HAL open science

Water use efficiency across scales: from genes to landscapes

Vincent Vadez, Raphael Pilloni, Alexandre Grondin, Amir Hajjarpoor, Hatem Belhouchette, Youssef Brouziyne, Ghani Chehbouni, Mohamed Hakim Kharrou, Rim Zitouna-Chebbi, Insaf Mekki, et al.

To cite this version:

Vincent Vadez, Raphael Pilloni, Alexandre Grondin, Amir Hajjarpoor, Hatem Belhouchette, et al.. Water use efficiency across scales: from genes to landscapes. Journal of Experimental Botany, 2023, 74 (16), pp.4770-4788. 10.1093/jxb/erad052 . hal-03993327v2

HAL Id: hal-03993327

https://hal.science/hal-03993327v2

Submitted on 28 Mar 2023

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Distributed under a Creative Commons Attribution - NonCommercial - NoDerivatives 4.0 International License

SOCIETY FOR EXPERIMENTAL BIOLOGY

Journal of Experimental Botany
https://doi.org/10.1093/jxb/erad052 Advance Access Publication 13 February, 2023
This paper is available online free of all access charges (see https://academic.oup.com/jxb/pages/openaccess for further details)

REVIEW PAPER

Water use efficiency across scales: from genes to landscapes

Vincent Vadez[1,2,3,*], Raphael Pilloni[1], Alexandre Grondin[1], Amir Hajjarpoor[1], Hatem Belhouchette[4], Youssef Brouziyne[5], Ghani Chehbouni[6], Mohamed Hakim Kharrou[6], Rim Zitouna-Chebbi[7], Insaf Mekki[7], Jérôme Molénat[8], Frédéric Jacob[8] and Jérôme Bossuet[9]

[1] French National Research Institute for Sustainable Development (IRD), UMR DIADE, University of Montpellier, 911 Av. Agropolis BP65401, 34394, Montpellier, France
[2] International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, 502 324, Telangana, India
[3] LMI LAPSE, CERAAS-ISRA, Thiès, Senegal
[4] ABSys, Université de Montpellier, CIHEAM-IAMM, CIRAD, INRAE, Institut Agro, Montpellier, France
[5] International Water Management Institute (IWMI), MENA Office, Giza 12661, Egypt
[6] International Water Research Institute (IWRI), Mohammed VI Polytechnic University (UM6P) UMR CESBIO, Benguerir 43150, Morocco
[7] INRGREF, Carthage University, B.P. 10, 2080 Ariana, Tunisia
[8] UMR LISAH, Université de Montpellier, INRAE, IRD, Institut Agro Montpellier, AgroParisTech, Montpellier, France
[9] Consultant, Exeter, UK

* Correspondence: Vincent.Vadez@ird.fr

Received 17 October 2022; Editorial decision 31 January 2023; Accepted 10 February 2023

Editor: Jianhua Zhang, Hong Kong Baptist University

Abstract

Water scarcity is already set to be one of the main issues of the 21st century, because of competing needs between civil, industrial, and agricultural use. Agriculture is currently the largest user of water, but its share is bound to decrease as societies develop and clearly it needs to become more water efficient. Improving water use efficiency (WUE) at the plant level is important, but translating this at the farm/landscape level presents considerable challenges. As we move up from the scale of cells, organs, and plants to more integrated scales such as plots, fields, farm systems, and landscapes, other factors such as trade-offs need to be considered to try to improve WUE. These include choices of crop variety/species, farm management practices, landscape design, infrastructure development, and ecosystem functions, where human decisions matter. This review is a cross-disciplinary attempt to analyse approaches to addressing WUE at these different scales, including definitions of the metrics of analysis and consideration of trade-offs. The equations we present in this perspectives paper use similar metrics across scales to make them easier to connect and are developed to highlight which levers, at different scales, can improve WUE. We also refer to models operating at these different scales to assess WUE. While our entry point is plants and crops, we scale up the analysis of WUE to farm systems and landscapes.

Keywords: Climate change, crop breeding, drought, farming systems, food security, landscape, water use efficiency, WUE.

© The Author(s) 2023. Published by Oxford University Press on behalf of the Society for Experimental Biology.
This is an Open Access article distributed under the terms of the Creative Commons Attribution License (https://creativecommons.org/licenses/by/4.0/), which permits unrestricted reuse, distribution, and reproduction in any medium, provided the original work is properly cited.

Downloaded from https://academic.oup.com/jxb/advance-article/doi/10.1093/jxb/erad052/7035358 by INRA - DOCUMENTATION user on 28 March 2023

Introduction

Agriculture is currently the largest consumer of water. However, as societies develop, the proportion of water use for non-agricultural purposes (industry, domestic) increases, and so does the competition between agriculture and non-agriculture actors. Climate change and its impact on precipitation and increasing temperatures also brings another level of complexity, increasing plant water demand and jeopardizing crop functioning, and indirectly decreasing surface, subsurface, and groundwater resources that supply the crops, whether that be via rainfall or irrigation. Therefore, agriculture in the 21st century needs to become more water efficient, and this goal can only be achieved by considering a holistic approach to water management and use in combination with crop improvement. The purpose of this review is to take that broader look at the functioning of plants and crops and at the multiscale levels of water efficiency, thereby going beyond the usual narrow focus on 'water use efficiency' of the plant science community.

Making efficient use of water in agriculture has been the object of much research, and it has been addressed at different scales, with different metrics, and different considerations. In the domain of plant science, 'water use efficiency' and 'transpiration efficiency' have been the main two metrics, broadly representing a quantity of biomass produced (from units of CO_2 to grams of biomass) per unit of water used in the wide sense (plant transpiration or crop evapotranspiration that includes both plant transpiration and soil evaporation), and over a timescale that can vary from sub-seconds to the entire duration of a crop cycle (Farquhar *et al.*, 1982; Condon et al, 2002, 2004; Vadez *et al.*, 2014; Hatfield *et al.*, 2019). The term 'efficiency' can also be expanded beyond biomass and be expressed (for example) in units of yield, income, calories, energy, feed value, and protein per unit of water use within the perspective of a farming system, giving a socio-economic angle to the notion of water use efficiency. In the domain of farm engineering, the term 'irrigation efficiency' is a common metric that represents the proportion of water (from reservoirs, rivers, and groundwater, for example; often referred to as 'blue water') that eventually reaches the roots of the crop (thus becoming 'green water', i.e. water contained in the soil profile) and is released back to the atmosphere through transpiration. Beyond tracking and minimizing the water that is lost on the way from the reservoirs to the irrigated fields, increasing irrigation efficiency is also about minimizing the fraction of the water that runs off the fields, gets evaporated, or percolates below the root zone. Whilst the quantity of percolated water is considered as a loss from an agronomical perspective, it is not a loss from a hydrological standpoint since this water infiltrates to recharge the groundwater tables and thus remains present to supply irrigation at the same location or elsewhere, and to fulfil ecosystem services. Finally, it is worth noting that the spatial approach we discuss here needs to be combined with a temporal dimension, where water pathways and subsequent availabilities for crops depend upon seasonal dynamics of both meteorological conditions and agricultural practices.

Therefore, increasing water use efficiency is in part about improving plant water use efficiency *per se* at the leaf, plant, crop, species, agronomy, hydrology, farm, and landscape levels. Beyond this, it is also about maximizing the socio-economic returns from water, not only from a monetary standpoint but also its environmental sustainability with regard to its preservation for future generations. In this review we consider how different research domains collectively address the question of making better use of water in agriculture, providing a broader view on what 'water use efficiency' really encompasses, and downscaling its meaning at each disciplinary level. We also aim to find ways, metrics, and equations to connect these scales of analysis. The common theme running through this review is to consider how different traits/crops/plants/anthropogenic actions can contribute to water use efficiency (taken in its broad sense), and whether existing observations and modelling methods can help in connecting these scales.

Transpiration efficiency at the plant, organ, and cell levels

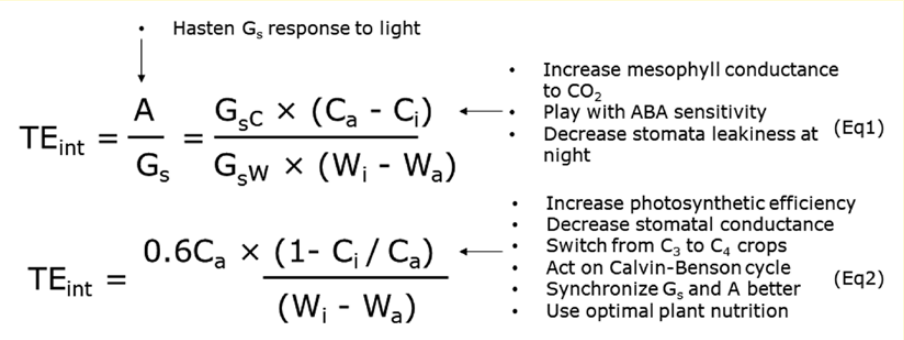
Many studies aimed at a better understanding of transpiration efficiency (TE) have focused on the organ or cell scales in order to avoid confounding effects of canopy architecture or soil–environment interactions (Vialet-Chabrand *et al.*, 2017; Hatfield *et al.*, 2019; Leakey *et al.*, 2019). At the leaf level, TE is referred to as 'intrinsic TE' (TE_{int}) and defined as A/G_s, where A is the CO_2 assimilation by the photosynthetic biochemistry and G_s is the stomatal conductance, or it is also defined as A/T, where T is the water lost by transpiration (see Box 1 for details and further derivations of the ratio). The time-frame is a second or less and the scale is that of a portion of a leaf. Equation 1 posits that possible means by which to increase A/T include increasing C_a–C_i by raising the CO_2 concentration gradient between the atmosphere and the stomatal chamber, improving the photosynthetic capacity or reducing stomatal conductance, or decreasing W_i–W_a by lowering the water-vapour gradient.

Improving TE_{int} by increasing photosynthetic activity is the current object of many studies (Long *et al.*, 2015). In C_3 plants, an exciting avenue for research is presented by converting their metabolism toward a C_4-like photosynthesis (Tardieu, 2022); however, inserting C_4 metabolism in C_3 plants is a challenging task, as observed in rice (Furbank, 2017; Sedelnikova *et al.*, 2018). A more realistic target might be to concentrate CO_2 towards the Rubisco active sites by increasing mesophyll conductance to CO_2, especially in leaves exposed to saturating light. To that end, manipulating the expression of plasma membrane intrinsic protein (PIP) aquaporins that are known to transport CO_2 from the liquid phase in mesophyll cells is of particular interest (Israel

Downloaded from https://academic.oup.com/jxb/advance-article/doi/10.1093/jxb/erad052/7035358 by INRA - DOCUMENTATION user on 28 March 2023

Box 1. Transpiration efficiency at the leaf scale

At the leaf level, TE in often called 'intrinsic transpiration efficiency' (TE_{int}) and defined as A/G_s, where A is the CO_2 assimilation by photosynthetic biochemistry and G_s is the stomatal conductance, or also as A/T, where T is transpiration. Two equations describing this basic framework have been proposed by Condon *et al.* (2004) and updated by Condon (2020), and are presented here. G_{sC} and G_{sW} are the stomatal conductance for CO_2 and water, respectively, C_a and C_i are the CO_2 concentration in the air and inside the stomatal chamber, respectively, and W_a and W_i are the vapour pressure in the air and inside the stomatal chamber, respectively. Equation 2 is a simplification of Eqn 1 where the ratio of G_{sC} to G_{sW} is approximated to 0.6 (Condon *et al.*, 2002). Text labels indicate possible levers affecting different terms of the equations.



	Scale/model type	Notes and references
Time-frame	< seconds	
Scale	Cell, leaf region, organ	
Models	G_s models	Tardieu *et al.* (2015) Buckley (2017) and Blatt *et al.* (2022) review different approaches for modelling stomatal conductance

et al., 2021). The expression and functioning of aquaporins have been associated with TE_{int} in rice (Nada *et al.*, 2014) and in the restriction of transpiration during high evaporative demand in soybean (Sadok *et al.*, 2010), pearl millet (Reddy *et al.*, 2017), and chickpea (Sivasakthi *et al.*, 2020). Another promising means for increasing plant photosynthesis is in accelerating the regeneration of ribulose-1:5 bisphosphate RuBP by increasing the levels of photosynthetic enzymes acting in the Calvin–Benson cycle (Long *et al.*, 2015; Simkin *et al.*, 2017) or by stimulating photosynthetic electron transport by overexpressing the Rieske FeS protein that is a key component of the cytochrome b_6f complex (Ermakova *et al.*, 2019; Simkin, 2019). In tobacco, overexpression of the enzymes fructose-1,6-bisphosphatase/sedoheptulose-1,7-biphosphatase from the Calvin–Benson cycle together with the red algal protein cytochrome c_6 serves this purpose and improves TE_{int} and plant biomass under field conditions (López-Calcagno *et al.*, 2020). However, whilst increasing TE_{int} by boosting photosynthetic activity has provided promising results at the cell/organ scale, more efforts are still needed to demonstrate its value in whole plants.

