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Review

Indicators of water use efficiency across diverse agroecosystems and spatiotemporal scales



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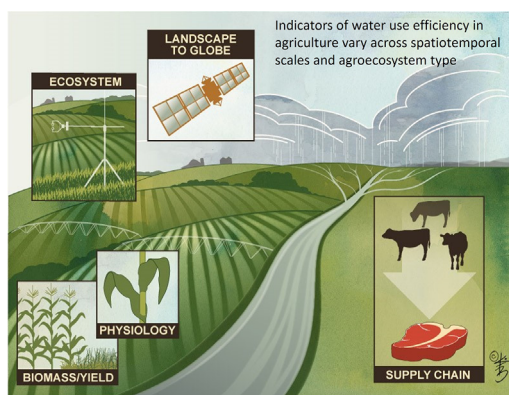
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HIGHLIGHTS

- Water use efficiency is the ratio of biomass produced to water consumed.
- Indicators of water use efficiency vary but are key to sustainable agriculture.
- There is no “silver bullet” indicator of water use efficiency.
- Indicators of water use efficiency can be compared across scales and agroecosystem.
- Indicators of water use efficiency can help adapting to agriculture to climate change.

GRAPHICAL ABSTRACT



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ABSTRACT

Understanding the relationship between water and production within and across agroecosystems is essential for addressing several agricultural challenges of the 21st century: providing food, fuel, and fiber to a growing human population, reducing the environmental impacts of agricultural production, and adapting food systems to climate change. Of all human activities, agriculture has the highest demand for water globally. Therefore, increasing water use efficiency (WUE), or producing ‘more crop per drop’, has been a long-term goal of agricultural management, engineering, and crop breeding. WUE is a widely used term applied across a diverse array of spatial scales, spanning from the leaf to the globe, and over temporal scales ranging from seconds to months to years. The measurement, interpretation, and complexity of WUE varies enormously across these spatial and temporal scales, challenging comparisons within and across diverse agroecosystems. The goals of this review are to evaluate common indicators of WUE in agricultural production and assess tradeoffs when applying these indicators within and across agroecosystems amidst a changing climate. We examine three questions: (1) what are the uses and limitations of common WUE indicators, (2) how can WUE indicators be applied within and across agroecosystems, and (3) how can WUE indicators help adapt agriculture to climate change? Addressing these agricultural challenges will require land managers, producers, policy makers, researchers, and consumers to evaluate costs and benefits of practices and innovations of water use in agricultural production. Clearly defining and interpreting WUE in the most scale-appropriate way is crucial for advancing agroecosystem sustainability.

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1. Introduction

Providing food, fuel, and fiber to a growing human population amidst climate change is one of the greatest sustainability challenges of the 21st century. Historically, rising agricultural demand was met by converting native vegetation to croplands or pastures and through technological innovations (Foley et al., 2005; Southgate, 2009). As a result, agricultural production is currently the dominant land use globally, accounting for 50 % of the habitable land on Earth (51 million km²), while the remaining area – forest, alpine, tundra, and desert ecosystems – present limited options for additional conversion (Ritchie and Roser, 2013; Tilman et al., 2011). Advances in breeding, mechanization, irrigation, and fertilization over the last half of the 20th century led to large increases in crop yields and livestock production globally, but at high environmental costs including water pollution, increased energy use, loss of natural ecosystems and biodiversity, and amplification of climate change (Foley et al., 2011; Springmann et al., 2018; Tilman et al., 2011). Thus, there is a need to balance increasing food production with reducing environmental impacts of agriculture to improve the short- and long-term sustainability of agroecosystems (Kleinman et al., 2018; Harmel et al., 2020).

The magnitude of this challenge is growing as climate change increases temperature, alters precipitation, and causes more frequent and extreme climatic events such as droughts, floods, and heat waves (IPCC, 2021). Agriculture, of all human activities, has the highest demand for water

globally and is tightly coupled with the hydrological cycle. Shifts in water availability resulting from climate change will have direct impacts on agricultural production (Hatfield and Dold, 2019). At the same time, surface or groundwater used for agriculture will have to compete with growing demands from urban and wildland water resource needs (Amarasinghe and Smakhtin, 2014). Understanding the myriad ways water is exchanged for provisioning, regulating, and supporting ecosystem services is critical for developing sustainable agroecosystems. However, indicators of water use in agricultural production vary widely across spatial scales (e.g., leaf to globe), climate zones (e.g., water-limited vs. nutrient-limited), agroecosystem types (e.g., maize vs. poultry), and management practices (e.g., irrigated vs. rainfed), making it difficult to determine which indicators to use when assessing dynamics and variability in agricultural water use (Fig. 1). A standardized approach to indicator development and use is critical for improving the efficiency and sustainability of water resources in agricultural production.

Resource use efficiency in ecology is defined as the “amount of biomass produced per unit of supplied resource”, with water, nutrients, light, carbon, and radiation as common limiting resources (Hodapp et al., 2019). Concepts underpinning resource use efficiency have deep agricultural roots. With the advent of industrial fertilizers, ideas emerged to define the optimal supply of resources to maximize the efficiency of agricultural production including the Law of the Minimum (Liebig, 1840), the Law of the Optimum (Liebscher, 1895), and the Law of Diminishing Returns

