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Water Use Efficiency (WUE) across scales: From genes to landscape

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Highlights

This paper reviews ways to improve water use efficiency beyond the plant level, across time and space scales, from cells, organs, and plants, to field, farm, and landscape.

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Abstract

Water scarcity will be one of the main issues of the 21st century, because of competing needs between civil, industrial, and agriculture use. While agriculture is the largest user of water, its share is bound to decrease as societies develop. Clearly, agriculture needs to become more water efficient. Improving water use efficiency (WUE) at the plant level is important although there is a long way into translating this at the farm/landscape level. As we move up from a cell/organ/plant scale to more integrated scales such as plot, field, farm system, and landscape, other factors need to be considered, including trade-offs, to possibly improve WUE. These include choices of crop variety/species, farm management, landscape design, infrastructure development, ecosystem functions, where human decisions matter. This review is a cross-disciplinary attempt to analyze ways to address WUE at these different scales where metrics of analysis are defined and trade-offs considered. The equations in this perspective paper use similar metrics across scales for an easier connection 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.

Key words: Climate change, food security, farming system, drought, landscape, breeding.

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Introduction

Agriculture is the largest consumer of water. Yet, 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 temperature increase also brings another complexity, increasing plant water demand, then jeopardizing crop functioning and indirectly surface, subsurface and ground water resources that supply these crops, either rainfed or irrigated. Therefore, agriculture of 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 to crop improvement. The purpose of this paper is to have that broader look on the functioning of plants and crops and on the multiscale levels of water efficiency, therefore going beyond the mere focus on “water use efficiency” of the plant science community.

Making an efficient use of water in agriculture has been the object of much research, and has been addressed at different scales, with different metrics and considerations. In the domain of plant science, “water use efficiency” or “transpiration efficiency” have been the main two metrics, which represent broadly a quantity of biomass produced (from units of CO₂ 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 time scale that vary from the sub-second scale to the duration of a crop cycle (Farqhar et al., 1982; Condon et al, 2002, 2004; Vadez et al., 2014; Hatfield and Dold 2019). The term “efficiency” can also be expanded beyond biomass and can be expressed in units of yield, income, calories, energy, feed value, protein (etc...) per unit of water use in a farming system perspective, giving a socio-economic angle to the notion of water use efficiency. In the domain of farm engineering, the term “irrigation efficiency” is a usual metric that represents the proportion of water (i.e. water from dams, reservoir, rivers, groundwater,..., i.e. 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 water reservoirs to irrigated fields, increasing irrigation efficiency is then about minimizing the part of water that runs off the fields, gets evaporated, or percolates below the root zone. If 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 infiltrated water recharges the groundwater tables, which supply irrigation at the same spot or elsewhere, and fulfill ecosystem services. Finally, it is worth noting that the spatial approach we discuss here needs

to be combined with a temporal dimension, where water paths 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, specie, 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. This paper/viewpoint will present how different research domains collectively address the question of making a 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, as well as finding ways, metrics, and equations to connect these scales of analysis. The thread line of the paper is to address how different trait / crops / plants / anthropogenic actions can contribute to water use efficiency, taken in the broad sense, and whether existing observations and modelling methods can help connecting these scales.

Transpiration efficiency (TE) at plant/organ/cell level

Many studies aiming at better understanding TE have focused at the organ or cell scales to avoid confounding effects of canopy architecture or soil environment interactions (Viale-Chabrand *et al.*, 2017; Hatfield and Dold, 2019; Leakey *et al.*, 2019). At the leaf level, TE is referred to as intrinsic TE and defined as A/G_s , where A is the CO₂ assimilation by photosynthetic biochemistry and G_s is the stomatal conductance, or, instantaneous TE and defined as A/T , where T is the water lost by transpiration (see Box 1 for details and further derivations of the ratio). The timeframe is the second or less and the scale is that of a portion of a leaf. Equation 1 posits that possible avenues to increase A/T would imply increasing $C_a - C_i$ by rising the CO₂ concentration gradient between the atmosphere and the stomata chamber, through improvement in photosynthetic capacity, or by decreasing $W_i - W_a$ by lowering the water vapour gradient through reducing stomatal conductance (Box 1).