Limiting G_s is another option to increase TE_{int}, but it may appear less attractive because it might result in a decrease in carbon fixation in the linear parts of the A versus G_s relationship (Tardieu, 2022), although it could be interesting in the non-linear parts of the relationship where any further increase in G_s is only rewarded by a marginal increase in A. Nevertheless, it is usually assumed that strategies aimed at reducing G_s come at the expense of biomass production and yield under optimal conditions (Condon *et al.*, 2002; Blum, 2009; Roche, 2015), and that they might be more useful under water limitation (Hughes *et al.*, 2017; Caine *et al.*, 2019; Mega *et al.*, 2019). However, this assumption is being challenged by an increasing number of reports showing that limiting G_s might not necessarily lead to a decrease in A (Franks *et al.*, 2015; Yang *et al.*, 2016; Dunn *et al.*, 2019). For instance, robust and large-scale lysimetric assessments of pearl millet, sorghum, and groundnut have challenged the common view that higher transpiration efficiency is bound to lower productivity, and have shown that higher TE is completely unrelated to total plant water use, which in turn is directly related to plant productivity (Vadez *et al.*, 2014). In another example, transgenic wheat plants overexpressing *Epidermal Patterning Factor* (*EPF*) show an increase in TE_{int} with no changes in A, biomass, and yield compared to control plants when the reduced stomatal density is no more than 50% of that of the

Downloaded from https://academic.oup.com/jxb/advance-article/doi/10.1093/jxb/erad052/7035358 by INRA - DOCUMENTATION user on 28 March 2023

controls (Dunn *et al.*, 2019). Transgenic tomato plants overexpressing 9-cis-epoxycarotenoid-dyoxygenase have higher ABA than the wild-type and show higher TE_{int} because of a lower stomatal conductance (Thompson *et al.*, 2007). Decreasing G_s by increasing plant sensitivity to ABA via overexpression of the ABA receptor *REGULATORY COMPONENT OF ABA RECEPOR 6* (*RCAR6*) in Arabidopsis also results in an unexpected increase in A and in a higher TE_{int} (Yang *et al.*, 2016). It is still unclear whether this ABA-related effect on A is the result of an increase in mesophyll conductance to CO_2, greater Rubisco activity, or is due to other pleiotropic aspects related to the effects of ABA on leaf characteristics, such as stomatal density or leaf epinasty, which could improve radiation interception (Thompson *et al.*, 2007; Yang *et al.*, 2016; Condon, 2020). Another interesting example comes from the overexpression in tobacco of *PHOTOSYSTEM II SUBUNIT S* (*PsbS*), which encodes a protein stimulating the non-photochemical quenching that protects the photosynthetic machinery under excessive light (Głowacka *et al.*, 2018). PsbS promotes thermal dissipation of excitation energy under high light and keeps the redox state of chloroplastic QUINONE A more oxidized, with the latter protein being an early signal for stomatal opening when it is reduced. Plants with increased *PsbS* expression growing in field conditions show increased non-photochemical quenching and lower G_s in response to light, resulting in a 25% reduction in water loss per CO_2 assimilated (Głowacka *et al.*, 2018). Limiting night transpiration by limiting G_s under dark conditions also contributes to the increase in TE (Coupel-Ledru *et al.*, 2016; Fricke, 2019).

The dynamic/temporal responses of G_s to environmental conditions have emerged as a novel approach in improving TE_{int}. In the field, fluctuations in light intensity and spectral quality that influence the photosynthetic photon flux density (PPFD) in term have large effects on A and G_s (Way *et al.*, 2012). However, stomatal responses are an order of magnitude slower than photosynthetic responses (minutes versus seconds), which leads to a disconnection between G_s and A. This relative lag in G_s limits A as stomata are slow to open under increasing PPFD, whilst unnecessary water loss continues after A has dropped under decreasing PPFD (Vialet-Chabrand *et al.*, 2017). Simulations suggest that synchronizing the behavior of G_s and A could increase TE_{int} by 20% in *Phaseolus vulgaris* under fluctuating PPFD (Lawson *et al.*, 2014). Manipulating stomatal movements to reduce the G_s response time and to improve water use and growth have been achieved in Arabidopsis by overexpressing *BLUE LIGHT-GATED K^+ CHANNEL 1* (*BLINK1*) specifically in guard cells (Papanatsiou *et al.*, 2019). The mean half-times of stomatal opening and closing upon exposure to light and dark, respectively, were accelerated by ~40% compared with the control plants, resulting in a 2.2-fold increase in biomass under fluctuating light without a cost in water use by the plant, thus increasing TE. Interestingly, large variations have been observed for A and G_s both among species (13 species varying in the shape of the stomata guard cells; McAusland *et al.*, 2016) and within species (in wheat, Salter *et al.*, 2019; in sorghum, Pignon *et al.*, 2021), and this has the potential to be exploited.

In summary, contrary to common belief, there may be several options to increase TE by adjusting G_s without significantly altering A, which would allow the development of water-efficient cultivars without significant yield trade-offs.

Transpiration efficiency at the plant and crop levels: interactions with the soil and atmosphere

Transpiration efficiency (TE) at this scale is measured in grams of biomass dry weight produced per unit of water transpired (B_d/T, g biomass l^{-1}), not taking into account soil evaporation. Sinclair *et al.* (1984) initially expressed TE as $k_d/\overline{(e_a^* - e)}_d$, where $(e_a^* e)_d$ is the gradient in vapour pressure between the leaf and the atmosphere at air temperature and the denominator represents a daily mean, and k_d is akin to the numerator term of Eqn 2 that reflects the C_i/C_a ratio (Box 1). In Box 2, we consider how to increase TE via the denominator term, $(e_a^* e)_d$, which is putatively an environmental factor, looking at daily or seasonal time-scales. The definition of TE implies that it will increase when the integration of the denominator over time is small. At a daily time-scale, this would mean avoiding transpiration during hours of the day with the highest vapour pressure deficit (VPD). At the time-scale of a crop season, avoiding periods with high VPD conditions would have the same effect, for example by early sowing. Although the numerator term is considered as constant for C_3 and C_4 species (4 Pa and 9 Pa respectively; Sinclair *et al.*, 1984), variations in TE among C_4 species have been found (Vadez *et al.*, 2021), which implies variations in the k_d term since the experiments were carried out side by side. Measuring TE is difficult, especially in the field (Cooper *et al.*, 1983), as it requires precise transpiration and biomass measurements, although a lysimetric method has managed to reconcile precision and throughput (Vadez *et al.*, 2014). These authors reported large variations in TE among panels of cultivated germplasms of sorghum, pearl millet, and groundnut. Many studies have used ^{13}C discrimination as a proxy for TE, although a number of them have reported limits to the value of this method (see Vadez *et al.*, 2014, for a detailed discussion and references).

Crop simulation has shown that restricting transpiration under high VPD can increase TE (Sinclair *et al.*, 2005). For the plant, this process translates into opening stomata and maximizing A when W_i–W_a is low due to low VPD in the air (Box 1) and closing stomata when VPD exceeds a certain threshold (Sinclair *et al.*, 2017). Stomatal closure under high VPD will limit A and increase leaf temperature because of decreased evaporative cooling, but since it is restricted to a period of a few hours, it is expected to avoid an excessive trade-off in terms of CO_2 fixation. Integrated over the time-course of a day (e.g. n=12 h; Box 2), the denominator term would exclude

Downloaded from https://academic.oup.com/jxb/advance-article/doi/10.1093/jxb/erad052/7035358 by INRA - DOCUMENTATION user on 28 March 2023

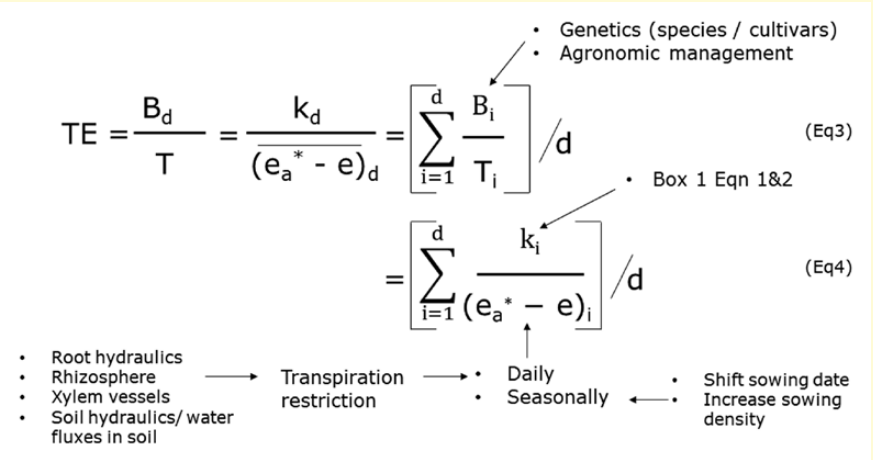
the high vapor pressure gradients of the midday hours, and thus increase TE. A similar integration could be carried out over the time-scale of a crop season, for example n=120 d. Clear agronomical benefits of phenotypes that restrict transpiration under high VPD in water-limited conditions have been demonstrated in maize (Messina *et al.*, 2015) and sorghum (Kholová *et al.*, 2014). Experimental evidence of genotypic variation for this trait has been reported in soybean (Fletcher *et al.*, 2007), pearl millet (Kholova *et al.*, 2010), chickpea (Zaman-Allah *et al.*, 2011), sorghum (Choudhary *et al.*, 2014), and wheat (Schoppach *et al.*, 2012).

As noted above, the first benefit of restricting transpiration under high VPD is to increase TE, and this has been demonstrated in sorghum lines introgressed with the *staygreen* QTL (Vadez *et al.*, 2011), which restricts transpiration under high VPD. This study was followed by a modelling assessment of the benefit of the restriction of transpiration on the yield in the same lines (Kholová *et al.*, 2014). In maize, some lines with relatively high TE more tightly regulate their transpiration response to increases in VPD and have a change-point at lower VPD levels than lines with lower TE (Ryan *et al.*, 2016). As far as we know, there have been no other experimental reports linking a milder transpiration response to VPD with higher TE, and additional experimental evidence is needed. Notably, pearl millet genotypes contrasting in their transpiration responses to high VPD (Kholova *et al.*, 2010) do not differ in terms of TE (Vadez *et al.*, 2013), suggesting that restriction of transpiration does not always increase TE. The interpretation given by Kholova *et al.* (2010) is that the observed restriction of transpiration could result from a mix of fully closed and fully open stomata, giving no benefit in intrinsic TE for the open stomata and yet still reducing the overall transpiration because of the closed stomata.

The second, and possibly most important benefit of the restriction of transpiration under high VPD comes from more parsimonious water use at early stages in the life cycle, which subsequently makes more water available to plants for the critical grain-filling stage. This has been shown in a number of crops such as pearl millet (Vadez *et al.*, 2013, 2014), chickpea

Box 2. Transpiration efficiency at the plant scale

Equation 3 defines TE as the ratio of biomass (B_d) to transpiration (T) and builds on an earlier equation (Sinclair *et al.*, 1984), that gives a daily TE value such as TE = $k_d/(e_a^* - e)_d$, where e_a^* is the saturation vapour pressure at air temperature, e is the vapour pressure in the air, the denominator $(e_a^* - e)_d$ represents a daily mean, and the term k_d is a factor that reflects the CO_2 concentration in the stomatal chamber, i.e. the C_i/C_a term of Eqn 2 in Box 1 (Condon *et al.*, 2002). The term $(e_a^* - e)_d$ then represents water vapor pressure deficit (VPD). In Eqns 3 and 4 below, the integration is conducted at the time-scale of days (d) to give a mean value of TE over i=1 to i=*d* days, and clearly other periods can be considered, such as hours. Text labels indicate possible levers either directly or indirectly affecting the terms of the equations.