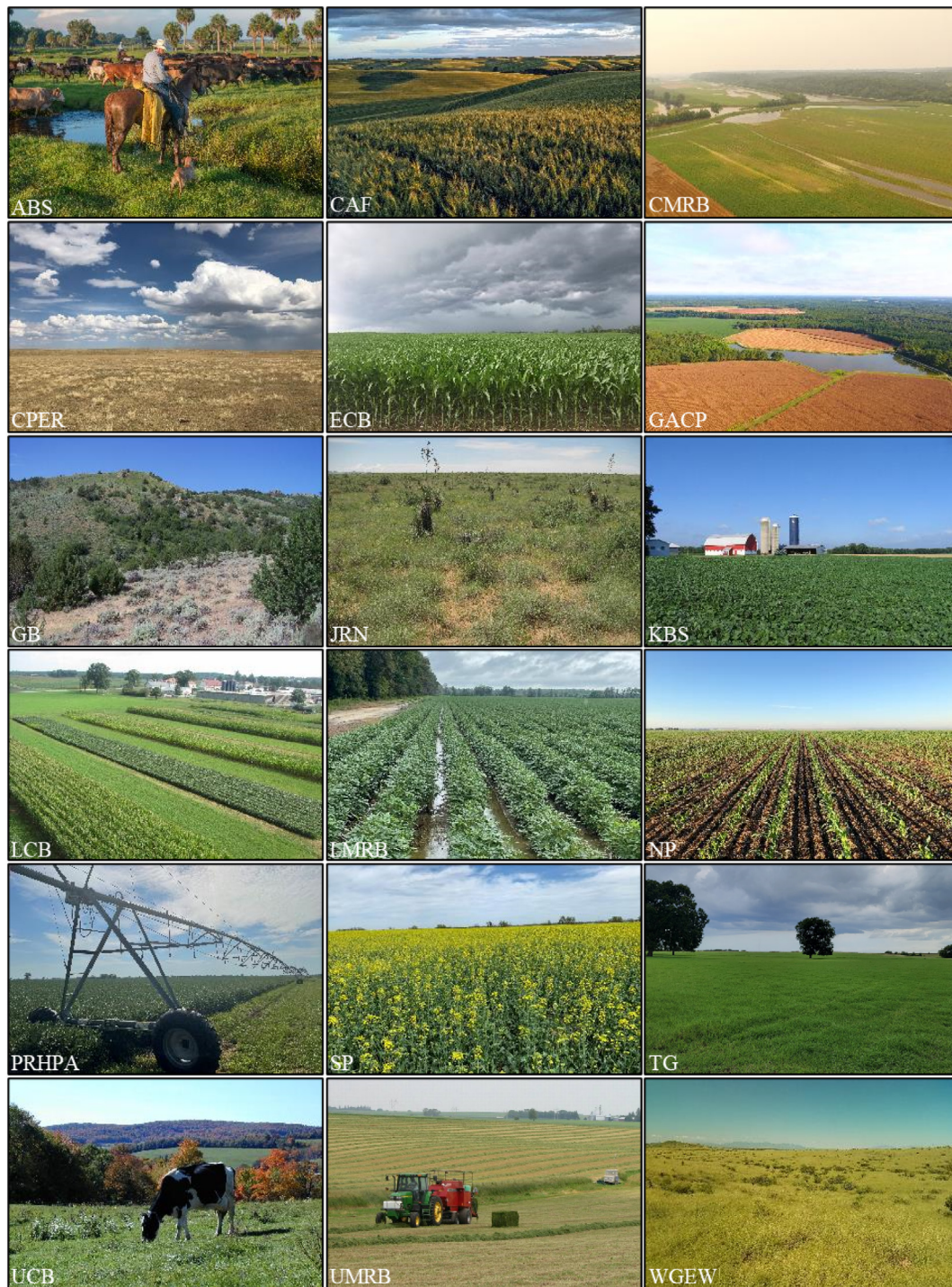


Fig. 1. Diversity of agroecosystem landscapes (croplands, pastures, and rangelands) represented by 18 sites of the Long-Term Agroecosystem research network (LTAR) in the United States. Research sites include: subtropical rangelands at Archbold Biological Station (ABS) in Florida (Photo credit: Carlton Ward); Wheat cropland at the R.J. Cook Agronomy Farm (CAF) in Washington (Photo Credit: Bryan Carlson); Mixed croplands at the Central Mississippi River Basin (CMRB) research station in Missouri (Photo credit: Curtis Ransom); Shortgrass steppe rangeland at the Central Plains Experimental Range (CPER) in Colorado; Corn cropland at the Eastern Corn Belt (ECB) research station in Ohio (Photo Credit: Kathryn Rumora); High elevation rangeland at the Great Basin (GB) research station in Idaho; Coastal Plain cropland at the Georgia Atlantic Coastal Plain (GACP) research station in Georgia (Photo credit: USDA-ARS); Chihuahuan desert rangeland at the Jornada Experimental Range (JRN) in New Mexico (Photo Credit: John Anderson); Soybean cropland and farmstead near Kellogg Biological Station (KBS) in Michigan (Photo Credit: Phil Robertson); Corn-Soybean-Alfalfa mixed cropland at the Lower Chesapeake Bay (LCB) research station in Maryland (Photo Credit: Michel Cavigelli); Soybean cropland at the Lower Mississippi River Basin (LMRB) research station in Mississippi (Photo Credit: Mark Griffith); Corn cropland at the Northern Plains (NP) research station in North Dakota (Photo Credit: Mark Liebig); Irrigated cropland at the Platte River/High Plains Aquifer (PRHPA) research station in Nebraska; Canola cropland at the Southern Plains (SP) research station in Oklahoma; Planted pasture near the Texas Gulf (TG) research station in Texas (Photo credit: Chad Hajda); Dairy farm near the Upper Chesapeake Bay (UCB) research station in New York (Photo Credit: Sarah Goslee); Haying alfalfa cropland near the Upper Mississippi River Basin (UMRB) research station in Wisconsin (Photo credit: Randy Mentz); Desert rangeland at the Walnut Gulch Experimental Watershed (WGEW) in Arizona (Photo credit: Russell Scott).

(Mitscherlich, 1909). These concepts continue to influence thinking about agroecosystems, particularly those where management can control the inputs of limiting resources such as irrigation and fertilizers. Water use efficiency (WUE) is an operationalized concept for resource use efficiency (as defined above) and is a common metric used to assess ratio of plant production to water consumed (Eq. (1); Sinclair et al., 1984; Howell, 2001; Morison et al., 2008; Tang et al., 2014).

Water use efficiency (WUE) : the amount of biomass produced per unit water.
$$WUE = \frac{\text{Production variable}}{\text{Water variable}} \quad (1)$$

Despite the simplicity of the WUE definition, there are many indicators of WUE in agricultural production settings ranging from plant breeding to irrigation to basin-scale water resource management (Hsiao et al., 2007; Howell, 2001). Hence, WUE indicators vary widely in spatiotemporal scales and measurement variables (Table 1; Fig. 2). The ratio of crop yield or carbon uptake to water consumed or used are common indicators of WUE, which are assessed over spatial scales ranging from the leaf to the globe and at time scales from seconds to years (Morison et al., 2008). The hydrological variables in the denominators of WUE calculations can also vary widely: from precipitation to irrigation to water used through evapotranspiration (ET), transpiration (T), and soil water depletion (Howell, 2001). At small spatial scales, WUE can be measured at the plant physiological-level using leaf gas-exchange to calculate the ratio of photosynthesis to stomatal conductance (i.e., intrinsic WUE) or at the ecosystem-level with eddy covariance to calculate the ratio of gross primary production (GPP) or net ecosystem production (NEP) to ET (i.e., ecosystem WUE; Table 1; Fig. 2). WUE is also assessed at the landscape to global scale through remote sensing, assessing variability in production via spectral indices (e.g., normalized difference vegetation index, NDVI) and modeled data products (e.g., NPP or GPP estimates; Wagle et al., 2016a, 2016b; Jiao et al., 2021). However, these common WUE indicators are broadly plant-centric, and can miss key elements of agriculture (e.g., livestock production). Moreover, many WUE indicators are limited to the farm or ranch scale. There are other indicators of water use for productivity in agroecosystems that do not fit classical definitions of WUE but have important implications for understanding the relationships between agricultural production and water across the supply chain, such as water footprints (Mekonnen and Hoekstra, 2011), water productivity (Molden et al., 2010), and life cycle assessments (Guinee et al., 2011; Fig. 2).

The goals of this review are to evaluate the measurement, estimation, interpretation, complexity, and limitations of the many indicators of WUE in agricultural production and assess the tradeoffs of their use when applying them across diverse agroecosystems in a changing climate. We discuss the use and limitations of WUE indicators within the scales pertinent to plant physiology, biomass and yield production, ecosystem fluxes, landscape-to-global scales, and agricultural supply chains. We then describe how to interpret and apply these multi-scalar indicators within and across diverse agroecosystems that vary in climate, production system, and

management practices. Finally, we evaluate the potential utility and efficacy of using WUE indicators for adapting agriculture to a changing climate amidst rising food demands and declining water resources in many regions of the world.

2. Indicators of water use efficiency

2.1. Hydrological variables – the denominators of WUE

As the denominator in WUE calculations, hydrological variables can span multiple WUE indicators and are used to quantify agricultural water use relative to a selected variable of agroecosystem productivity. These hydrological variables range in spatial scale from the leaf (e.g., stomatal conductance, T), to the field (e.g., precipitation, irrigation, ET), to the globe (e.g., gridded precipitation), and across the supply chain (e.g., water footprint; Table 1; Tang et al., 2014). Hydrological variables can be differentiated into two types of water use – consumptive and non-consumptive. Consumptive water use is defined as water that is utilized through ET, incorporated into products or crops, consumed by livestock, or otherwise removed from an immediate water environment (e.g., surface or groundwater; Falkenmark and Lannerstad, 2005). For agroecosystems, consumptive water use is often the denominator of the WUE calculation and includes variables such as ET, T, and stomatal conductance, and is also used in calculations of water footprints, water productivity, and life cycle assessments (Table 1; Pfister and Bayer, 2014). Any remaining water goes to non-consumptive use such as recharging aquifers and or supplying water to freshwater and coastal ecosystems (Falkenmark and Lannerstad, 2005). There are also hydrological variables used in calculating WUE that simply measure the input of water into the agroecosystem (e.g., precipitation and irrigation) and do not differentiate between consumptive and non-consumptive water use.