[Please insert Box 1 about here]

Improving intrinsic TE by increasing photosynthetic activity is the current object of many studies (Long *et al.*, 2015). In C3 plants, an exciting avenue consists in converting their

metabolism toward a C₄-like photosynthesis (Tardieu, 2022). However, inserting C₄ metabolism in C₃ plants is a challenging task as observed in rice (Furbank, 2016; Sedelnikova *et al.*, 2018). A more realistic target may consist in concentrating CO₂ toward the RuBP carboxylase/oxygenase (Rubisco) active sites by increasing mesophyll conductance to CO₂, especially in leaves exposed to saturating light. To that end, manipulating the expression of PIP aquaporins that are known to transport CO₂ from liquid phase in mesophyll cells is of particular interest (Israel *et al.*, 2021). Aquaporins expression or function have also been associated with intrinsic TE in rice (Nada and Abogadallah, 2014) and transpiration restriction at high evaporative demand in soybean (Sadok and Sinclair, 2010), pearl millet (Reddy *et al.*, 2017) and chickpea (Sivasakthi *et al.*, 2020). Another promising avenue to increase plant photosynthesis consist in accelerating ribulose-1:5-bisphosphate RuBP regeneration by increasing the levels of photosynthetic enzymes acting in the Calvin-Benson cycle (Long *et al.*, 2015; Simkin *et al.*, 2017) or stimulating the photosynthetic electron transport by overexpressing the Rieske FeS protein that is a key component of the cytochrome *b₆f* complex (Ermakova *et al.*, 2019; Simkin, 2019). In tobacco, overexpression of enzymes fructose-1,6-bisphosphatase/sedoheptulose-1,7-bisphosphatase from the Calvin-Benson cycle together with the red algal protein cytochrome *c₆* served this purpose and improved intrinsic TE and plant biomass in field conditions (López-Calcano *et al.*, 2020). In sum, while increasing intrinsic TE by boosting the photosynthetic activity has reported several potential avenues at the cell/organ scale, more efforts are still needed to demonstrate their value in whole plants.

Limiting *G_s* is another option that may appear less attractive to increase TE and may result in a decrease in carbon fixation in the linear parts of the *A* vs *G_s* relationship (Tardieu, 2022) although it could be interesting in the non-linear parts of that relationship where any further increase in *G_s* is only rewarded by a marginal *A* increase. Nevertheless, it is usually assumed that conservative stomatal strategies come at the expense of biomass production and yield under optimal conditions (Condon *et al.*, 2002; Blum, 2009; Roche, 2015), and that they may 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* may not necessarily lead to a decrease in *A* (Franks *et al.*, 2015; Yang *et al.*, 2016, 2019; Dunn *et al.*, 2019). For instance, robust and large-scale lysimetric assessments also challenged this common view that higher TE is bound to lower productivity, and showed in large sets of pearl millet, sorghum, and groundnut that higher TE was totally unrelated to total plant water use, itself relating directly to plant productivity (Vadez *et al.*,

2014). In another instance, transgenic wheat plants overexpressing the *Epidermal Patterning Factor (EPF)* showed increase in intrinsic TE with no change in *A*, biomass and yield as compared to control plants only when reduced stomatal density was no more than 50 % of that of control plants (Dunn *et al.*, 2019). Transgenic plants over-expressing the 9-cis-epoxycarotenoid-dioxygenase enzyme had higher ABA than the wild type and showed higher TE 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 RECEPTOR 6 (RCAR6)* also resulted in an unexpected increase in *A* and resulted in a higher intrinsic TE (Yang *et al.*, 2016). It is still unclear whether this ABA-related effect on *A* is related to an increase in mesophyll conductance to CO₂, greater Rubisco activity, or other pleiotropic aspects related to ABA effect on leaf characteristics such as stomatal density or leaf epinasty that could improve radiation interception (Thompson *et al.*, 2007; Yang *et al.*, 2016; Condon, 2020). Another interesting example come from the overexpression in tobacco of the *PHOTOSYSTEM II SUBUNIT S (PsbS)*, 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 keep the redox state of chloroplastic QUINONE A more oxidized, the later protein being an early signal for stomatal opening when reduced (Głowacka *et al.*, 2018). Plants with increased *PsbS* expression growing in field conditions showed increased non-photochemical quenching and lower *G_s* in response to light resulting in a 25% reduction in water loss per CO₂ assimilated (Głowacka *et al.*, 2018). Limiting night transpiration by limiting *G_s* under dark conditions also contribute to increase TE (Coupel-Ledru *et al.*, 2016; Fricke, 2019).