	Scale/model type	Notes, references, and links
Time-frame	Day(s) to months	Up to a crop cycle
Scale	Plant, crop	
Models	Functional–structural plant models (FSPM). Crop models in Box 3	CPlantBox (Zhou *et al.*, 2020); https://www.quantitative-plant.org/model/cplantbox

Downloaded from https://academic.oup.com/jxb/advance-article/doi/10.1093/jxb/erad052/7035358 by INRA - DOCUMENTATION user on 28 March 2023

Box 3. WUE at the crop/field scale

At this scale transpiration efficiency is generally termed water use efficiency (WUE_{field}) and is the ratio of grain yield to water used, either coming from rainfall or irrigation (Eqn 5). Yield can be disaggregated in the equation Yield = T × TE × HI (Passioura, 1977), where HI is the harvest index, and T and TE are brought in from Box 2. In Eqn 6, this ratio is reduced into a sum of daily ratios of TE to the proportions of water lost to evaporation and to run-off, which is then integrated over a season of n days. This equation indicates that soil evaporation and run-off need to be minimized to maximize WUE. Text labels indicate possible levers directly affecting the terms of the equations.

$$WUE_{field} = \frac{\text{Grain Yield}}{\text{Irrigation + Rainfall}} = \frac{T \times TE \times HI}{T + Evap + Run\text{-}off} \quad \text{(Eq5)}$$

$$= \left[\sum_{i=1}^{n} \frac{TE_i}{1 + Evap_i/T_i + Run\text{-}off_i/T_i}\right] \times HI/n \quad \text{(Eq6)}$$

- Box 2
- Increase sowing density
- Orientate rows North-South
- Use adequate plant nutrition
- Increase light penetration in canopy
- Irrigation at key times
- Increase soil storage capacity
- Increase sowing density
- Use North-South row orientation
- Use mulching
- Increase sowing density
- Use terracing, levelling
- Use contour bunds

	Scale/model type	Notes, references, and links
Time-frame	Months	Crop cycle
Scale	Crop, field	
Models	Process-based crop simulation models such as: APSIM; DSSAT; WOFOST; DAISY; CROPSYST; AQUACROP; SSM	https://www.apsim.info/ https://dssat.net/ https://www.wur.nl/en/research-results/research-institutes/environmental-research/facilities-tools/software-models-and-databases/wofost.htm https://daisy.ku.dk/ http://sites.bsyse.wsu.edu/cs_suite/cropsyst/ https://www.fao.org/aquacrop/en/ http://ssm-crop-models.net/

(Zaman-Allah *et al.*, 2011), and maize (Messina *et al.*, 2015). Similar responses have been observed in modern Spanish durum wheat lines grown under drought stress in field conditions (Medina *et al.*, 2019). Water availability during the grain-filling period is indeed critical, and it has been shown to have a high return in terms of grain yield per mm of water, for example 55 kg ha^{-1} mm^{-1} in wheat (Manschadi *et al.*, 2006), ~40 kg ha^{-1} mm^{-1} in chickpea (Zaman-Allah *et al.*, 2011), and 37–45 kg ha^{-1} mm^{-1} in pearl millet (Vadez *et al.*, 2013). This also tells us that improving transpiration 'efficiency' is not only about improving the physiology of plant transpiration (Box 1) but also about understanding time periods when the crop has critical water needs (Box 3). In that sense, the equation Yield = T×TE×HI, where T is water used for transpiration and HI is the harvest index (Passioura, 1977), can no longer be seen as the combination of linear terms, but as the combination of terms whose importance varies among them and over time (see Box 3, and below).

Late-night transpiration, as was reported in wheat (Tamang *et al.*, 2019), has been proposed as an avenue for research towards increasing TE, on the assumption that it would set the plant for an early onset of photosynthesis in the morning under more favorable VPD conditions, possibly related to a

Downloaded from https://academic.oup.com/jxb/advance-article/doi/10.1093/jxb/erad052/7035358 by INRA - DOCUMENTATION user on 28 March 2023

higher pre-dawn water status. That said, night-time transpiration is not associated with any photosynthesis and would need to be limited. Up to 30% of plant water loss can take place at night in grapevines (Coupel-Ledru *et al.*, 2016) and up to 55% in wheat (Schoppach *et al.*, 2014), so that reducing night-time transpiration would be a way of improving TE.

What drives the restriction of transpiration?

According to the gradients in potential, water moves from the soil pores to the roots, and then through the plant to the stomatal chamber to be transpired as vapour into the air (Tyree, 1997). Hydraulic resistances have been identified at different levels in this continuum, affecting the water gradient between the soil and the plant, gradients within the plant, and between the plant and the air. Typically, resistances across the soil, across the soil–root interface, across the root to the root xylem, and along the xylem are used to model water flow through a series of analytical solutions/functions (e.g Couvreur *et al.*, 2012; Abdalla *et al.*, 2022; Koehler *et al.*, 2022). Accurate estimates of how soil water stress affects plant transpiration are essential for reliable mechanistic model predictions (Verhoef *et al.*, 2014) so that reliable exploration of possible effects on TE can be carried out. There is still a need for such estimates, and models that can easily represent mesophyll behavior in response to environmental drivers are still rare (Zhang *et al.*, 2022).

Soil hydraulic conductivity can drastically limit water uptake and is considered as a main driver of stomatal closure for plants in drying soils (Carminati *et al.*, 2020; Carminati and Javaux, 2020; Abdalla *et al.*, 2022). Its effects can interact with crop species/genotypes. As an illustration, maize and sorghum genotypes have been observed to have lower TE in a sandy soil than in a high clay Vertisol, whereas TE is similar in both soils in pearl millet (Vadez *et al.*, 2021). It has been proposed that species fitness could be specific to soil type and its interaction with the environment (low/high VPD). Plants respond to soil matric potential (suction) rather than soil water content (SWC), a concept that has long been understood and is widely accepted. The magnitude of matric potential depends on SWC, the size of the soil pores, the surface properties of the soil particles, and the surface tension of the soil water (Whalley *et al.*, 2013). Thus, in summary, a putative role of soil in possibly explaining restrictions of transpiration needs to be clarified (Box 2).

Experimental evidence further suggests that root phenotypes such as long and dense root hairs postpone soil limitation in drying soils by reducing the drop in matric potential at the interface between the roots and soil in transpiring plants (Carminati *et al.*, 2017; Cai *et al.*, 2022; Schnepf *et al.*, 2022). The nature of the rhizosphere also has the potential to disrupt the connection between the soil and the plant. Engineering rhizospheric characteristics, for example by increasing mucilage production, might open up new avenues for crop production management and lead to increases in water use efficiency (Ahmed *et al.*, 2018). In addition to their role in water capture, roots have been proposed to act as hydraulic rheostats, able to adjust their hydraulic radial conductance through alterations of apoplastic barriers (Calvo-Polanco *et al.*, 2021; Salas-González *et al.*, 2021) or aquaporin functions (Maurel *et al.*, 2010; Vadez, 2014). A typical example comes from the correspondence observed between aquaporin expression, diurnal variations in root hydraulic conductivity, and transpiration, which can be interpreted as a means for preventing a drop in water potential in the leaf when transpiration is high (Tsuda *et al.*, 2000). Restriction of transpiration under high VPD has indeed been related to root conductance and its control by root and shoot aquaporins (Sadok *et al.*, 2010; Reddy *et al.*, 2017, 2022; Sivasakthi *et al.*, 2020), but also to leaf area (Choudhary *et al.*, 2020) and to the root-to-shoot ratio (Affortit *et al.*, 2022). Xylem vessels are responsible for hydraulic axial conductance of water from the roots to the shoots, and reductions in xylem conductance have been associated with increases in TE in wheat (Richards *et al.*, 1989; Hendel *et al.*, 2021).

In summary, there are two main benefits to restricting transpiration under high VPD, namely higher TE and more water for grain filling. Several root traits and soil characteristics are likely to have a strong influence on the restriction, and will tend to decrease the denominator term of Eqn 4 (Box 2) and thereby increase TE overall.

Water use efficiency at the species and agronomy level

This scale of assessment is at the level of field plots, and transpiration efficiency is generally referred to as water use efficiency (WUE_{field}). The usual metric is either grain or biomass yield per millimeter of water used (kg ha^{-1} mm^{-1}) from either rainfall or irrigation (Box 3). For an easier connection to the other scales, WUE_{field} can also be expressed with the metrics presented above (Box 2), by converting yield into the product of plant transpiration T, TE, and the harvest index (HI; Passioura, 1977), and by separating rainfall and irrigation into the transpiration component T minus a component of soil evaporation and run-off (Eqn 5, Box 3). Equation 6 is then a daily integration over an entire crop cycle, following the integration developed in Box 2. As a result, it becomes clear that increasing WUE_{field} is about increasing transpiration efficiency (as detailed in the previous two sections) *and* minimizing soil evaporation and run-off.

Run-off occurs when rainfall (more rarely irrigation) is in excess of what the soil can absorb. The term 'precipitation use efficiency' (PUE) can be used and is an integration of the yield increments that occur consecutive to any rainfall. Research on the capacity of soil to store more water has been aimed at improving PUE under such rain-fed conditions (Hatfield *et al.*, 2001). For example, over-tilling of bare soil leads to decreases

Downloaded from https://academic.oup.com/jxb/advance-article/doi/10.1093/jxb/erad052/7035358 by INRA - DOCUMENTATION user on 28 March 2023

in its water- and nutrient-storage capacities that in turn decrease the potential WUE of the future crop (Cresswell *et al.*, 1993). A scale-up of PUE is precipitation storage efficiency (PSE), which defines the capacity of a soil to be a more or less useful reserve for future crops. PSE is negatively affected by over-tilling (Tanaka *et al.*, 1987) and it has been reported that it can be increased by up to 40% by using herbicides to control weeds instead of conventional tillage (Wicks, 1968). It has been demonstrated that PSE, PUE, and WUE are related (Nielsen *et al.*, 2005) (Box 3), and thus soil management practices can potentially be used to increase WUE.

As far as soil evaporation is concerned, early vigor is a plant trait that has long been favored by breeders, as it ensures rapid coverage of the ground and efficient competition against weeds. A faster soil coverage could also come from an increased sowing density, and this would reduce the evaporation component of the equations for WUE_{field} (Box 3). There are also promising avenues to explore for decreasing irrigation needs and improving WUE_{field} in semi-arid regions by using advanced agronomic practices such as those related to conservation tillage (DeLaune *et al.*, 2012) and mulching (Igbadun *et al.*, 2012; Liao *et al.*, 2021), which are considered as effective means for improving irrigation efficiency by reducing the fraction of water lost through non-beneficial soil evaporation. They can also allow for the control of weeds, reduction of soil compaction, improvements in nutrient management, and the incorporation of additional nutrients into the soil (McCraw *et al.*, 1991; Shaxson *et al.*, 2003). It has been reported that plastic film and straw mulching also reduces the impact of raindrops on the soil surface, subsequently reducing soil dispersion and thereby enhancing water infiltration, reducing run-off, and increasing soil water storage (Li *et al.*, 2013).

As far as the TE component of Eqn 6 is concerned (Box 3), the WUE_{field} of crops can be affected by the management applied and be optimized by the right interaction of genotype and management (G×M) for a given environment (E) (Hsiao *et al.*, 2007; Messina *et al.*, 2009). In pearl millet, low soil-P treatments have been reported to decrease WUE (Beggi *et al.*, 2015), and it has been shown that both the intrinsic TE (A/T, Box 1) and TE at the plant level (B_i/T, Box 2) are decreased by ~10-fold by a low soil-P treatment (Payne *et al.*, 1992). It should be noted that low P nutrition has also been shown to reduce plant hydraulic conductance (Radin, 1990). A number of studies also show increased WUE as soil fertility increases (e.g. in wheat, Fan *et al.*, 2005; and in maize, Faloye *et al.*, 2019). Therefore, poor fertility is bound to decrease the TE component of Box 3, something that is food for thought when agriculture needs to be more water-efficient while also aiming at using less nutrients. Increasing the sowing density in maize has been shown to increase WUE (French and Schultz, 1984; Hatfield *et al.*, 2001), and is interpreted as an effect of a limited leaf area index. In cotton, a higher sowing density was found to affects the microclimate within the canopy, with light transmission through the canopy in some genotypes increasing light interception (Yang *et al.*, 2014). As an alternative interpretation, the benefit could also have been the result of a combination with a decrease in VPD within the canopy (Box 2), allowing photosynthesis to continue at the lower VPD, and hence achieving higher gains in intrinsic TE_{int} (Box 1). Indeed, recent work on sorghum has highlighted a significant increase in WUE when the sowing density of plants is doubled, with large genotypic variation being found in the response (Pilloni, 2022). This can be contrasted with a lower WUE found in a skip-row planting system and dry environment, and a higher WUE found in a skip-row system and a wetter environment (Abunyewa *et al.*, 2010). In the dense-canopy conditions used by Pilloni (2022), high WUE was recorded in genotypes with a strong transpiration response to the evaporative demand, which was seemingly caused by a higher light penetration within the canopy. The benefit thereby came from the association of an agronomic management modification (density) and a genetic trait related to canopy architecture that allowed light penetration within the canopy. The plant architectural traits seem to have been driving the diversity in the response. According to Niinemets (2010), the traits that most control the distribution and efficiency of light use at the plant level are the angle distribution of the leaves and the spatial aggregation of the foliage. From a canopy perspective, the way leaves are spatially distributed and how biomass is allocated to them varies significantly. Unfortunately, leaf areas are still largely represented using 2D metrics (m^2), and more work is needed to better understand and measure leaf areas in 3D, and hence to better gauge the role they play in light distribution through the canopy and what effects they have on the microclimate within the canopy.