Selecting an appropriate hydrological variable to assess WUE is influenced by the scope of the research question as well as the scale of the productivity variable. For example, stomatal conductance, as well as leaf-level and whole-plant T are commonly used to calculate WUE at the plant physiological scale. At the field scale, ET is a common variable for estimating crop water consumption more directly than precipitation. Furthermore, WUE estimates of different crops or production systems should ideally be made with hydrological variables that are measured in consistent and comparable methods. Selecting a hydrological variable for WUE can also be influenced by data availability and uncertainty. For instance, precipitation is a widely measured hydrological variable, with high spatial and temporal instrumentation coverage globally, and commonly is commonly used in WUE calculations (Fick and Hijmans, 2017). Other hydrological variables, such as ET, are more limited in spatiotemporal coverage and are associated with higher uncertainty than precipitation (Nouri et al., 2013; Ochoa-Sanchez et al., 2019). However, ET estimates from merged measurements, satellite data, and models are becoming increasingly available (Mu et al., 2007; Melton et al., 2021; Anderson et al., 2021).

2.2. Physiological WUE indicators

Researchers calculate WUE at the plant physiological-level to connect agroecosystem water budgets and WUE with basic physiological plant traits associated with carbon assimilation and water loss. This approach provides a powerful tool to understand the role that plant physiological traits play in agroecosystem WUE. At the leaf-level, intrinsic water use efficiency (WUE_i) is calculated as the rate of net CO_2 assimilation per stomatal conductance (A_{net}/g_s), and instantaneous water use efficiency (WUE_{leaf}) is the rate of net CO_2 assimilation per transpiration rate (A_{net}/T). Leaf gas exchange is generally measured with portable infrared gas analyzers attached to a leaf cuvette. Plant leaves are enclosed in the leaf cuvette and changes in carbon dioxide and water concentrations are measured as a function of time. C_3 , C_4 , and CAM photosynthetic pathways have inherent differences in WUE because of differing photosynthetic biochemistries and stomatal regulation (Hatfield and Dold, 2019). For example, C_4 plants have naturally higher

Table 1
Examples of water use efficiency variables in agroecosystems across various scales.

Scale	Production variable (numerator)	Water variable (denominator)
Physiological	- Net photosynthesis	- Stomatal conductance
	- Carbohydrate production	- Transpiration
Biomass	- Forage	- Precipitation
	- Grain yield/harvest index	- Irrigation
	- Aboveground biomass	- Evapotranspiration
Ecosystem	- Net ecosystem production	- Precipitation
	- Gross primary production	- Evapotranspiration
Landscape/region	- Normalized difference vegetation index	- Gridded precipitation
		- Modeled evapotranspiration
Supply chain	- Water productivity	- Water footprint

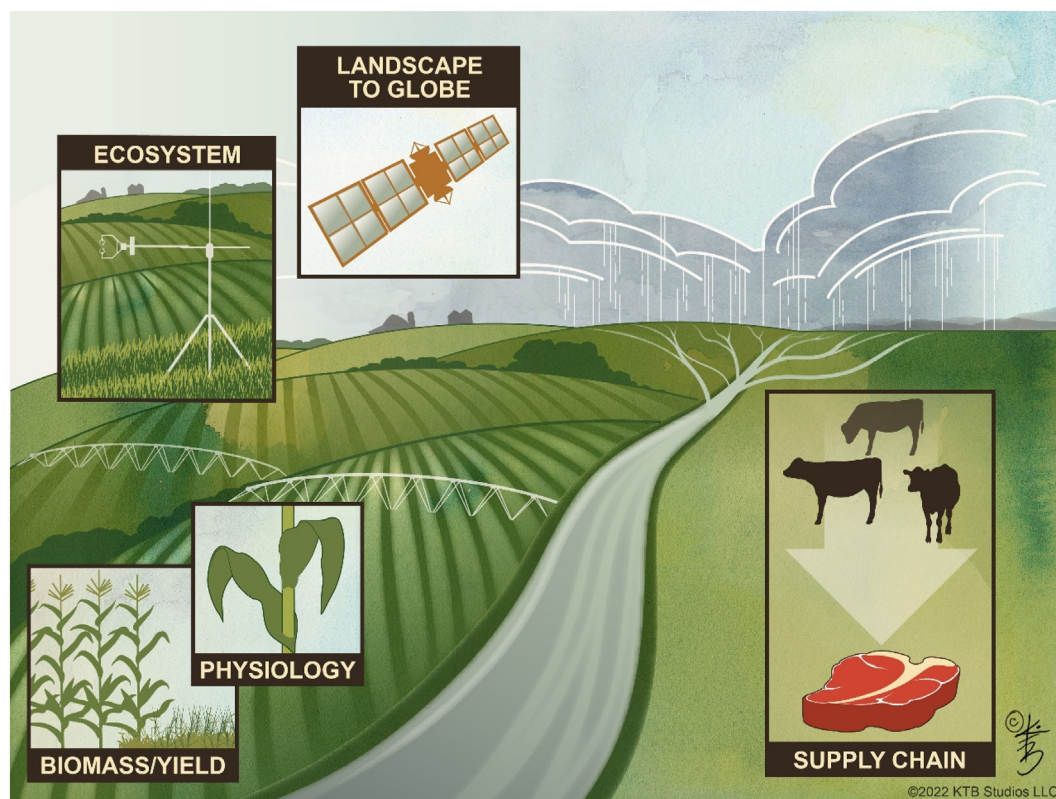


Fig. 2. Agroecosystem water use efficiency indicators across multiple spatial scales, climate, production systems, and management practices.

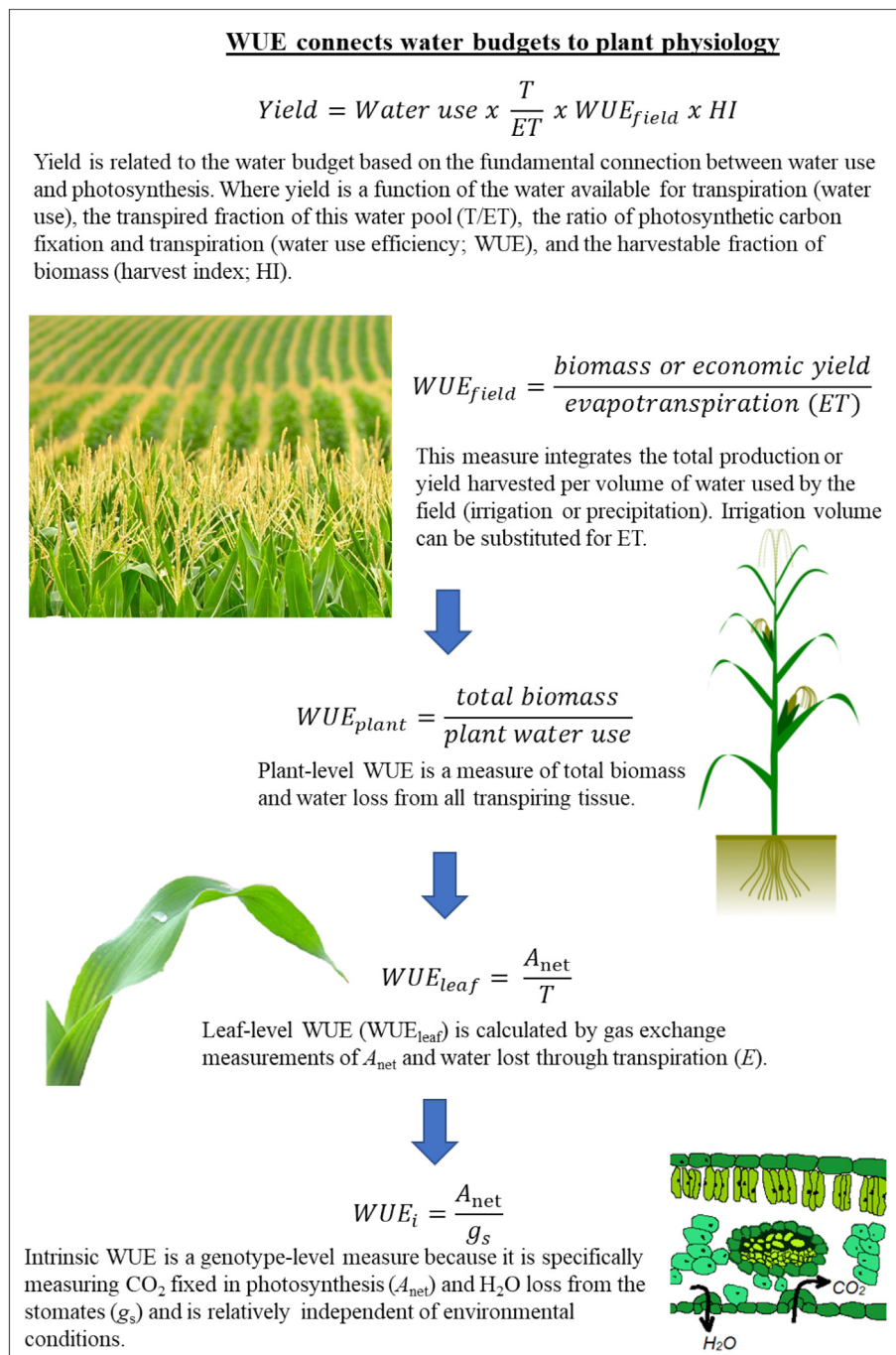
WUE than C_3 plants because their CO_2 concentrating mechanism increases CO_2 around Rubisco in the bundle sheath cells, so that lower g_s (and water loss) can provide sufficient CO_2 for photosynthesis.

