plants was transformative to climate, and the acclimation of present species to rapid global changes is likely to have major influences as well. Global change is expected to intensify the global hydrologic cycle. Although a ~6% decrease in ET under elevated  $[CO_2]$  may be offset by an increased VPD, much less is known about the impact of altered energy partitioning on shorter timescales or high-intensity atmospheric processes that drive meteorological events. There is no tool currently capable of explicitly resolving turbulent atmospheric processes and climate patterns as well as accurately representing the physiological and ecosystem energy balance consequences of global change. A key advancement in global change research will be the development of tools that are capable of resolving the impact of multiple global change factors on ecosystems at the scale of mechanistic understanding along with their interactions with and feedbacks on climate. Such tools will be necessary to scale from the size of the experimental plots in the empirical studies described above to those that are most relevant for resolving the impacts on the landscape and global scales.

### SUMMARY POINTS

1. Since the evolution of higher plants, evapotranspiration from terrestrial ecosystems has played a dominant role in the global hydrologic cycle.
2. Water is the most limiting factor for ecosystem carbon uptake for much of the earth's terrestrial ecosystems.
3. Anthropogenic activity will play an increasing role in determining the demand for and cycling of water.
4. Increasing  $CO_2$  concentrations will significantly reduce the rate of water loss per unit of carbon gain and increase the water use efficiency of terrestrial ecosystems. However, this will likely be offset by the concurrent rise in atmospheric temperatures and vapor pressure deficit.
5. The water-saving effect of elevated  $CO_2$  can be diminished under strong water-limiting conditions where the  $CO_2$ -induced increase in leaf area overcompensates for the lower stomatal conductance, resulting in higher water use.
6. Accurately projecting the future of ecosystem water use will require new empirical data from field experiments, coupled with sophisticated tools capable of resolving interactions among global change factors and feedbacks between the terrestrial ecosystem and the atmosphere.

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The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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