WUE can be linked to crop architecture, orientation, and associations with other plants–

In the previous section we have shown that adapting the management of an annual crop can directly affect its water budget. The same is true for perennial crops, but in this case the management also needs to be adapted to the landscape. A striking example is that of the vineyard, where the orientation of the rows of plants affects how the soil temperature and water content vary with depth (Hunter *et al.*, 2020), and this can have an impact on water availability at the scale of the landscape. The main factor that is affected by row orientation in perennial crops is the distribution of light resources through the canopy. A change in orientation in a Shiraz vineyard from north–south to east–west was found to significantly reduce the transpiration by up to 13% without any significant reduction in yield and its components, thus leading to an increase in WUE (Buesa *et al.*, 2017). It was suggested that the better distribution of radiation received by the rows orientated east–west during the hot and dry season and the low photosynthetic efficiency of the north–south vines during the afternoon contributed to the increased WUE.

Downloaded from https://academic.oup.com/jxb/advance-article/doi/10.1093/jxb/erad052/7035358 by INRA - DOCUMENTATION user on 28 March 2023

These differences in canopy structure and the link to WUE can be also considered in the case of intercropping between annuals or between perennials and annuals. For example, maize yield in a maize–coffee tree intercropping system has been found to be increased by 50–80%, depending on the intercropping distance, compared to maize grown alone (Huxley *et al.*, 1994). This was possibly due to lower direct radiation, a milder microclimate effect due to tree transpiration, and lower exposure of the maize to wind. Reduced exposure to wind would decrease the evaporative demand to the benefit of WUE, and ultimately yield (Chaves *et al.*, 2016; Hatfield *et al.*, 2019). These case studies show the importance of planning combinations of crops within agroecosystems that can best use the different resources and tolerate the environmental constraints that drive the pattern of water consumption (see landscape section below).

Increasing WUE through better irrigation efficiency

Irrigation efficiency (IE), defined as the ratio of water used by the crop for transpiration to total water applied, is the traditional concept of efficiency in irrigation engineering (Israelson, 1950, Jensen, 2007). Equation 7 in Box 4 separates irrigation into the components directed to crop transpiration, soil evaporation, run-off (similar to Box 3), and percolation below the root zone.

Improvement of IE at the field level can be achieved by reducing evapotranspiration from weeds, and by adopting practices such as optimizing the timing of irrigation, reducing waterlogging, and using advanced irrigation techniques to reduce the wetted area (Batchelor *et al.*, 2014; Hatfield *et al.*, 2019). A series of new irrigation practices and technologies have been

Box 4. Increasing WUE at the field scale with better irrigation efficiency

Irrigation efficiency (IE) represents the proportion of irrigated water that will eventually be used for plant transpiration and hence for growth. Here, Eqns 7 and 8 only focus here on the 'T' component from the previous Boxes 1–3. The integration also in Eqn 8 is done over a season of n days. Equation 7 introduces a component of water percolation below the root zone (Perc). Although they are not represented in the equations, water losses can also occur during the transfer from the source to the field, or during the application of irrigation. This can be measured as the conveyance efficiency, defined as the ratio of water diverted from the source (reservoir, river, pumping station) to the water reaching the field (Rogers *et al.*, 1997; Howell, 2003), and as the field application efficiency, defined as the ratio of water needed by the crop to the amount of water available at the field inlet (Bos and Nugteren, 1990). Text labels indicate possible levers directly affecting the terms of the equations. DI, deficit irrigation; RDI, regulated deficit irrigation; PRD, partial root-zone drying.

- Suppress weeds
- Use supplemental irrigation
- Play with DI, RDI, and PRD

$$IE = \frac{T}{Irrigation} = \frac{T}{T + Evap + Run\text{-}off + Perc} \quad \text{(Eq7)}$$

$$= \left[\sum_{i=1}^{n} \frac{1}{1 + \underbrace{Evap_i/T_i + Run\text{-}off_i/T_i}_{} + Perc_i/T_i} \right] \Big/ n \quad \text{(Eq8)}$$

- Box 3
- Use mulch + drip-irrigation

- Optimize irrigation timing & duration
- Increase soil storage capacity

	Scale/model type	Notes, references, and links
Time-frame	Months	Crop cycle, years
Scale	Field, irrigation basin	
Mod-els	Crop models of Box 3. Irrigation management models such as:HYDRUS; CROPWAT; or other Agrohydrology models such as Soil Water Atmosphere Plant (SWAP)	https://www.pc-progress.com/en/default.aspx?hydrus https://www.fao.org/land-water/databases-and-software/cropwat/en/ https://www.swap.alterra.nl/

Downloaded from https://academic.oup.com/jxb/advance-article/doi/10.1093/jxb/erad052/7035358 by INRA - DOCUMENTATION user on 28 March 2023

developed to enhance WUE based on the physiological mechanisms of crop responses to water deficit. These irrigation strategies encompass deficit irrigation, regulated deficit irrigation, and partial root-zone drying irrigation, and can be applied by surface-, sprinkler-, or drip-irrigation methods, or possibly by subsurface methods to avoid soil evaporation (El-Hendawy *et al.*, 2008; Jovanovic *et al.*, 2020).

Deficit irrigation (DI) is a water-saving strategy that permits a certain level of crop water stress to exist continuously throughout the season without compromising crop yield significantly (Pereira *et al.*, 2002; Manning *et al.*, 2018). Regulated deficit irrigation (RDI) allows water stress at certain phenological stages during which plants are less sensitive, while fully meeting the irrigation needs of the crop at critical growth stages (Romero *et al.*, 2013). Partial root-zone drying (PRD) irrigation is a technique that allows half of the root system to experience drying while the other half is irrigated. PRD targets the plant physiological response through the production of abscisic acid (ABA) by the drying roots, which reduces leaf expansion and stomatal conductance (thus affecting C_i/C_a in Box 1) while the wetted roots maintain a favorable plant water status (Galindo *et al.*, 2018). It has been reported that RDI and PRD improve WUE mainly through enhancing the guard-cell signal transduction network that reduces leaf transpiration (Schroeder *et al.*, 2001), through optimized stomatal control that improves the ratio of photosynthesis to transpiration (Iqbal *et al.*, 2020), and through a reduction in the evaporative surface area (Xie *et al.*, 2012). However, there is still debate about the importance of ABA signalling in regulating WUE in plants subjected to PRD (e.g. Perez-Perez *et al.*, 2012) because ABA production in the part of the root exposed to drying might not be sustained over time (Dodd *et al.*, 2008).

In rain-fed agriculture of semi-arid regions, supplemental irrigation (SI) has emerged as a promising practice for climate resilience. It consists of applying limited amounts of water at critical growth stages when rainfall fails to provide sufficient moisture for normal crop growth in order to improve and stabilize yields (Oweis *et al.*, 2012) (Box 4). Several studies have reported substantial increases in crop yields using this method. For example, Oweis *et al.* (2000) showed that, in combination with early sowing and the availability of appropriate levels of nitrogen, the WUE of rain-fed wheat can be substantially improved by adopting a level of SI equivalent to only one-third to two-thirds of the full irrigation requirement. Timely SI at the jointing and anthesis growth stages of wheat can result in high grain yields and nitrogen use efficiency while achieving higher WUE (Wu *et al.*, 2018), and chickpea yield can be increased 30% by applying 40 mm irrigation at the beginning of seed growth (Vadez *et al.*, 2011).

Finally, crop management and irrigation techniques can be combined to further increase irrigation efficiency. In a modelling study that analysed the effects of mulching and drip-irrigation, Zhang *et al.* (2022) found that a combination of the two treatments significantly improved the crop yield and WUE compared to irrigation with no mulching. The improvements were affected by climatic and soil conditions, crop type, and water consumption, with the technique being more effective in planting areas with rainfall or water consumption less than 400 mm and in areas with soil of medium texture.

Maximizing WUE at the farm system level

Water efficiency at the farm level is often calculated as the ratio of total farm production to the total amount of irrigation water used. In economic terms the word 'production' usually means the gross margin of a farm (revenue minus production costs), and so this efficiency can also be expressed in terms of the number of calories produced by the crops grown on the farm, and/or by the negative or positive externalities that a farm can produce, for example the quantity of water used, nitrogen leached, changes in soil organic matter, erosion, and drainage.

Efficiency is often considered on a per-hectare basis for easy comparisons at the regional level. To better understand this overall efficiency, it is often necessary to calculate and analyse intermediate efficiencies. These may be expressed by type of crop, crop practice, irrigation system, or biophysical system. The concept of water efficiency at the farm level is rarely used for rain-fed crops. Finally, the concept of irrigation efficiency at the farm level is often used to characterise and analyse the performance of farms with regard to the quantities of irrigation water involved, to put forward and test the effects of technical (e.g. new varieties, new rotation, tillage) and socio-economic (e.g. water pricing, subsidies for more efficient irrigation systems) alternatives meant to improve water efficiency and consequently the overall performance of the farm, or to better understand the determinants that affect overall water efficiency (soil effects, rotation, irrigation systems).

The concept of water efficiency at the farm level

The stochastic frontier production approach is the most widely used method to analyse technical efficiency in production (Battesse *et al.*, 1995). Irrigation water technical efficiency (IWTE) measures how an individual farmer's water use compares with that of the most efficient water user. The comparison is made while controlling for the effects of all other factors affecting efficiency (Yigezu *et al.*, 2013). $IWTE_i$, where 'i' represents a farm, is calculated following Karagiannis *et al.*, (2003) (Box 5). This efficiency formulation is based on three considerable simplifications: all production factors other than water are less limiting, all these factors act in the same way on production, and all these production factors are substitutable. For this reason, these factors are often expressed in monetary terms for easier aggregation, such as production costs, and not in quantitative terms; in this case, we refer to irrigation

Downloaded from https://academic.oup.com/jxb/advance-article/doi/10.1093/jxb/erad052/7035358 by INRA - DOCUMENTATION user on 28 March 2023

technical cost efficiency, ITCE (Akridge, 1989) (Eqn 10, Box 5). This formulation implies that improving farm efficiency can come from acting either on the denominator (e.g. switching from flooding to drip irrigation), the numerator (e.g. improving crop yields by using more efficient varieties), or both. In practice this concept is complicated to apply, especially in an arid context where several limiting factors act at the same time (e.g. labour, access to resources and the market) and where several production objectives are targeted (e.g. food, economic, social, environmental). In this context, comparing and especially understanding the efficiency of a farm in relation to water involves verifying that no other factor is limiting, and that water is the only determining factor in the total performance of the system being analysed. Here, the main issue in calculating efficiency is not the mathematical formulation of efficiency, but the availability and quality of data (see Appendix S1 for more details).

Water efficiency, production, and resilience in arid areas

It is often assumed that better efficiency in the use of irrigation water should make it possible to safeguard water resources, improve crop production per hectare, reduce production costs by reducing irrigation inputs, potentially reduce nitrate leaching and, finally and more globally, improve farmer income. This type of assumption must be treated with great caution when the analysis is carried out at the farm level. Several dryland countries have indeed implemented support policies to promote sprinkler- and drip-irrigation instead of submersion, and this has led to higher productivity per hectare. However, intervening on the water component alone has only allowed a modest improvement of irrigation efficiency, because several other production factors have remained limiting (e.g. labour availability, adapted and certified seeds, fertility). In addition, access to water is often not available at the right time for the

Box 5. WUE at the farm scale

Irrigation water technical efficiency (IWTE) measures how an individual farmer's water use compares with that of the most efficient water user. $IWTE_i$, where 'i' represents a farm, is determined according to Eqn 9, where X_1 represents the units of inputs other than water, W_2 represents the minimum feasible water use needed to produce the optimal units of output, C, and A represents the quantity of non-optimal units of output that would be obtained from the same level of X_1 combined with a non-optimal quantity of irrigation water, W_2. The ratio W_1/W_2 expresses the proportion of irrigation water that is lost, or alternatively the proportion saved $[1-(W_1/W_2)]$. It also enables the determination of the maximum possible reduction in water use (W_1-W_2). If water is not available at the right time, this leads to a reduction in the denominator in Eqn 9 (Box 9; quantity of irrigation water, W_2) but a fairly small increase in the numerator, mostly expressed by the gross margin on the farm. The irrigation technical cost efficiency (ITCE) is defined for the *i*th studied farm ($ITCE_i$) in Eqn 10, where $S_{W,i}$ is the observed share of the cost of irrigation water (W) out of the total of all input costs of the *i*th studied farm, and $S_{j,i}$ is the corresponding share of the cost of the *j*th input. By definition, the shares of the costs of all the inputs must add up to 1 and since $IWTE_i$ takes values between 0 and 1 (Eqn 9), it implies that ITCEi is the same.