Whole-plant WUE is the relationship between plant biomass and total water use and is a function of photosynthetic carbon assimilation, transpiration, and assimilated carbon losses such as respiration. Variability in whole plant WUE results from differences in genotypes, photosynthetic pathway, plant functional types (e.g., grasses versus shrubs), resource availability, and drought response mechanisms (Morison and Gifford, 1984; Eamus, 1991; Araus et al., 2002; Nelson et al., 2004). Lastly, foliar discrimination against the ^{13}C isotope ($\Delta^{13}C$) varies with photosynthetic pathway (Farquhar, 1989) and is correlated with whole plant WUE among genotypes within a species (Hubick et al., 1986; Condon et al., 2004; Ellsworth and Cousins, 2016; Feldman et al., 2018; Ellsworth et al., 2020).

A major focus in plant physiology-based WUE is scaling from basic metabolism and photosynthesis to whole-plant and field scales to identify ecosystem-level implications of plant response to the environment. Scaling basic metabolism and photosynthesis through the leaf and plant levels to the agroecosystem scale requires understanding the physiological factors that influence WUE at each level and how they are mechanistically linked (Box 1). WUE can be derived from models of CO_2 assimilation and stomatal conductance such as the Ball-Berry model and its derivations (Ball et al., 1987; Farquhar, 1980). Scaling from the leaf to the entire canopy has been accomplished in the 'big leaf model' and the 'two-leaf model' by conducting leaf-level modeling of photosynthesis and water loss on a hypothetical leaf equal in size to the entire canopy leaf area, which can be divided into sun and shade components (de Pury and Farquhar, 1997; Wu et al., 2018). Currently, more complex 3-D models of leaf canopy architecture are being developed to better predict canopy photosynthesis and transpiration (Chang et al., 2019; Song et al., 2013). Scaling from the leaf to the whole plant can improve the mechanistic understanding of the role of photosynthetic and transpiration parameters on whole plant WUE. For example, plant breeding and crop management can benefit from a better understanding of how leaf physiology affects whole plant traits in testing

varieties across scales (Wu et al., 2016). Plant responses to global change drivers, such as increased CO_2 , temperature, and drought have been a large research focus and can be more effectively understood by scaling between plant and agroecosystem levels. For example, measurements of WUE of invasive species, plant growth responses to grazing, experimental manipulations such as Free Air CO_2 Enrichment (FACE) projects, rainfall manipulations, and common garden experiments have shed light on the physiological factors that contribute to rangeland agroecosystem WUE (Ainsworth and Long, 2005; Nippert et al., 2009; Ashbacher and Cleland, 2015; Mata-Gonzalez et al., 2021; Doescher et al., 1997; Caldwell et al., 1981; Zhang et al., 2020).

There are several challenges to assessing physiological WUE across scales. First, physiological WUE is a complex trait with multiple components, with each component trait only having a small effect on WUE (Leakey et al., 2019). Improving physiological WUE requires better defining each component trait and its influence on WUE and developing phenotyping platforms to rapidly measure these traits. Genetic mapping has led to improved understanding of their genetic architecture, and multiple genes driving WUE have been discovered (Feldman et al., 2018; Ellsworth et al., 2020; Masle et al., 2005; Karaba et al., 2007). The second challenge is that measurement and instrumentation limitations reduce the ability to identify, define, and measure the component traits of WUE. For example, leaf-level gas exchange provides very accurate snapshots of WUE but vary along a leaf blade and among leaves based on their location within the canopy, age, nutrient status, and time of day. Consequently, gas exchange-based measures of WUE do not reflect the diurnal cycle of WUE or the mean WUE for the entire canopy or over the life of the plant or production cycle (Medrano et al., 2015). Often single measurements of leaf WUE do not agree with measures of whole plant WUE, which include non-leaf carbon and water losses not included in leaf WUE (Medrano et al., 2015). Whole plant WUE is most commonly measured using a lysimeter approach that provides accurate measures of water loss. Carbon gain measurements through time can be done using imaging, but accuracy is limited by the ability to identify and measure all plant-associated pixels



Box 1. Water use efficiency from the plant to the field. Modified from Current Opinion in Plant Biology (Ellsworth and Cousins, 2016) with permission from Elsevier.

and the robustness of the pixel to biomass relationship, while direct and mostly destructive sampling can give accurate measurements of carbon gain/biomass but are limited to a single time point per plant (Gehan et al., 2017; Feldman et al., 2018). Chamber-based studies allow gas exchange of a whole plant to be measured continuously, and they may provide the ability to better understand the relationship between individual leaves and whole plant WUE (Perez-Priego, 2021; Pieters et al., 2022). Chamber-based methods to monitor gas exchange and belowground processes such as root respiration have limitations due to chamber size because larger chambers are more difficult to construct and chamber effects on gas exchange measurements can require corrections, but progress is being made to improve their effectiveness (Patono et al., 2022; Pérez-Priego et al., 2015; Pieters et al., 2022). Lysimeter and chamber-based studies

provide precise measurements and can be informative, but nonetheless they are an artificial situation that presents challenges to translating the results to the field scale. In contrast, in situ measurements of whole plant WUE can remove the artificiality of the pot studies, but they are seldom made because accounting for all pathways of carbon gain and water loss is challenging. Sap flow technique can be used to measure water loss but calculating plant mass is difficult, especially when including belowground biomass or multiple time points in the growth of an individual plant. As in lysimeter studies, biomass production can be calculated from image analysis, allometry, or destructive harvesting. Theoretically, the physiological relationship of WUE varies across scales. However, measurement and instrumentation limitations restrict the ability to empirically validate these physiological models beyond the sub-leaf and leaf levels, further

restricting model refinement. Nonetheless, technological and scientific advancements are quickly overcoming these challenges such that many indicators will soon be measured or estimated more accurately.

2.3. Biomass/grain yield WUE

WUE in agricultural production is often measured in terms of above-ground biomass or grain yield, per unit water input or water consumed. Unlike plant physiological WUE at the leaf-level, which presents snapshots in time (seconds to minutes), biomass/grain yield WUE integrates plant responses over longer time scales (e.g., a growing season) and are often reported frequently in long-term site records (Yost et al., 2016, 2017). These WUE indicators serve as key variables to assess agricultural production from both food production and economic perspectives and can be useful when comparing similar variables (e.g., grain yield to grain yield) and can encompass different spatial (e.g., plots, fields, and small watersheds) and temporal (e.g., seasonal to annual) scales (Yost et al., 2019).