The dynamic / temporal responses of *G_s* to environmental conditions is a novel approach that has emerged in the literature in order to improve TE. In the field, fluctuations in light intensities and spectral qualities influencing the photosynthetic photon flux density (PPFD) largely influence *A* and *G_s* (Way and Pearcy, 2012). However, stomatal responses are an order of magnitude slower than photosynthetic responses (minutes versus seconds) which lead to a disconnection between *G_s* and *A*. This lag in *G_s* relative to *A* limits *A* as stomata are opening under increasing PPFD while it maintains unnecessary water loss after *A* has dropped under decreasing PPFD (Violet-Chabrand *et al.*, 2017). Simulations suggested that synchronization behavior in *G_s* and *A* could increase intrinsic TE by 20% in *Phaseolus vulgaris* under fluctuating PPFD (Lawson and Blatt, 2014). Manipulating stomatal movements to reduce *G_s* response time and improve water use and growth have been

achieved in *Arabidopsis thaliana* by overexpressing the *BLUE LIGHT-GATED K⁺ CHANNEL 1 (BLINK1)* specifically in guard cells. Mean half-time stomatal opening upon light exposure and closing upon dark exposure were accelerated by around 40% as compared with the control plants resulting in a 2.2 fold increase in biomass under fluctuating light without cost in water use by the plant, therefore increasing TE (Papanatsiou *et al.*, 2019). Interestingly, large variation have been observed for *A* and *G_s* among (McAusland *et al.*, 2016 in thirteen species varying in the shape of the stomata guard cells) and within species (Salter *et al.*, 2019 in wheat; Pignon *et al.*, 2021 in sorghum) which could be exploited. In summary, despite common belief, there appears to be several options to increase TE by tuning *G_s* without significantly altering *A*, which would allow to develop water efficient cultivars without significant yield trade-offs.

TE at plant/crop level – interaction with the environment (soil, atmosphere)

Transpiration efficiency (TE) at this scale is measured in grams of biomass dry weight produced per unit of water transpired (DW/T, in g biomass L⁻¹ water transpired), which then does not take into account the soil evaporation part, and operate at timescale of at least a day. This definition has been also expressed as $k_d / (e_a^* - e)_d$, (Sinclair *et al.*, 1984) (see Box 2 for details and further derivations of the equation). The purpose of the current section is mostly to address avenues to increase TE via the denominator term $((e_a^* - e)_d)$, which is putatively an environmental factor, while k_d is akin to the numerator term of Equation 2 that reflects the C_i/C_a ratio (see Box 1 and previous section for details on how to influence this ratio). The TE definition implies that TE would increase when the integration of the denominator over time is small. At a daily timescale, this would mean avoiding transpiration during periods of the day with the highest VPD. At the timescale of a crop season, avoiding periods with high VPD conditions would have the same effect, by early sowing for instance. Although the numerator term is considered as constant for C₃ and C₄ species (4 and 9 Pa respectively) (Sinclair *et al.*, 1984), results showed TE variations among C₄ species (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 more recent lysimetric method reconciled precision and throughput (Vadez *et al.*, 2014). Using large panels of cultivated germplasm of sorghum, pearl millet and groundnut, Vadez *et al.* (2014) reported large TE variation among germplasm. Many studies have used ¹³C discrimination as a proxy for TE, although a number of studies

have reported limits to the value of the method (see Vadez et al., 2014 for a detailed discussion and references).

Restricting transpiration under high VPD, has been shown to increase TE by crop simulation (Sinclair et al., 2005). This process translates for the plant 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 a decreased evaporative cooling, but since it is restricted to a few hours, it is expected to avoid excessive trade-off on CO₂ fixation. Integrated over the time course of a day, say, 12 hours ($n = 12$, 'i' in hours, Box 2), the numerator term would exclude the high vapor pressure gradients values of the midday hours, and then increase TE. The same could be integrated over the time scale of a crop season, say, $n=120$ days. Transpiration restriction to VPD demonstrated the unequivocal agronomical benefits of this phenotype under water limited conditions, as in maize (Messina *et al.*, 2015) and sorghum (Kholová *et al.*, 2014). Experimental evidence of genotypic variation for this trait has been reported in several species, i.e. soybean (Fletcher et al., 2007), pearl millet (Kholova et al., 2010), chickpea (Zaman-Allah et al., 2011), sorghum (Choudhary et al., 2014), wheat (Schoppach and Sadok, 2012).