- Local stakeholder decision
- Balance between water and other input (fertilizer, labor, etc...)
- Irrigation type

$$IWTE_i = X_1C/X_1A = W_1/W_2; \qquad 0 < IWTE_i < 1 \qquad \text{(Eq9)}$$

$$ITCE_i = S_{W,i} \times IWTE_i + \sum_{j=1}^{j} S_{j,i} \qquad \text{for } j \neq W \qquad \text{(Eq10)}$$

- Support farmer decisions by comparing his/her cost efficiency in irrigation water application to the most cost efficient user(s) of irrigation water

	Scale/model type	Notes, references, and links
Time-frame	Crop cycle	
Scale	Farm/several fields	
Models	Bio-economic models and simulators such as: IMPACT; DAHBSIM	https://www.ifpri.org/publication/international-model-policy-analysis-agricultural-commodities-and-trade-impact-model-0 https://www.ifpri.org/publication/dynamic-agricultural-household-bio-economic-simulator-dahbsim-model-description

Downloaded from https://academic.oup.com/jxb/advance-article/doi/10.1093/jxb/erad052/7035358 by INRA - DOCUMENTATION user on 28 March 2023

crop (e.g. during grain-filling). This leads to a reduction in the denominator in Eqn 9 (Box 9; quantity of irrigation water, W_2) but a fairly small increase in the numerator, mostly expressed by the gross margin on the farm. Since irrigation rates are calculated for optimal yields and not yields limited by other factors, then a possible side-effect of not calculating the irrigation requirement correctly can be an increase of leaching as excess water is applied (El Ansari *et al.*, 2020).

Based on this, it is essential to combine the irrigation efficiency indicator with indicators that express all the ecosystem services (see also 'WUE at the landscape level' below), with the aim of maximizing irrigation and production while minimizing externalities. This brings us back to a trade-off analysis in which neither efficiency nor production in its different components should be considered separately. This is all the more important as the most efficient farms in the drylands today are those that are poor, with very limited access to resources (low numerator and denominator in Eqn 9.

The limits of water efficiency

By massively subsidising the renewal of irrigation systems, dryland countries have sought to improve irrigation efficiency, increase farmer incomes, and preserve water resources; however, two unexpected effects have occurred. First, saving water per hectare has also led to an increase in the area of land that is irrigated, and hence in total water use, and second, the improvement of irrigation efficiency has either led to a simplification of the cropping system, or the partial/total replacement of traditional cropping systems based on cereals and legumes with more profitable crops. While this has led to significant increases in farmer income per hectare, it has also decreased the diversity of cropping systems on farms, and increased crop protection treatments. The quest for greater irrigation efficiency via the simplification of cropping systems has also been followed by a reduction in the diversity of food intake in farm households, leading to unbalanced diets as most or all of the production is now marketed (Chenoune *et al.*, 2017). It may seem paradoxical, but the quest for greater irrigation efficiency has been followed by a direct or indirect risk of non-resilience for farms in drylands (Souissi *et al.*, 2018; Hossard *et al.*, 2021), because these farms have either become too dependent on water (Nasrallah *et al.*, 2020), or the simplification of cropping systems that has followed the search for more efficient systems has made these systems less flexible (e.g. in the choice of crop succession or substitution) in the event of a climate shock.

WUE at the landscape level

Going beyond the farm level is the landscape level, where it is essential to modulate water storage on the basis of trade-offs between the various and possibly antagonist water-user needs (see Box 6). Beyond satisfying those needs, modulating water levels within different compartments (e.g. root zone, aquifers, surface reservoirs) is critical for the sustainability of systems that depend on rainfall directly (infiltration for rain-fed crops) or indirectly (irrigation from aquifers or surface reservoirs).

Landscape level: definition, concepts, and levers of action for WUE

The notion of 'landscape' carries different meanings and its definitions are numerous (Aznar *et al.*, 2006). Landscape is considered in this review as a portion of a territory from a few km² to a few tens of km². Agricultural landscapes are characterized, among other things, by their composition and configuration (Liu *et al.*, 2020). The composition includes the different types of land uses and crops over agricultural soils, as well as various man-made infrastructures that influence water flows. The configuration is the way in which the composition is organized in space. Composition and configuration of agricultural landscapes evolve over time, according to farmer choices. The composition then represents an important lever for WUE at the landscape scale (WUE_{land}), as this is where the choice can be made between water-efficient and -inefficient crops (Box 6).

Analysing and controlling WUE_{land} requires understanding various water uses and related ecosystem services: production of blue water for agricultural, domestic, and industrial uses, availability of green water for non-cultivated terrestrial ecosystems (e.g. forest, scrubland), and preservation of aquatic environments (e.g. lakes, rivers, wetlands). In doing so, the analysis of water availability and uses leads to the delineation of landscapes according to the watershed, a hydrological spatial unit that enables the determination of the drivers of soil water availability such as hydrological fluxes (infiltration, run-off, evaporation, transpiration, groundwater recharge) and their interactions within the hydrological cycle (Vereecken *et al.*, 2015). Increasing the WUE of crops might have a negative impact on other water uses within the watershed that therefore have to be both taken into account and quantified. In other words, at the landscape level, the challenge is to establish trade-offs between one or more ecosystem functions of the soil water supply that we seek to modulate in time and space to increase the WUE of crops, and between other ecosystem functions that we also seek to modulate, such as variations the flow of streams. The landscape approach to WUE must therefore be part of a global approach of water management (Habibi Davijani *et al.*, 2016; Psomas *et al.*, 2016), within which water is considered as a resource for agriculture and other human uses, but also as a living environment for plants and animals. The approach therefore requires involving a diversity of stakeholders and social groups with diverse and possibly antagonistic interests (e.g. national and local authorities, water production and distribution companies, fishermen, environmental non-governmental organizations), a diversity that goes far beyond the circle of farmers or groups of farmers (Koontz *et al.*, 2014).

Downloaded from https://academic.oup.com/jxb/advance-article/doi/10.1093/jxb/erad052/7035358 by INRA - DOCUMENTATION user on 28 March 2023

Box 6. WUE at the landscape scale

WUE at the landscape scale (WUE_{land}) is presented in Eqn 11 as ratios of different possible metrics, which can include gross or net primary productivity (GPP or NPP). WUE_{land} can also be expressed as an interaction function between the distribution of different crops/species within the landscape (the 'Environment', Envt), the management (Mgt, e.g. rainfed, irrigated, fertilized, weeded), and the crops/species chosen by farmers, averaged across the many crops/species of the landscape, and divided by 'Water'. The latter includes several hydric indicators such as rainfall, watershed wetting (rainfall minus run-off, including infiltration for crops and underlying aquifers), root-zone water content, and withdrawals from reservoirs, and it is akin to the denominator of Eqn 5 (Box 3). The major difference with Boxes 1–4 is that WUE_{land} needs to be aggregated both in time ('*i*') as seen in Boxes 1–4, and in space ('j'), and this for the many crops/species of the landscape, each occupying a *j*th portion of the space. This is developed in Eqn 12. The first part of the equation takes into account the 'Environment' and the 'Management' effects, weighted by the area covered by each combination (where *m* is the total number of combinations). The second part of the equation is akin to WUE_{field} (Box 3) and is an aggregation over time 'i', within each of the *j*th portions of the space occupied by a crops/species. The text labels indicate possible levers directly affecting the terms of the equations. In addition, the bold arrows and text also indicates unavoidable interactions/ trade-offs; for instance with the WUE of other adjacent landscapes, between the landscape design and non-farming stakeholders, and with the need for ecosystem services such as river flow.

$$WUE_{land} = \frac{\text{Biomass; yield; "GPP/NPP"}}{\text{Rainfall + Irrigation}} = \frac{\overline{\text{Envt} \times \text{Mgt} \times (\text{Crops / Species})}}{\text{Water}} \quad \text{(Eq11)}$$

$$WUE_{Land} = \left[\sum_{j=1}^{m} \frac{Envt_j \times Mgt_j \times Area_j}{\sum_{j=1}^{m} Area_j}\right] \times \left[\sum_{i=1}^{n} \frac{TE_i}{1 + Evap_i/T_i + Run\text{-}off_i/T_i}\right] \times HI/n \quad \text{(Eq12)}$$

- Policy maker decisions
- Landscape design
- Farmer decisions
- Boxes 1-3
- Boxes 3-4

Adjacent Landcapes

- **Need for ecosystem services**
- **Effects of man-made infrastructures**
- **Decisions from non-farming stakeholders**

	Scale/model type	References and links
Time-frame	Day(s) to phenological stages, from one to several crop cycles, up to decades	
Scale	Fields, land-use classes, watersheds, aquifers	
Mod-els	Hydrological and agro-hydrological, models such as: SWAT; ParFlow; APEX or Coupled hydrological and crop growth models Integrated models such as MHYDAS-Small-Reservoirs Watershed and land-management models such as WEAP	https://swat.tamu.edu/ https://parflow.org/ https://epicapex.tamu.edu/ Lebon *et al.* (2022) https://www.sei.org/projects-and-tools/tools/weap/

The landscape-specific levers for steering and optimizing WUE_{land} are two-fold (Box 6). The first lever is the choice of landscape composition (Stroosnijder *et al.*, 2012). This involves first determining the crop species and varieties adapted to the climatic conditions and soil-water availability, second specifying agricultural practices to be implemented for modulating rainwater infiltration or limiting evaporation (e.g. type of ploughing and date, seeding density and date, grassing, mulching), and third determining effective man-made infrastructures to appropriately distribute rainwater between landscape compartments (Eqn 12, Box 6). The main landscape infrastructures are rainwater harvesting systems such as reservoirs, terraces, and contour trenches or ridges that follow the topographic levels (Habets *et al.*, 2018; Lasage *et al.*, 2015). The second lever for controlling WUE_{land} consists of determining the landscape configuration, namely the spatial allocation of crops and practices at the scales of sub-fields and field patchworks (Colin *et al.*, 2012), and the implementation of landscape infrastructures

Downloaded from https://academic.oup.com/jxb/advance-article/doi/10.1093/jxb/erad052/7033358 by INRA - DOCUMENTATION user on 28 March 2023

in specific areas related to the pedological substrate and hydrographic network. This determination relies on scientific or expert knowledge about the environment, climate, and hydrology across the whole landscape (Laudon *et al.*, 2018). Beyond water resource management, determining the landscape composition and configuration is the basis of landscape agroecology (Jeanneret *et al.*, 2021) (Eqn 12, Box 6).

WUE at the landscape level: biophysical metrics and scales

WUE_{land} can be quantified in relation to the water pathways at the scale of a local watershed of a few km^2 to a regional watershed of a few tens of km^2 (Wilson *et al.*, 2022) (Box 6). Because WUE_{land} aggregates WUE from the many crops/vegetation within the landscape, the aggregation is at scales of both time (Boxes 1–) and space. Aggregation at small scales of space include the ratios presented in Boxes 3 and 4, and these are expanded to gross/net primary productivity to plant transpiration or crop evapotranspiration at the scale of an agricultural field, and over time-scales that range from days to the full crop cycle (Box 6). Aggregation at larger spatial scales will include a mix of rain-fed and irrigated crops at different sizes and rely on a variety of hydric indicators such as rainfall, watershed wetting (the difference between rainfall and run-off, and including watershed-scale infiltration for crops and underlying aquifers), root-zone water content for crops only, and withdrawals from reservoirs used for irrigation (Du *et al.*, 2018; Abeshu *et al.*, 2021). These large-scale aggregations can be placed into different categories and allow the measurement of efficiency at different scales (land-use classes, watersheds, aquifers). These large-scale metrics are also defined across various time-scales, from days to the whole crop-cycle, including specific periods related to phenological stages when the balance between water needs and water availability is critical, as discussed above (e.g. grain-setting at the beginning of spring for rain-fed crops under semi-arid climates) (see Box 3).

Current research paths

WUE can be evaluated using actual data obtained by monitoring the implementation and subsequent impacts of new cropping systems or landscape infrastructures (*ex post* approaches), or using forecasts to evaluate the potential impacts of changes in landscape composition/configuration (*ex ante* approaches). *Ex post* evaluation allows changes to be assessed experimentally in real conditions with non-academic stakeholders, whilst *ex ante* approaches can provide guidance to stakeholders in the context of long-term adaptations linked to global changes. Both approaches have to be considered simultaneously in the design and assessment of integrated water management policies (Hashemi *et al*, 2019).

At the landscape scale, the current challenge is to evaluate WUE_{land} both from an integrated viewpoint across the watershed, which is the analysis/decision level of interest for decision-makers, and from a local viewpoint from the perspective of the agricultural field, which is the analysis/decision level for farmers. This scientific challenge presents various research avenues (Eqn 12, Box 6). The first avenue is the development of observation methods at defined spatial scales for characterizing the landscape composition and configuration, including classes, delineations, geometries, and functional properties, and for characterizing these variables in relation to WUE indicators, namely rainfall, evapotranspiration, run-off, and soil moisture. Recent research has focused on various innovations and limitations related to the assessment of these variables using remote sensing (Jacob *et al.*, 2014; Weiss *et al*, 2020; Deliry *et al.*, 2021; Chen *et al.*, 2022). The second avenue is the design of agro-hydrological models that simulate both crop functioning and water fluxes within a landscape in a coupled manner (e.g., Lebon *et al.*, 2022). Agro-hydrological models are potential tools for *exante* assessment of WUE at the landscape scale when evaluating possible choices of cropping systems or landscape management modes in accordance with predicted climate scenarios (Krysanova *et al.*, 2015). The third avenue is the formulation of scenarios about how the landscape composition and configuration will evolve. Such scenarios, which should be compatible with the formalisms of agro-hydrological models for evaluation purposes, require the design of landscape modeling tools that can be used with participative protocols in order to take into account the drivers of stakeholder strategies (De Girolamo and Lo Porto, 2012).