In rangeland systems, biomass is usually quantified as the annual above-ground net primary production (ANPP), with seasonal or annual precipitation input as a common hydrological variable (e.g., rain/precipitation use efficiency; Huxman et al., 2004). In rangelands with herbivores (native or livestock), it can be challenging to fully account for net carbon flows or ANPP as a portion of the plant growth is consumed by grazing animals. For croplands, the productivity component is the marketable portion of the plant: grain yield for cereal grain crops, vegetable or fruit yield (which may be the belowground fraction, e.g., tubers), and aboveground biomass for hay and bioenergy crops. WUE is calculated based on the relevant time scale for the water utilized by that crop, thus time scale may be a growing season, or even multiple years when considering crop rotations or cropping systems.

While measurements such as grain yield or ANPP are useful when comparing WUE between similar agricultural production variables, it can be

challenging when making such comparisons across different agroecosystems and plant measurement variables. Long-term cropland data in Eastern Nebraska (2000–2014) show how WUE can vary through time, and how variability is influenced by crop type (maize vs switchgrass), plant fraction (ANPP vs grain yield), and management (fertilizer rate; Fig. 3). Direct comparisons of the effect of management or climate on WUE are best made with consistent measurements, such as between crop type but within plant fraction or between plant fractions, but within crop type. For example, switchgrass is more sensitive to increased nitrogen than maize, when examining responses of WUE and variability of the ANPP plant fraction (Fig. 3). Furthermore, production-based WUE estimated from only the aboveground biomass does not account for the energy requirements of certain grains (starch-based versus protein-based) and the allocation of carbon to belowground biomass. Such information is important when comparing potential ecosystem services of different crops or production systems.

Another challenge in calculating biomass/grain yield WUE is the inclusion of non-cash crops, such as cover crops, as these affect consumptive water use and storage (Unger and Vigil, 1998), but can have additional ecosystem service benefits (Haruna et al., 2018). In addition, fallow periods must be accounted for in rainfed areas that utilize fallow periods to leave soil moisture for the cash crop. For example, Jones and Popham (1997) calculated efficiency across different temporal scales by dividing grain yield by harvest-to-harvest available water. Under this approach, grain sorghum WUE was greater for a continuous sorghum system compared to sorghum in a wheat-sorghum-fallow system (12 months versus 16 months, respectively).

2.4. Ecosystem WUE indicators

WUE at the patch or ecosystem scale reflects the amount of water and carbon transferred between the land surface to the atmosphere and is

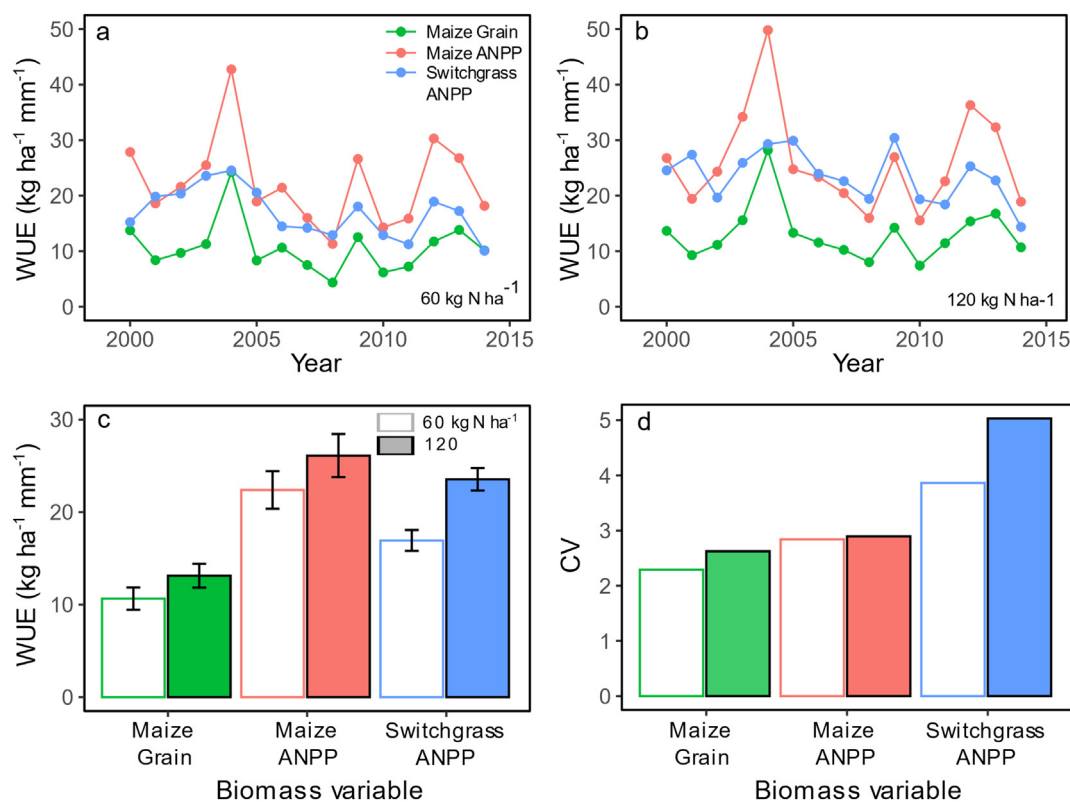


Fig. 3. Biomass/Grain Yield WUE. Water use efficiency (WUE) for maize and switchgrass was calculated using grain yield (Grain) or aboveground net primary production (ANPP) for the production variable and growing season precipitation (April–September) as the water variable (e.g., $WUE = ANPP/growing\ season\ precipitation$). Research was conducted in Eastern Nebraska (2000–2014) under different nitrogen (N) fertilizer rates (60 and 120 kg N ha⁻¹). (a, b) WUE over time for each biomass variable at two different N fertilizer rates. (c) Mean WUE by biomass variable and fertilizer rate, with standard error bars. (d) Coefficient of variation (CV) by biomass variable and fertilizer rate. Data available at <https://agros-usdaars.opendata.arcgis.com/pages/reap>.

commonly measured using micrometeorological approaches beginning first with Bowen ratio instrumentation (Sinclair et al., 1975) and now, more commonly, using the eddy covariance technique (Baldocchi, 2003; Burba, 2019). Eddy covariance can provide nearly continuous (e.g., 30-minute intervals) measurements of both loss of water (ET) and the net carbon dioxide exchange (i.e., NEP) at a patch scale of $\sim 10^4\text{--}10^6\text{ m}^2$. This extent is typically called the ecosystem scale because of the multiple biophysical components within it (e.g., soils, different flora and fauna; Baldocchi, 2003). One major advantage of using eddy covariance measurements to evaluate WUE is the ability to determine near instantaneous WUE for every half-hour to quantify diurnal cycles of WUE. Characterizing high-frequency response to weather variations is important for understanding how agroecosystems are impacted by changing climate. Continuous eddy covariance measurements can also be integrated to determine ecosystem WUE over various time periods (i.e., from hourly to annually). Long-term and continuous eddy covariance measurements offer valuable and directly comparable datasets to evaluate ecosystem WUE across production systems, regions of the globe, and gradients in soils, climate, land use, management, and disturbance (Pastorello et al., 2020). Eddy covariance measurements provide information on the effects of environmental drivers and management practices on WUE (Chi et al., 2017) and can provide ground validation for remote sensing assessments (Lu et al., 2017).