Conclusions

It is a long way from intrinsic transpiration efficiency at the leaf level to the improvement of water use efficiency at farm system/landscape level. In this review we have attempted to draw a path and show the connections, as well as the trade-offs, between increasing biological, physical, hydrological, and human scales. While additive efficiency gains can be made at each of these different scales, overall gains in water use efficiency can only be made if the scales are connected and if the numerous trade-offs along the way are meaningfully addressed. In this context, human decisions, often moulded by societal/policy influences, very likely represent the main level of influence on landscape WUE, for example the choice of a water-efficient crop species, a water-efficient irrigation system, or a landscape allocation/design that will maximize return on water. However, even when these choices are made, there remains a lot of room for WUE improvement from the plant/crop perspective, following the agronomic levers presented in Box 3, and using water-efficient cultivars developed from plant traits described in Boxes 1 and 2. Equation 12 in Box 6 is our attempt to put together the levers that exist to increase WUE from the organ/plant/crop/field perspective (Boxes 1–4) with the aspects of the human and societal dimension that only

Downloaded from https://academic.oup.com/jxb/advance-article/doi/10.1093/jxb/erad052/7035358 by INRA - DOCUMENTATION user on 28 March 2023

appear when plants/crops become part of a landscape, and to highlight necessary trade-offs (for instance for ecosystem services) within and beyond the landscape scale.

Supplementary data

The following supplementary data are available at JXB online.

Appendix S1. The availability and quality of data as an important limiting factor in the analysis of water use efficiency.

Acknowledgements

The paper was written and supported under the Make Our Planet Great Again (MOPGA) ICARUS project (Improve Crops in Arid Regions and Future Climates), and written within the scope and with the support of the ClimBeR initiative of CGIAR, itself supported by the France-CGIAR Action Plan on Climate Change.

Author contributions

All authors participated in the overall design of the paper and in the writing of the individual sections;VV collated and developed the sections to produce the complete review, and developed the Boxes, all with input from the other authors.

Conflict of interest

The authors declare that they have no conflicts of interest in relation to this work.

Funding

The Make Our Planet Great Again (MOPGA) ICARUS project (Improve Crops in Arid Regions and Future Climates) is funded by the Agence Nationale de la Recherche (ANR, grant ANR-17-MPGA-0011).

Data availability

No new data were generated in this review.

References

Abdalla M, Ahmed MA, Cai G, Wankmüller F, Schwartz N, Litig O, Javaux M, Carminati A. 2022. Stomatal closure during water deficit is controlled by below-ground hydraulics. Annals of Botany **129**, 161–170.

Abeshu GW, Li HY. 2021. Horton Index: conceptual framework for exploring mult-scale links between catchment water balance and vegetation dynamics. Water Resources Research **57**, e2020WR029343.

Abunyewa A, Ferguson RB, Wortmann CS, Lyon DJ, Mason SC, Klein RN. 2010. Skip-row and plant population effects on Sorghum grain yield. Agronomy Journal **102**, 296–302.

Affortit P, Effa-Effa B, Ndoye MS, *et al*. 2022. Physiological and genetic control of transpiration efficiency in African rice, *Oryza glaberrima* Steud. Journal of Experimental Botany **73**, 5279–5293.

Ahmed MA, Zarebanadkouki M, Ahmadi K, Kroener E, Kostka S, Kaestner A, Carminati A. 2018. Engineering rhizosphere hydraulics: pathways to improve plant adaptation to drought. Vadose Zone Journal **17**, 160090.

Akridge JT. 1989. Measuring productive efficiency in multiple product agribusiness firms: a dual approach. American Journal of Agriculture Economics **71**, 116–125.

Aznar O, Michelin Y, Perella G, Turpin N. 2006. Landscape at the crossroads, towards a 'geo-economic' analysis of rural landscapes. First Workshop on Landscape Economics, Angers, Horticulture National Institute, 9–10 June 2006, 2006. 17.

Batchelor C, Reddy VR, Linstead C, Dhar M, Roy S, May R. 2014. Do water-saving technologies improve environmental flows? Journal od Hydrology **518**, 140–149.

Battesse GE, Coelli TJ. 1995. A model for technical inefficiency effects in a stochastic frontier production function for panel data. Empirical Economics **20**, 325–332.

Beggi F, Falalou H, Buerkert A, Vadez V. 2015. Tolerant pearl millet (*Pennisetum glaucum* (L.) R. Br.) varieties to low soil P have higher transpiration efficiency and lower flowering delay than sensitive ones. Plant and Soil **389**, 89–108.

Blatt MR, Jezek M, Lew VL, Hills A. 2022. What can mechanistic models tell us about guard cells, photosynthesis, and water use efficiency? Trends in Plant Science **27**, 166–179.

Blum A. 2009. Effective use of water (EUW) and not water-use efficiency (WUE) is the target of crop yield improvement under drought stress. Field Crops Research **112**, 119–123.

Bos MG, Nugteren J. 1990. On irrigation efficiencies, 4th edn. Publication 19. Wageningen, the Netherlands: International Institute for Land Reclamation and Improvement.

Buckley TN. 2017. Modeling stomatal conductance. Plant Physiology **174**, 572–582.

Buesa I, Caccavello G, Merli MC, Poni S, Intrigliolo DS. 2017. East–west vineyard trellis system orientation improves water use efficiency and productivity of potted grapevines. Acta Horticulturae **1188**, 35–42.

Cai G, Ahmed MA, Abdalla M, Carminati A. 2022. Root hydraulic phenotypes impacting water uptake in drying soils. Plant, Cell & Environment **45**, 650–663.

Caine RS, Yin X, Sloan J, *et al*. 2019. Rice with reduced stomatal density conserves water and has improved drought tolerance under future climate conditions. New Phytologist **221**, 371–384.

Calvo-Polanco M, Ribeyre Z, Dauzat M, *et al*. 2021. Physiological roles of Casparian strips and suberin in the transport of water and solutes. New Phytologist **232**, 2295–2307.

Carminati A, Ahmed MA, Zarebanadkouki M, Cai G, Lovric G, Javaux M. 2020. Stomatal closure prevents the drop in soil water potential around roots. New Phytologist **226**, 1541–1543.

Carminati A, Javaux M. 2020. Soil rather than xylem vulnerability controls stomatal response to drought. Trends in Plant Science **25**, 868–880.

Carminati A, Passioura JB, Zarebanadkouki M, Ahmed MA, Ryan PR, Watt M, Delhaize E. 2017. Root hairs enable high transpiration rates in drying soils. New Phytologist **216**, 771–781.

Chaves MM, Costa JM, Zarrouk O, Pinheiro C, Lopes CM, Pereira JS. 2016. Controlling stomatal aperture in semi-arid regions—the dilemma of saving water or being cool? Plant Science **251**, 54–64.

Chen S, Arrouays D, Mulder VL, *et al*. 2022. Digital mapping of *GlobalSoilMap* soil properties at a broad scale: a review. Geoderma **409**, 115567.

Chenoune R, Allen T, Komarek AM, Paloma SGY, Flichman G, Capillon A, Belhouchette H. 2017. Assessing consumption-production-resources nexus decisions for rice-focused agricultural households in Sierra Leone. Land Use Policy **67**, 597–607.

Choudhary S, Guha A, Kholova J, Pandravada A, Messina CD, Cooper M, Vadez V. 2020. Maize, sorghum, and pearl millet have highly

Downloaded from https://academic.oup.com/jxb/advance-article/doi/10.1093/jxb/erad052/7033358 by INRA - DOCUMENTATION user on 28 March 2023

contrasting species strategies to adapt to water stress and climate change-like conditions. Plant Science **295**, 110297.

Choudhary S, Sinclair TR, Messina CD, Cooper M. 2014. Hydraulic conductance of maize hybrids differing in transpiration response to vapor pressure deficit. Crop Science **54**, 1147–1152.

Colin F, Moussa R, Louchart X. 2012. Impact of the spatial arrangement of land management practices on surface runoff for small catchments. Hydrological Processes **26**, 255–271.

Condon AG. 2020. Drying times: plant traits to improve crop water use efficiency and yield. Journal of Experimental Botany **71**, 2239–2252.

Condon AG, Richards RA, Rebetzke GJ, Farquhar GD. 2002. Improving intrinsic water-use efficiency and crop yield. Crop Science **42**, 122–131.

Condon AG, Richards RA, Rebetzke GJ, Farquhar GD. 2004. Breeding for high water-use efficiency. Journal of Experimental Botany **55**, 2447–2460.

Cooper PJM, Keatinge JDH, Hughes G. 1983. Crop evapotranspiration: a technique for calculation of its components by field measurements. Field Crops Research **7**, 299–312.

Coupel-Ledru A, Lebon E, Christophe A, Gallo A, Gago P, Pantin F, Doligez A, Simonneau T. 2016. Reduced nighttime transpiration is a relevant breeding target for high water-use efficiency in grapevine. Proceedings of the National Academy of Sciences, USA **113**, 8963–8968.

Couvreur V, Vanderborght J, Javaux M. 2012. A simple three-dimensional macroscopic root water uptake model based on the hydraulic architecture approach. Hydrology and Earth System Sciences **16**, 2957–2971.

Cresswell HP, Painter DJ, Cameron KC. 1993. Tillage and water content effects on surface soil hydraulic properties and shortwave albedo. Soil Science Society of America Journal **57**, 816–824.

De Girolamo AM, Lo Porto A. 2012. Land use scenario development as a tool for watershed management within the Rio Mannu Basin. Land Use Policy **29**, 691–701.

DeLaune PB, Sij JW, Park SC, Krutz LJ. 2012. Cotton production as affected by irrigation level and transitioning tillage systems. Agronomy Journal **104**, 991–995.

Deliry SI, Avdan U. 2021. Accuracy of unmanned aerial systems photogrammetry and structure from motion in surveying and mapping: a review. Journal of the Indian Society of Remote Sensing **49**, 1997–2017.

Dodd IC, Egea G, Davies WJ. 2008. Abscisic acid signalling when soil moisture is heterogeneous: decreased photoperiod sap flow from drying roots limits abscisic acid export to the shoots. Plant, Cell a&nd Environment **31**, 1263–1274.

Du L, Mikle N, Zou Z, Huang Y, Shi Z, Jiang L, McCarthy HR, Liang J, Luo Y. 2018. Global patterns of extreme drought-induced loss in land primary production: identifying ecological extremes from rain-use efficiency. Science of the Total Environment **628**, 611–620.

Dunn J, Hunt L, Afsharinafar M, Meselmani MA, Mitchell A, Howells R, Wallington E, Fleming AJ, Gray JE. 2019. Reduced stomatal density in bread wheat leads to increased water-use efficiency. Journal of Experimental Botany **70**, 4737–4748.

El Ansari L, Chenoune R, Yigezu YA, Gary C, Belhouchette H. 2020. Trade-offs between sustainability indicators in response to the production choices of different farm household types in drylands. Agronomy **10**, 998.

El-Hendawy SE, Hokam EM, Schmidhalter U. 2008. Drip irrigation frequency: the effects and their interaction with nitrogen fertilization on sandy soil water distribution, maize yield and water use efficiency under Egyptian conditions. Journal of Agronomy and Crop Science **194**, 180–192.

Ermakova M, Lopez-Calcagno PE, Raines CA, Furbank RT, von Caemmerer S. 2019. Overexpression of the Rieske FeS protein of the Cytochrome *b6f* complex increases C_4 photosynthesis in *Setaria viridis*. Communications Biology **2**, 314.

Faloye OT, Alatise MO, Ajayi AE, Ewulo BS. 2019. Effects of biochar and inorganic fertiliser applications on growth, yield and water use efficiency of maize under deficit irrigation. Agricultural Water Management **217**, 165–178.

Fan T, Stewart BA, Yong W, Junjie L, Guangye Z. 2005. Long-term fertilization effects on grain yield, water-use efficiency and soil fertility in the dryland of Loess Plateau in China. Agriculture, Ecosystems & Environment **106**, 313–329.

Farquhar GD, O'Leary MH, Baxter JA. 1982. On the relationship between carbon isotope discrimination and intercellular carbon dioxide concentration in leaves. Australian Journal of Plant Physiology **9**, 121–137.

Fletcher AL, Sinclair TR, Allen LH. 2007. Transpiration responses to vapor pressure deficit in well watered 'slow-wilting' and commercial soybean. Environmental and Experimental Botany **61**, 145–151.