Eddy covariance-measured NEP can be partitioned into GPP and ecosystem respiration (ER) with relatively well-constrained uncertainties (Lasslop et al., 2010). As a result, eddy covariance measurements make it possible to determine WUE at the ecosystem scale as the ratio of GPP to ET (Hu et al., 2008; Law et al., 2002; Wagle et al., 2016b) and/or the ratio of NEP to ET (Emmerich, 2007; Monson et al., 2010; Wagle et al., 2016a, 2016b; Biederman et al., 2016), representing either net or gross carbon uptake, respectively. In addition, slopes of the regression of carbon gain (NEP or GPP) vs. water loss (ET or T) can be used to determine WUE at different temporal scales (i.e., hourly, daily, monthly, seasonally, or annually; Emmerich, 2007; Kuglitsch et al., 2008; Law et al., 2002; Wagle et al., 2016a). Stomatal regulation, which is a function of vapor pressure deficit (VPD), regulates carbon assimilation and T (Jarvis and McNaughton, 1986). As a result, intrinsic WUE (WUE_i) can be calculated as carbon assimilation (GPP)/stomatal conductance (G_c) (Schulze and Hall, 1982) or inherent WUE (IWUE) by multiplying WUE (GPP/ET) by mean daylight VPD (GPP \times VPD/ET) (Beer et al., 2007; Law et al., 2002). Due to their dependence on environmental conditions, these WUE metrics are more directly comparable to physiological-scale WUE determined by the ratio of leaf assimilation to stomatal conductance (e.g., Medlyn et al., 2017). Using WUE_i and IWUE metrics can be more appropriate than WUE for assessing the adaptive adjustment of ecosystem physiology to environmental conditions (Beer et al., 2007).

There are several challenges regarding the use of eddy covariance for WUE. First, ecosystem-level carbon uptake (NEP or GPP) and water loss (ET or T) measured by or derived from eddy covariance assesses only the land area contributing to the measured fluxes, ranging from less than a hundred meters to several kilometers depending on several factors (e.g., tower height, weather conditions, and canopy characteristics). Secondly, high equipment costs, complex logistical requirements, and difficulty of interpreting fluxes in complex heterogeneous landscapes limit the coverage directly achievable with eddy covariance. Finally, NEP and ET measurements from eddy covariance systems represent integrated, above-canopy fluxes, which are not direct measures of the canopy functional fluxes of GPP and T. Instead, NEP and ET are confounded by ER and evaporation (E), respectively. Biophysical processes occurring in plants and soils can more greatly influence NEP than GPP, as NEP is a more complicated process involving both plants and microbial communities. As a result, GPP and ET generally show a higher correlation than do NEP and ET (Biederman et al., 2016). In practice, ET is often considered equivalent to T for select measurement periods, with the common practice being to filter out several days with and after rainfall so that E may be assumed to be negligible. This allows one to determine T-based WUE at the ecosystem scale without direct measurement of T. However, this assumption seems

inadequate, as non-negligible E can continue over a week or more following rainfall events (Moran et al., 2009), and daily E can account for 15–20 % of daily ET even during peak growths in dry periods (Wagle et al., 2021). Thus, the assumption of negligible E results in overestimates of vegetation water requirement and lower WUE (Wu et al., 2015). Estimations of WUE based on T rather than ET (Gong et al., 2017; Hu et al., 2008) can account for variable amounts of E and improve WUE estimates (Scott et al., 2021; Wagle et al., 2021). Even though GPP and T are not directly measured by eddy covariance systems, calculating WUE using partitioned GPP and T can provide meaningful ecosystem WUE for cross-site comparisons (Nelson et al., 2020; Wagle et al., 2021).

2.5. Landscape-to-global scale WUE indicators

Researchers, land managers, and decision-makers require reliable WUE estimates at the landscape, regional, national, and global scales, yet many measurements of WUE (e.g., physiological, grain yield, eddy covariance) are measured at much smaller scales and often do not capture the inherent variability present at broader scales. Satellite-based remote sensing (e.g., Landsat, Sentinel, and MODIS) is available globally at various spatial and temporal resolutions, allowing mechanistic linking of smaller-scale WUE indicators to broader spatial extents (Cai et al., 2021). For example, satellite remote sensing has been proposed as a low-cost and scalable solution to fill widespread gaps in monitoring of irrigation water use in both developed and developing countries, bypassing the technical, socioeconomic, and political challenges that to date have constrained in-situ monitoring (Foster et al., 2020). In an assessment of global WUE estimated from satellite remote sensing, Sun et al. (2016) indicated that different mechanisms govern response of WUE to increasing precipitation, highlighting the importance of scale-dependent interactions. Remote sensing is also used to assess impacts of drought across national (Ahmadi et al., 2019), continental (Funk et al., 2019), and global (Yu et al., 2017; Huang et al., 2017) scales.

The numerator, or production variables used in calculating remote sensing-based WUE, can be direct measures of spectral reflectance, often expressed as vegetation indices related to photosynthetic activity (e.g., NDVI; enhanced vegetation index - EVI), or an indirectly estimated variable derived from empirical relationships between spectral reflectance and ground measurements, process-based models (e.g., light-use efficiency; modeled NEP from the Soil Moisture Active Passive mission: Jones et al., 2017), or a combination of direct and indirect measures. For example, the MODIS GPP product uses a light-use efficiency model parameterized with a fraction of photosynthetically active radiation (or FPAR) and land cover derived from spectral reflectance (Heinsch et al., 2003). In addition, thermal infrared remote sensing (TIR) can effectively augment Landsat TIR retrievals that serve to improve models to estimate ET (Anderson et al., 2021). Biotic variables represent land surface conditions at a single point in time (e.g., NDVI, EVI, SIF) or conditions accumulated over a period of time (e.g., annual GPP or NPP, annual integrated-NDVI).

The denominator in remote sensing-based WUE estimates can include gridded precipitation, vapor pressure deficit, ET or T, soil moisture, or irrigation. Generally, remote sensing-based estimates of the denominator for WUE are derived from process-based models (e.g., MODIS ET product, Mu et al., 2007; SMAP product, Chan et al., 2018; Colliander et al., 2017) or use interpolation from weather station networks, resulting in varying uncertainty depending on terrain complexity and the distance of the grid cell to the nearest weather station. While soil moisture can be estimated directly from active (e.g., RADAR) or passive spectral reflectance, developing direct relationships is hindered by interactions between soil and vegetation reflectance and high spatial heterogeneity (both laterally and with depth) as compared to the resolution of available measurements (e.g., SMAP; Mohanty et al., 2017).

Despite the many benefits of continuously monitored indicators of WUE in space and time, remote sensing-based WUE has several limitations. The utility, application, and performance of all remotely sensed data products are influenced by many factors (e.g., source, method, ground resolved

distance or cell grain size, and revisit frequency; Wu and Li, 2009). Simplified algorithms and parameter estimates lead to uncertainties in remote-sensed estimates of biomass, GPP, and ET (Cai et al., 2021). Since the hydrological variable (i.e., the denominator) is typically derived from process-based models or interpolation, it is often challenging to obtain highly resolved estimates with low uncertainty. Additionally, commonly used spectral reflectance measures (i.e., greenness) indicate photosynthetic capacity rather than actual photosynthesis, highlighting the need to improve direct measures of physiological function such as solar-induced fluorescence (SIF; Smith et al., 2019; Wang et al., 2022).

Several emerging opportunities exist or are planned with the potential for downscaling remote sensing observations and model estimates. New sensor constellations (e.g., Planet) and data fusion techniques (e.g., Spatial and Temporal Adaptive Reflectance Fusion Model; Gao et al., 2006; and the Harmonized Landsat-Sentinel dataset by NASA; Claverie et al., 2018) are now providing daily and near-real time remote sensing at relatively fine spatial resolution (1–30 m). Emerging satellite observations (e.g., ECOSTRESS, OCO-3), and future satellite missions (e.g., GeoCarb, TEMPO, Sentinel-4) are expected to provide enhanced opportunities for characterizing and understanding how GPP, ET, and WUE vary over the course of the day in response to temperature, water stress, and management practices (Xiao et al., 2021). In addition, innovative measurements, such as SIF, along with robust methods for data integration with OCO-3 for monitoring drought stress using neural networks (e.g., Zhang et al., 2018; Li et al., 2020) are expected to overcome current challenges with the temporal and spatial resolution for quantifying indicators of water status and use.

2.6. Water use indicators across supply chains

Indicators of WUE in agroecosystems discussed thus far are calculated on small (e.g., leaf, field) or large scales (e.g., basin, globe) and are generally plant-centric, focusing on carbon uptake or plant production related variables (e.g., photosynthesis, grain yield, biomass). However, bringing an agricultural product from the field to the dinner plate involves a large, complex commodity chain, utilizing multiple water resources, and increasing the total water use of a given product. Here, we highlight three approaches that can provide a more holistic assessment of water use across the supply chain: water footprints (Hoekstra et al., 2011), water productivity (Molden et al., 2010), and life cycle assessments (LCA, Eq. (2); Guinee et al., 2011; Fig. 2). These approaches allow producers, consumers, and resource managers to assess both the economic and environmental tradeoffs of entire production systems.

Water Footprint : the total volume of freshwater used to produce a product, measured over the full supply chain as water consumed (blue and greenwater) and/or polluted (grey water; Hoekstra et al., 2011).

Water Productivity : the ratio of net benefits from agricultural systems (e.g., biomass, crop yields, revenue) to the amount of water used to produce the benefits (Holden et al., 2010).

Life Cycle Assessment : assess the environmental impacts of a production system along the entire supply chain (Guinee et al., 2011).

(2)

A water footprint is a comprehensive indicator of freshwater resource appropriation for an individual person, product, commodity chain, river basin, nation, etc. Water footprints are one of several environmental assessment methods that help gauge the impact of human activity on natural resources (Pfister and Hellweg, 2009). The concept of a water footprint incorporates three aspects of water use: green water (precipitation stored in the root zone and consumed by plants), blue water (surface or groundwater resources that are evaporated or incorporated into a product), and grey water (the amount of fresh water required to assimilate pollutant loads to achieve existing ambient water quality standards; Mekonnen and Hoekstra, 2011). Water footprints can be utilized at global scales, for

specific local agricultural production, or for future trend scenarios (Lovarelli et al., 2016). The concept of virtual water trading also relies heavily on the water footprint method to assess the water use in exported or imported products (Hanasaki et al., 2010).

Water productivity is the closest of the supply chain-focused water use indicators to the standard definition of WUE because it calculates the ratio of net benefits of agriculture to water use (“physical water productivity”; Molden et al., 2010). However, another indicator, economic water productivity, is defined as the value derived per unit of water used, which can be increased by either reducing the costs or increasing the value generated by water use (Molden et al., 2010). For example, economic yields can be increased by breeding plants with a higher harvest index (e.g., the weight of the harvested product as a percentage of total plant weight), which can produce more revenue per unit of water consumed through transpiration. While economic productivity is frequently used to consider the profit generated per unit of water, it can also include non-market values (positive or negative) to generate a more holistic perspective. Such economic valuations of environmental uses are critical when determining tradeoffs and opportunity costs for water use.

Life cycle assessments are typically considered “cradle to grave” and product-focused, while water footprint analyses have a water management focus and define the boundaries based on the specific goal of the analysis (Boulay et al., 2013). Life cycle assessment is a comprehensive method that evaluates the environmental impacts of a product along the entire commodity chain from production to transportation, consumption, and disposal. Life cycle assessments generally consider land use impacts, material use, greenhouse gas emissions, and pollution production in addition to water use impacts (Guinee et al., 2011).

These three indicators are useful tools for evaluating the water used in bringing an agricultural product to market. A common limitation across these water use indicators is data availability at various scales. Information on water use may be available at time scales or resolutions much coarser than what is needed for a local impact study. Uncertainties will vary spatially based on the availability and quality of data. For example, detailed records of surface water withdrawals may exist in some states or countries, but not in others, which adds uncertainty to blue water estimations. These supply chain water use indicators also have methodological limitations. Life cycle assessments focus on the negative environmental impacts of a production process but do not incorporate the positive ecosystem services that a system may provide (van der Werf et al., 2020). Also, both indicators are based on production amount and not the nutritional quality of the food. The functional unit for life cycle assessments and water footprints is typically “kg” or mass, but there is a progress toward considering nutrient quality indexes in the LCA evaluation (Sonesson et al., 2019). To align different production systems for comparisons, it may be more effective to utilize a functional unit related to nutrition, such as the Nutrient Rich Foods index or an individual nutrient like protein, to be able to compare various commodities with drastically different production methods such as beans, beef, rice, and poultry (Drewnowski, 2010; Sabate et al., 2015).

3. Discussion

Increasing WUE or producing ‘more crop per drop’ of water has been a major goal of agriculture, reflected by the diversity of WUE indicators in agricultural production. Each indicator carries a set of costs and benefits, measures patterns and processes at a specific spatial and temporal scales, and informs certain aspects of management and production. Given that each WUE indicator has benefits and limitations, there is no ‘silver bullet’ WUE indicator to fully assess how agricultural practices and innovations impact water resources and productivity. Focusing on a single WUE indicator in complex agricultural systems may be misleading and fail to consider additional water consumed or costs involved in production (Giordano et al., 2021). Furthermore, optimizing a single WUE indicator (e.g., leaf-level WUE) over other indicators may have unintended impacts at different spatial scales or other resources and production goals.

Selecting a WUE indicator or set of indicators depends on the research question, agricultural practice, innovation, or policy at hand. For example, biomass-based WUE indicators (e.g., grain yield per mm of rainfall) can be used to evaluate how a given management practice (e.g., N fertilization) influences the relationship of agricultural productivity (e.g., grain yield) to variability in precipitation. Moreover, ecosystem-level indicators of WUE are often used to evaluate how innovation in agriculture (e.g., adaptive livestock management) can influence environmental sustainability (e.g., net ecosystem carbon balance; Spiegel et al., 2022). Looking more broadly across the supply chain, WUE indicators can also be employed in LCAs that quantify the water used in bringing an agricultural product to the consumer (Guinee et al., 2011). Importantly, WUE indicators can inform economic analyses that assess the costs and benefits of alternate water use management choices, across multiple scales and diverse agroecosystems. In this light, standardization and communication about WUE indicators is critical for sustainability outcomes in agroecosystems at multiple scales.

3.1. WUE indicators – spanning scales

WUE indicators in agricultural production span a wide range of spatio-temporal scales and measurement types (Table 1; Fig. 2). Combining multiple spatial scales can improve our mechanistic understanding of how management or climate change influences the relationship between water use and productivity. For example, leaf-level plant WUE indicators, such as intrinsic WUE, can evaluate how elevated CO₂ may increase the rate of CO₂ assimilation per unit of water transpired (Leakey et al., 2019). However, scaling the leaf-level impact of rising CO₂ on WUE to grain yield will improve mechanistic understanding of the costs and benefits of rising CO₂ for food production (Box 1). Combining physiological measurements with both ecosystem and biomass indicators can provide an improved mechanistic understanding of leaf- to ecosystem-level dynamics of water and carbon.

Utilizing WUE indicators from several spatial scales can fill gaps and identify how management and innovation ultimately affect WUE from farm to table. There remain several challenges to achieving this holistic understanding of agricultural water use and productivity dynamics. For example, ground-based measurements of agricultural production (e.g., grain yield or eddy covariance), are limited in spatial extent, often stopping at the farm or ranch gate. As a result, both production and water use measures may fail to capture the impacts of environmental heterogeneity and diverse management practices that occur across farms or regions. This challenge can be overcome by filling such spatial gaps with satellite remote sensing observations. A variety of remote sensing-based CO₂ and ET prediction methods and models have been developed and validated using eddy covariance data and used to estimate water and productivity at regional to global scales (Allen et al., 2007; Choudhury et al., 1994; Gillies et al., 1997; Glenn et al., 2007; Kustas and Norman, 1996; Monteith, 1972; Prince and Goward, 1995; Running et al., 2004; Wagle et al., 2017; Xiao et al., 2004). On the other hand, large-scale indicators often rely on simplified parameter estimates, which can be too coarse for local assessments and can benefit from ground-level indicators. For example, biomass measurements and eddy covariance towers can provide ‘ground truthing’ to inform remote sensing. Combining ground-based WUE indicators with broader-scale indicators such as eddy covariance and remote sensing measurements of ET can help capture such regional variability and improve estimates of WUE for production systems and over complete commodity life cycles.