Franks PJ, Doheny-Adams TW, Britton-Harper ZJ, Gray JE. 2015. Increasing water-use efficiency directly through genetic manipulation of stomatal density. New Phytologist **207**, 188–195.

French RJ, Schultz JE. 1984. Water use efficiency of wheat in a Mediterranean-type environment. I. The relation between yield, water use and climate. Australian Journal of Agricultural Research **35**, 743–764.

Fricke W. 2019. Night-time transpiration – favouring growth? Trends in Plant Science **24**, 311–317.

Furbank RT. 2017. Walking the C_4 pathway: past, present, and future. Journal of Experimental Botany **67**, e1–e10.

Galindo A, Collado-González J, Griñán I, *et al*. 2018. Deficit irrigation and emerging fruit crops as a strategy to save water in Mediterranean semi-arid agrosystems. Agricultural Water Management **202**, 311–324.

Głowacka K, Kromdijk J, Kucera K, Xie J, Cavanagh AP, Leonelli L, Leakey ADB, Ort DR, Niyogi KK, Long SP. 2018. *Photosystem II Subunit S* overexpression increases the efficiency of water use in a field-grown crop. Nature Communications **9**, 868.

Habets F, Molénat J, Carluer N, Douez O, Leenhardt D. 2018. The cumulative impacts of small reservoirs on hydrology: a review. Science of the Total Environment **643**, 850–867.

Habibi Davijani M, Banihabib ME, Nadjafzadeh Anvar A, Hashemi SR. 2016. Multi-objective optimization model for the allocation of water resources in arid regions based on the maximization of socioeconomic efficiency. Water Resources Management **30**, 927–946.

Hashemi MS, Bagheri A, Rizzoli AE. 2019. The role of ex-post and ex-ante integrated assessment frameworks in conceptualization of the modeling process in the context of integrated water resources management. Water Resources **46**, 296–307.

Hatfield JL, Dold C. 2019. Water-use efficiency: advances and challenges in a changing climate. Frontiers in Plant Science **10**, 103.

Hatfield JL, Sauer TJ, Prueger JH. 2001. Managing soils to achieve greater water use efficiency: a review. Agronomy Journal **93**, 271–280.

Hendel E, Bacher H, Oksenberg A, Walia H, Schwartz N, Peleg Z. 2021. Deciphering the genetic basis of wheat seminal root anatomy uncovers ancestral axial conductance alleles. Plant, Cell & Environment **44**, 1921–1934.

Hossard L, Fadlaoui A, Ricote E, Belhouchette H. 2021. Assessing the resilience of farming systems on the Saïs plain, Morocco. Regional Environmental Change **21**, 36.

Howell TA. 2003. Irrigation efficiency. In: Stewart BA, Howell TA. eds. Encyclopedia of water science. New York: Marcel Dekker, 467–472.

Hsiao TC, Steduto P, Fereres E. 2007. A systematic and quantitative approach to improve water use efficiency in agriculture. Irrigation Science **25**, 209–231.

Hughes J, Hepworth C, Dutton C, Dunn JA, Hunt L, Stephens J, Waugh R, Cameron DD, Gray JE. 2017. Reducing stomatal density in barley improves drought tolerance without impacting on yield. Plant Physiology **174**, 776–787.

Hunter JJK, Tarricone L, Volschenk C, Giacalone C, Melo MS, Zorer R. 2020. Grapevine physiological response to row orientation-induced spatial radiation and microclimate changes. OENO One **54**, 411–433.

Huxley PA, Pinney A, Akunda E, Muraya P. 1994. A tree/crop interface orientation experiment with a *Grevillea robusta* hedgerow and maize. Agroforestry Systems **26**, 23–45.

Igbadun Henry E, Ramalan AA, Oiganji E. 2012. Effects of regulated deficit irrigation and mulch on yield, water use and crop water productivity of onion in Samaru, Nigeria. Agricultural Water Management **109**, 162–169.

Downloaded from https://academic.oup.com/jxb/advance-article/doi/10.1093/jxb/erad052/7035358 by INRA - DOCUMENTATION user on 28 March 2023

Iqbal R, Raza MAS, Toleikiene M, *et al*. 2020. Partial root-zone drying (PRD), its effects and agricultural significance: a review. Bulletin of the National Research Center **44**, 159.

Israel D, Khan S, Warren CR, Zwiazek JJ, Robson TM. 2021. The contribution of PIP2-type aquaporins to photosynthetic response to increased vapour pressure deficit. Journal of Experimental Botany **72**, 5066–5078.

Israelson OW. 1950. Irrigation principles and practices. Wiley, New York.

Jacob F, Weiss M. 2014. Mapping biophysical variables from solar and thermal infrared remote sensing: focus on agricultural landscapes with spatial heterogeneity. IEEE Geoscience and Remote Sensing Letters **11**, 1844–1848.

Jeanneret P, Aviron S, Alignier A, Helfenstein J, Herzog F, Kay S, Petit S. 2021. Agroecology landscapes. Landscape Ecology **36**, 2235–2257.

Jensen M. 2007. Beyond irrigation efficiency. Irrigation Science **25**, 233–245.

Jovanovic N, Pereira LS, Paredes P, Pôças I, Cantore V, Todorovic M. 2020. A review of strategies, methods and technologies to reduce non-beneficial consumptive water use on farms considering the FAO56 methods. Agricultural Water Management **239**, 106267.

Karagiannis G, Tzouvelekas V, Xepapadeas A. 2003. Measuring irrigation water efficiency with a stochastic production frontier: an application to Greek out-of-season vegetable cultivation. In: Pashardes P, Swanson T, Xepapadeas A. eds. Current issues in the economics of water resource management. Economy & Environment, vol. **23**. Dordrecht: Springer, 85–101.

Kholova J, Hash CT, Kumar PL, Yadav RS, Kocova M, Vadez V. 2010. Terminal drought-tolerant pearl millet *Pennisetum glaucum* (L.) R. Br. have high leaf ABA and limit transpiration at high vapour pressure deficit. Journal of Experimental Botany **61**, 1431–1440.

Kholová J, Murugesan T, Kaliamoorthy S, *et al*. 2014. Modelling the effect of plant water use traits on yield and stay-green expression in sorghum. Functional Plant Biology **41**, 1019–1034.

Koehler T, Moser DS, Botezatu A, *et al*. 2022. Going underground: soil hydraulic properties impacting maize responsiveness to water deficit. Plant and Soil **478**, 43–58.

Koontz TM, Newig J. 2014. From planning to implementation: top-down and bottom-up approaches for collaborative watershed management. Policy Studies Journal **42**, 416–442.

Krysanova V, Srinivasan R. 2015. Assessment of climate and land use change impacts with SWAT. Regional Environmental Change **15**, 431–434.

Lasage R, Verburg PH. 2015. Evaluation of small-scale water harvesting techniques for semi-arid environments. Journal of Arid Environments **118**, 48–57.

Laudon H, Sponseller RA. 2018. How landscape organization and scale shape catchment hydrology and biogeochemistry: insights from a long-term catchment study. WIREs Water **5**, e1265.

Lawson T, Blatt MR. 2014. Stomatal size, speed, and responsiveness impact on photosynthesis and water use efficiency. Plant Physiology **164**, 1556–1570.

Leakey ADB, Ferguson JN, Pignon CP, Wu A, Jin Z, Hammer GL, Lobell DB. 2019. Water use efficiency as a constraint and target for improving the resilience and productivity of C_3 and C_4 crops. Annual Review of Plant Biology **70**, 781–808.

Lebon N, Dagès C, Burger-Leenhardt D, Molénat J. 2022. A new agro-hydrological catchment model to assess the cumulative impact of small reservoirs. Environmental Modelling & Software **153**, 105409.

Li SX, Wang ZH, Li SQ, Gao YJ, Tian XH. 2013. Effect of plastic sheet mulch, wheat straw mulch, and maize growth on water loss by evaporation in dryland areas of China. Agricultural Water Management **116**, 39–49.

Liao Y, Cao HX, Xue WK, Liu X. 2021. Effects of the combination of mulching and deficit irrigation on the soil water and heat, growth and productivity of apples. Agricultural Water Management **243**, 106482.

Liu J, Liu X, Wang Y, Li Y, Jiang Y, Fu Y, Wu J. 2020. Landscape composition or configuration: which contributes more to catchment hydrological flows and variations? Landscape Ecology **35**, 1531–1551.

Long SP, Marshall-Colon A, Zhu XG. 2015. Meeting the global food demand of the future by engineering crop photosynthesis and yield potential. Cell **161**, 56–66.

López-Calcagno PE, Brown KL, Simkin AJ, Fisk SJ, Vialet-Chabrand S, Lawson T, Raines CA. 2020. Stimulating photosynthetic processes increases productivity and water-use efficiency in the field. Nature Plants **6**, 1054–1063.

Manning DT, Lurbé S, Comas LH, Trout TJ, Flynn N, Fonte SJ. 2018. Economic viability of deficit irrigation in the Western US. Agricultural Water Management **196**, 114–123.

Manschadi AM, Christopher J, Devoil P, Hammer GL. 2006. The role of root architectural traits in adaptation of wheat to water-limited environments. Functional Plant Biology **33**, 823–837.

Maurel C, Simonneau T, Sutka M. 2010. The significance of roots as hydraulic rheostats. Journal of Experimental Botany **61**, 3191–3198.

McAusland L, Vialet-Chabrand S, Davey PA, Baker NR, Brendel O, Lawson T. 2016. Effects of kinetics of light-induced stomatal responses on photosynthesis and water-use efficiency. New Phytologist **211**, 1209–1220.

McCraw D, Motes J E. 1991. Use of plastic mulch and row covers in vegetable production. OSU Cooperative Extension Service, Extension Facts, 6034. Stillwater, Oklahoma: Oklahoma State University.

Medina S, Vicente R, Nieto-Taladriz MT, Aparicio N, Chairi F, Vergara-Diaz O, Araus JL. 2019. The plant-transpiration response to vapor pressure deficit (VPD) in durum wheat is associated with differential yield performance and specific expression of genes involved in primary metabolism and water transport. Frontiers in Plant Science **9**, 1994.

Mega R, Abe F, Kim JS, *et al*. 2019. Tuning water-use efficiency and drought tolerance in wheat using abscisic acid receptors. Nature Plants **5**, 153–159.

Messina CD, Hammer GL, Dong Z, Podlich D, Cooper M. 2009. Modelling crop improvement in a G×E×M framework via gene–trait–phenotype relationships. In: Sadras V, Calderini D. eds. Crop physiology. Academic Press, 235–581.

Messina CD, Sinclair TR, Hammer GL, Curan D, Thompson J, Oler Z, Gho C, Cooper M. 2015. Limited-transpiration trait may increase maize drought tolerance in the US corn belt. Agronomy Journal **107**, 1978–1986.

Nada RM, Abogadallah GM. 2014. Aquaporins are major determinants of water use efficiency of rice plants in the field. Plant Science **227**, 165–180.

Nasrallah A, Belhouchette H, Baghdadi N, Mhawej M, Darwish T, *et al.* 2020. Performance of wheat-based cropping systems and economic risk of low relative productivity assessment in a sub-dry Mediterranean environment. European Journal of Agronomy **113**, 125968.

Nielsen DC, Unger PW, Miller PR. 2005. Efficient water use in dryland cropping systems in the Great Plains. Agronomy Journal **97**, 364–372.

Niinemets U. 2010. A review of light interception in plant stands from leaf to canopy in different plant functional types and in species with varying shade tolerance. Ecological Research **25**, 693–714.

Oweis T, Hachum A. 2012. Supplemental irrigation: a highly efficient water-use practice. Aleppo, Syria: ICARDA.

Oweis T, Zhang H, Pala M. 2000. Water use efficiency of rainfed and irrigated bread wheat in a Mediterranean environment. Agronomy Journal **92**, 231–238.

Papanatsiou M, Petersen J, Henderson L, Wang Y, Christie JM, Blatt MR. 2019. Optogenetic manipulation of stomatal kinetics improves carbon assimilation, water use, and growth. Science **363**, 1456–1459.

Passioura JB. 1977. Grain yield, harvest index and water use of wheat. Journal of the Australian Institute of Agricultural Science **43**, 117–120.

Payne WA, Drew MC, Hossner LR, Lascano RJ, Onken AB, Wendt CW. 1992. Soil phosphorus availability and pearl millet water-use efficiency. Crop Science **32**, 1010–1015.

Pereira LS, Oweis T, Zairi A. 2002. Irrigation management under water scarcity. Agricultural Water Management **57**, 175–206.

Perez-Perez JG, Dodd IC, Botia P. 2012. Partial rootzone drying increases water-use efficiency of lemon Fino 49 trees independently of root-to-shoot ABA signalling. Functional Plant Biology **39**, 366–378.

Downloaded from https://academic.oup.com/jxb/advance-article/doi/10.1093/jxb/erad052/7033358 by INRA - DOCUMENTATION user on 28 March 2023

Pignon CP, Leakey ADB, Long SP, Kromdijk J. 2021. Drivers of natural variation in water-use efficiency under fluctuating light are promising targets for improvement in Sorghum. Frontiers in Plant Science **12**, 627432.

Pilloni R. 2022. Agronomical and physiological study of the response of sorghum and pearl millet crops to higher sowing density in the semi-arid tropics. PhD thesis, University of Montpellier.

Psomas A, Panagopoulos Y, Konsta D, Mimikou M. 2016. Designing water efficiency measures in a catchment in Greece using WEAP and SWAT models. Procedia Engineering **162**, 269–276.

Radin JW. 1990. Responses of transpiration and hydraulic conductance to root temperature in nitrogen- and phosphorus-deficient cotton seedlings. Plant Physiology **92**, 855–857.

Reddy PS, Tharanya M, Sivasakthi K, Srikanth M, Hash CT, Kholova J, Sharma KK, Vadez V. 2017. Molecular cloning and expression analysis of *Aquaporin* genes in pearl millet [*Pennisetum glaucum* (L) R. Br.] genotypes contrasting in their transpiration response to high vapour pressure deficits. Plant Science **265**, 167–176.

Reddy PS, Dhaware MG, Sivasakthi K, Divya K, Nagaraju M, Sri Cindhuri K, Kavi Kishor PB, Bhatnagar-Mathur P, Vadez V, Sharma KK. 2022. Pearl millet aquaporin gene PgPIP2;6 improves abiotic stress tolerance in transgenic tobacco. Frontiers in Plant Science **13**, 820996.

Richards RA, Passioura JB. 1989. A breeding program to reduce the diameter of the major xylem vessel in the seminal roots of wheat and its effect on grain yield in rain-fed environments. Australian Journal of Agricultural Research **40**, 943–950.

Roche D. 2015. Stomatal conductance is essential for higher yield potential of C_3 crops. Critical Reviews in Plant Sciences **34**, 429–453.

Rogers DH, Lamm FR, Alam M, Trooien TP, Clark GA, Barnes PI, Mankin K. 1997. Efficiencies and water losses of irrigation systems. Irrigation management series. Manhattan: Kansas State University Cooperative Extension Service.

Romero P, Gil-Muñoz R, del Amor FM, Valdés E, Fernández JI, Martinez-Cutillas A. 2013. Regulated deficit irrigation based upon optimum water status improves phenolic composition in Monastrell grapes and wines. Agricultural Water Management **121**, 85–101.

Ryan AC, Dodd IC, Rothwell SA, Jones R, Tardieu F, Draye X, Davies WJ. 2016. Gravimetric phenotyping of whole plant transpiration responses to atmospheric vapour pressure deficit identifies genotypic variation in water use efficiency. Plant Science **251**, 101–109.

Sadok W, Sinclair TR. 2010. Transpiration response of 'slow-wilting' and commercial soybean (*Glycine max* (L.) Merr.) genotypes to three aquaporin inhibitors. Journal of Experimental Botany **61**, 821–829.

Salas-González I, Reyt G, Flis P, *et al*. 2021. Coordination between microbiota and root endodermis supports plant mineral nutrient homeostasis. Science **371**, 6525.

Salter WT, Merchant AM, Richards RA, Trethowan R, Buckley TN. 2019. Rate of photosynthetic induction in fluctuating light varies widely among genotypes of wheat. Journal of Experimental Botany **70**, 2787–2796.

Schnepf A, Carminati A, Ahmed MA, *et al*. 2022. Linking rhizosphere processes across scales: opinion. Plant and Soil **478**, 5–42.

Schoppach R, Sadok W. 2012. Differential sensitivities of transpiration to evaporative demand and soil water deficit among wheat elite cultivars indicate different strategies for drought tolerance. Environmental and Experimental Botany **84**, 1–10.

Schoppach R, Wauthelet D, Jeanguenin L, Sadok W. 2014. Conservative water use under high evaporative demand associated with smaller root metaxylem and limited trans- membrane water transport in wheat. Functional Plant Biology **41**, 257–269.

Schroeder JI, Kwak JM, Allen GJ. 2001. Guard cell abscisic acid signalling and engineering drought hardiness in plants. Nature **410**, 327–330.

Sedelnikova OV, Hughes TE, Langdale JA. 2018. Understanding the genetic basis of C_4 Kranz anatomy with a view to engineering C_3 crops. Annual Review of Genetics **52**, 249–270.

Shaxson F, Barber R. 2003. Optimizing soil moisture for plant production, the significance of soil porosity. FAO Soils Bulletin, 79. Rome, Italy: Food and Agriculture Organization of the United Nations.

Simkin AJ. 2019. Genetic engineering for global food security: photosynthesis and biofortification. Plants **8**, 586.

Simkin AJ, Lopez-Calcagno PE, Davey PA, Headland LR, Lawson T, Timm S, Bauwe H, Raines CA. 2017. Simultaneous stimulation of sedoheptulose 1,7-bisphosphatase, fructose 1,6-bisphophate aldolase and the photorespiratory glycine decarboxylase-H protein increases CO_2 assimilation, vegetative biomass and seed yield in Arabidopsis. Plant Biotechnology Journal **15**, 805–816.

Sinclair TR, Devi J, Shekoofa A, Choudhary S, Sadok W, Vadez V, Riar M, Rufty T. 2017. Limited-transpiration response to high vapor pressure deficit in crop species. Plant Science **260**, 109–118.

Sinclair TR, Hammer GL, van Oosterom EJ. 2005. Potential yield and water-use efficiency benefits in Sorghum from limited maximum transpiration rate. Functional Plant Biology **32**, 945–952.

Sinclair TR, Tanner CB, Bennett JM. 1984. Water use efficiency in crop production. BioScience **34**, 36–40.

Sivasakthi K, Tharanya M, Zaman-Allah M, Kholová J, Thirunalasundari T, Vadez V. 2020. Transpiration difference under high evaporative demand in chickpea (*Cicer arietinum* L.) may be explained by differences in the water transport pathway in the root cylinder. Plant Biology **22**, 769–780.

Souissi I, Boisson J, Mekki I, Therond O, Flichman G, Belhouchette H 2018. Impact assessment of climate change on farming systems in the South Mediterranean area: a Tunisian case study. Regional Environmental Change **18**, 637–650.

Stroosnijder L, Moore D, Alharbi A, Argaman E, Biazin B, van den Elsen E. 2012. Improving water use efficiency in drylands. Current Opinion in Environmental Sustainability **4**, 497–506.

Tamang BG, Schoppach R, Monnens D, Steffenson BJ, Anderson JA, Sadok W. 2019. Variability in temperature-independent transpiration responses to evaporative demand correlate with nighttime water use and its circadian control across diverse wheat populations. Planta **250**, 115–127.

Tanaka DL, Aase JK. 1987. Fallow method influences on soil water and precipitation storage efficiency. Soil and Tillage Research **9**, 307–316.

Tardieu F. 2022. Different avenues for progress apply to drought tolerance, water use efficiency and yield in dry areas. Current Opinion in Biotechnology **73**, 128–134.

Tardieu F, Simonneau T, Parent B. 2015. Modelling the coordination of the controls of stomatal aperture, transpiration, leaf growth, and abscisic acid: update and extension of the Tardieu–Davies model. Journal of Experimental Botany **66**, 2227–2237.

Thompson AJ, Andrews J, Mulholland BJ, *et al*. 2007. Overproduction of abscisic acid in tomato increases transpiration efficiency and root hydraulic conductivity and influences leaf expansion. Plant Physiology **143**, 1905–1917.

Tsuda M, Tyree MT. 2000. Plant hydraulic conductance measured by the high pressure flow meter in crop plants. Journal of Experimental Botany **51**, 823–828.

Tyree MT. 1997. The Cohesion–Tension theory of sap ascent: current controversies. Journal of Experimental Botany **48**, 1753–1765.

Vadez V. 2014. Root hydraulics: the forgotten side of root in drought adaptation. Field Crops Research **165**, 15–24.

Vadez V, Choudhary S, Kholova J, Hash CT, Srivastava R, Ashok Kumar A, Prandavada A, Anjaiah M. 2021. Transpiration efficiency: insights from comparisons of C_4 cereal species. Journal of Experimental Botany **72**, 5221–5234.

Vadez V, Deshpande SP, Kholova J, Hammer GL, Borrell AK, Talwar HS, Hash CT. 2011. Stay-green quantitative trait loci's effects on water extraction, transpiration efficiency and seed yield depend on recipient parent background. Functional Plant Biology **38**, 553–566.

Vadez V, Kholova J, Medina S, Aparna K, Anderberg H. 2014. Transpiration efficiency: new insights into an old story. Journal of Experimental Botany **65**, 6141–6153.

Vadez V, Kholova J, Yadav RS, Hash CT. 2013. Small temporal differences in water uptake among varieties of pearl millet (*Pennisetum glaucum*

Downloaded from https://academic.oup.com/jxb/advance-article/doi/10.1093/jxb/erad052/7035358 by INRA - DOCUMENTATION user on 28 March 2023

(L.) R. Br.) are critical for grain yield under terminal drought. Plant and Soil **371**, 447–462.

Vereecken H, Huisman JA, Hendricks Franssen HJ, Brüggemann N, Bogena HR, Kollet S, Javaux M, van den Kruk J, Vanderborght J. 2015. Soil hydrology: recent methodological advances, challenges, and perspectives. Water Resources Research **51**, 2616–2633.

Verhoef A, Egea G. 2014. Modeling plant transpiration under limited soil water: comparison of different plant and soil hydraulic parameterizations and preliminary implications for their use in land surface models. Agricultural and Forest Meteorology **191**, 22–32.

Vialet-Chabrand SRM, Matthews JSA, McAusland L, Blatt MR, Griffiths H, Lawson T. 2017. Temporal dynamics of stomatal behavior: modeling and implications for photosynthesis and water use. Plant Physiology **174**, 603–613.

Way DA, Pearcy RW. 2012. Sunflecks in trees and forests: from photosynthetic physiology to global change biology. Tree Physiology **32**, 1066–1081.

Weiss M, Jacob F, Duveiller G. 2020. Remote sensing for agricultural applications: a meta-review. Remote Sensing of Environment **236**, 111402.

Whalley WR, Ober ES, Jenkins M. 2013. Measurement of the matric potential of soil water in the rhizosphere. Journal of Experimental Botany **64**, 3951–3963.

Wicks GA. 1968. Soil water storage during fallow in the Central Great Plains as influenced by tillage and herbicide treatments. Soil Science Society of America Journal **32**, 591–595.

Wilson CG, Papanicolaou AN, Abban BKF, Freudenberg VB, Ghaneeizad SM, Giannopoulos CP, Hilafu HT. 2022. Comparing spatial and temporal variability of the system water use efficiency in a Lower Mississippi River watershed. Journal of Hydrology: Regional Studies **42**, 101141.

Wu B, Zhang H, Wang D. 2018. Timely supplemental irrigation changed nitrogen use of wheat by regulating root vertical distribution. Journal of Plant Nutrition and Soil Science **181**, 396–408.

Xie K, Wang XX, Zhang R, Gong X, Zhang S, Mares V, Gavilan C, Adolfo P, Roberto Q. 2012. Partial root-zone drying irrigation and water utilization efficiency by the potato crop in semi-arid regions in China. Scientia Horticulturae **134**, 20–25.

Yang G, Luo X, Nie Y, Zhang X. 2014. Effects of plant density on yield and canopy micro environment in hybrid cotton. Journal of Integrative Agriculture **13**, 2154–2163.

Yang Z, Liu J, Tischer SV, Christmann A, Windisch W, Schnyder H, Grill E. 2016. Leveraging abscisic acid receptors for efficient water use in Arabidopsis. Proceedings of the National Academy of Sciences, USA **113**, 6791–6796.

Yigezu YA, Ahmed MA, Shideed K, AW-Hassan A, El-Shater T, Al-Atwan S. 2013. Implications of a shift in irrigation technology on resource use efficiency: a Syrian case. Agricultural Systems **118**, 14–22.

Zaman-Allah M, Jenkinson DM, Vadez V. 2011. A conservative pattern of water use, rather than deep or profuse rooting, is critical for the terminal drought tolerance of chickpea. Journal of Experimental Botany **62**, 4239–4252.

Zhang Y, Liu B, Jia G, *et al*. 2022. Scaling up from leaf to whole-plant level for water use efficiency estimates based on stomatal and mesophyll behaviour in *Platycladus orientalis*. Water **14**, 263.

Zhou X, Schnepf A, Vanderborght J, Leitner D, Lacointe A, Vereecken H, Lobet G. 2020. CPlantBox, a whole-plant modelling framework for the simulation of water- and carbon-related processes. In silico Plants **2**, diaa001.

Downloaded from https://academic.oup.com/jxb/advance-article/doi/10.1093/jxb/erad052/7033358 by INRA - DOCUMENTATION user on 28 March 2023