To maximize the potential benefits of combining WUE indicators from multiple scales, several technical challenges must be recognized. First, uncertainty associated with measurements at different scales must be accounted for properly. Inaccuracies in estimates of ET, yield, and irrigation can propagate throughout the scaling process in a water footprint analysis, resulting in footprint values differing by 100 % for a single field (van der Laan et al., 2019). Second, indicators vary in their temporal sensitivities to environmental drivers across spatial scales – from seconds (e.g., leaf-level photosynthesis) to the entire growing season (e.g., grain yield). Finally, combining multiple indicators requires an assessment of the

correlations among different indicators of WUE. Indicators may be redundant (highly correlated), complementary (information gained when combined), or divergent (provide different signals to the same phenomena; Browning et al., 2021). Complementary indicators of WUE in productivity will provide the most improved holistic and mechanistic understanding of how management or climate change drivers influence the relationship between WUE and productivity, while divergent indicators may obscure such relationships.

3.2. WUE indicators – comparing agroecosystems

Agroecosystems span an incredibly diverse range of climatic and edaphic conditions due to advances in crop and livestock genetics, production technologies, and resource management strategies (Fig. 1). Across diverse environments (e.g., deserts to rainforests), resource efficiency can vary due to limitations in water, nutrients, light, and radiation (Hodapp et al., 2019). In water-limited agroecosystems, optimizing WUE may be the primary goal, while in water-excess systems, mineral nutrients may be the primary limiting resource and the focus of management (Cossani and Sadras, 2018). Cross-site comparisons of productivity can allow researchers to evaluate the efficiency of production at regional to national scales, identify generalizable relationships between water and production, and assess food security vulnerabilities and adaptations to climate change.

Given the diversity of agroecosystems, selecting an optimal WUE indicator or combination of indicators for comparing agroecosystems requires a common currency that indicates WUE at comparable spatial and temporal scales and is measured with consistent methods at a frequency that adequately captures environmental variability. Eddy covariance and remote sensing are examples of measurements with consistent methods and continuous data collection that allow for direct comparisons of agroecosystems and regional-level responses (e.g., Wagle et al., 2019, 2021). Additionally, such measurements are often limited to long-term research stations and specific to local questions. Coordinated research networks can aid with standardizing measurements for direct comparisons of diverse agriculture.

While there are options to compare environmental responses across agroecosystems, direct comparisons of food production-related indicators are more challenging. Biomass measurements (e.g., grain yield, ANPP) often vary by the production system, making comparisons across croplands and rangelands or different types of crops challenging (Fig. 3). Furthermore, higher WUE for one crop can mask the potentially higher water requirements in comparison to alternative crops in a region – a crucial factor in evaluating the environmental sustainability of water allocation to agriculture as well as regional crop choice. Evaluating the energy and nutritional density of foods in relation to water use along food production chains is an emerging option that produces a common currency (calories, protein, or nutritional density) across diverse agricultural products (Sonesson et al., 2017).

3.3. WUE indicators – adapting to climate change

Crop yields and livestock production have increased substantially since the 1960s to meet rising demands from a human population that grew in both size and affluence (Thornton, 2010; Southgate, 2009; Ritchie and Roser, 2013). Agricultural production will need to keep pace with continued growth in demand, yet climate change, declining freshwater resources, and urbanization may limit yield growth potential. There is evidence that current rates of yield increase for key crops (maize, rice, wheat, and soybeans) are far below what is needed to meet future demands (Ray et al., 2013). Temperature- and precipitation-related climate change drivers can affect food production through shifts in climate envelopes, seasonal changes, and increased extreme events (IPCC, 2021). Crop yield reductions have been observed in lower latitudes globally and are projected to decline further over the next century (Rosenzweig et al., 2014). Global mean NPP in rangelands is projected to decline by 2050, resulting in a 7–10 % decline in total livestock production and economic losses of \$9.7–12.6 billion (Boone et al., 2018).

Many of the direct and indirect effects of global change on agricultural production are related to impacts on water resources. Changes in precipitation amount and pattern, increased extreme events (e.g., droughts and deluges), and higher rates of evaporation will alter water inputs, storage, and loss, with direct effects on productivity (IPCC, 2021; Zhang et al., 2021). Irrigation has been an important tool for increasing crop yields but represents the single largest anthropogenic demand for freshwater, accounting for 70 % of global water withdrawals (Shiklomanov and Rodda, 2003). Declining freshwater availability, higher evaporative losses, and competition with urban and environmental water demand will make irrigation water management more challenging. For example, water availability in the western U.S. has declined due to reduced snowpack and snowmelt, increased droughts and floods, forest cover loss, and evaporative losses (Dettinger et al., 2015). In many water-limited regions of the globe, groundwater aquifers are the sole source of perennial freshwater, providing a buffer against water deficits, but are being depleted at unsustainable rates. Withdrawals from the Ogallala Aquifer in the U.S. Great Plains, which provides water to one-fifth of the total US agricultural harvest, are drastically outpacing recharge rates and threaten drinking and irrigation water supplies. In Kansas, 30 % of the groundwater from this aquifer has been removed with another 39 % projected to be withdrawn over the next 50 years. Given the recharge rates in this region, it would take 500–1300 years to completely refill the aquifer if depleted (Steward et al., 2013).

Water use in agricultural production will have to compete with growing demands of urbanization. By 2030, population growth is projected to increase urban water demand by 80 % (Amarasinghe and Smakhtin, 2014). This sets up potential urban-rural conflicts for water resources, particularly in regions where cities have priority for water over other sectors (Florke et al., 2018), and highlights the importance of examining opportunity costs of water uses. Assessing the relationship between water use and production across diverse agroecosystems and spatial scales is also essential to enhance resilience and adapt agriculture to climate change. Improving irrigation management and restoring soil structure and hydrological function can enable producers and managers to increase the resilience of water resources to climate variability and extremes. Crop and livestock breeding can select for genotypes that have higher resilience to climate variability and extremes. Indicators of WUE and production at the leaf, whole plant, and ecosystem levels can help assess how water stress affects water use along the soil-plant-atmosphere continuum. WUE indicators can also be used to track climate impacts to enable producers to adapt management to changing conditions on the farm and ranch. Water footprints can be developed from measured or modeled data, and therefore it is possible to evaluate the impact of projected climate scenarios on water use in agricultural production (Chen et al., 2021; Yesilkoy and Saylan, 2021).

4. Conclusions

Understanding the relationship between water and agricultural production within and across agroecosystems is critical for providing food, fuel, and fiber to a growing human population, while reducing environmental impacts and adapting to climate change. Increasing the efficiency of water use in the agricultural enterprise by producing ‘more crop per drop’, or higher WUE, has been a long-term goal of agricultural management, engineering, technological innovations, and crop breeding. However, each indicator of WUE in agricultural production has benefits and limitations, and therefore the key is to select an indicator or set of indicators that best address the scientific question, policy, agricultural management, or technological innovation. Optimizing a single WUE indicator (e.g., leaf-level WUE) over other indicators may have unintended impacts at different spatial scales or other resources and production goals. Traditional measurements of WUE are often plant-centric and limited in scale to the farm or ranch, and therefore may miss important water-related impacts at regional scales or across the food production system. Agriculture already has the highest demand for water globally and water resources are projected to become impacted by climate change and competition from other water

demands, such as urbanization. Indicators of WUE in agricultural production can help balance production demands with sustainability goals.

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Data availability

No data was used for the research described in the article.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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