[Please insert Box 2 about here]

As mentioned above, the first benefit of the transpiration restriction under high VPD is to increase TE. This has been shown in sorghum, where TE measured in the condition of a terminal stress was higher in germplasm lines (Kakker et al., unpublished), or in sorghum lines introgressed with staygreen QTL (Vadez et al., 2011), that restricted transpiration under high VPD. This was followed by a modelling assessment of the benefit of the transpiration restriction on yield in these same lines (Kholova et al., 2014). In maize, some lines with higher TE more tightly regulated their transpiration response to an increased VPD and had a change point at lower VPD levels than lines with lower TE (Ryan et al., 2016). As far as we know, there has been no other experimental report linking a milder transpiration response to VPD and higher TE, and additional experimental evidence is needed. Notably, pearl millet genotypes contrasting in the transpiration response to high VPD (Kholova et al., 2010) did not differ for TE (Vadez et al., 2013), suggesting that transpiration restriction does not always increase TE. The interpretation given in Kholova et al (2010) is that the transpiration restriction could result from a mix of fully close and fully open stomata, giving no intrinsic

TE benefit for the open stomata and yet reducing overall transpiration because of the close stomata.

The second benefit of the transpiration restriction under high VPD, and possibly the most important, comes from a more parsimonious water use at an early stage, which 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 (Zaman-Allah et al., 2011) and maize (Messina et al., 2015). Similar responses were observed in modern Spanish durum wheat lines grown under drought stress in field conditions (Medina *et al.*, 2019). Water availability at the grain filling period is indeed critical and has shown to have high grain yield return per mm of water, i.e. 55 kg ha⁻¹ mm⁻¹ water in wheat (Manshadi et al., 2006), about 40 kg ha⁻¹ mm⁻¹ in chickpea (Zaman-Allah et al., 2011), or 37-45 kg ha⁻¹ mm⁻¹ in pearl millet (Vadez et al., 2013). It 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 (Passioura et al., 1977, where T is water used for transpiration and HI is the harvest index) 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 next section and Box 3).

Late night transpiration, as was reported in wheat (Tamang et al., 2019), has been proposed as an avenue toward increasing TE, with the interpretation that this night time transpiration would also set the plant for an early onset of photosynthesis in the morning at more favorable VPD conditions, possibly related to a higher pre-dawn water status. That said, night time transpiration is not associated to any photosynthesis and would need to be limited. Up to 30% of plant water loss can take place at night in grape vines (Coupel-Ledru et al., 2016) - up to 55% in wheat (Schoppach et al., 2014), so that reducing night time transpiration would be a way of improving TE.

What possibly drives the transpiration restriction? - Water moves from the soil pores to the roots, and through the plant to the stomatal chamber to be transpired as vapour in the air according to the water potential gradient (Tyree, 1997). Hydraulic resistances have been identified at different levels in this continuum, affecting water gradient between the soil and the plant, within the plant or 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). However, accurate estimates of how soil

water stress affects plant transpiration are essential for reliable mechanistic model predictions (Verhoef and Egea, 2014), so that reliable exploration of possible effects on TE can be done. This is still needed 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 under drying soils (Carminati and Javaux, 2020; Carminati *et al.*, 2020; Abdalla *et al.*, 2022). It could interact with crop species / genotypes. An illustration of that came from the observation that maize and sorghum genotypes had lower TE in a sandy soil than in a high clay Vertisol, whereas TE was similar in both soils in pearl millet (Vadez et al., 2021). It was then proposed that species fitness should be specific to soil type and its interaction with environment (low/high VPD). Plants respond to soil matric potential (suction) rather than soil water content (SWC), which has long been understood and 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). In sum, a putative role of soil in possibly explaining transpiration restriction would need to be clarified (Box 2).

Experimental evidences further suggest 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 root and soil in transpiring plants (Cai et al., 2022; Carminati et al., 2017; Schnepf et al., 2022). Rhizosphere has also the potential to disrupt the connection between the soil and the plant. Engineering rhizospheric characteristics, by increasing mucilage production for example, may open up new avenues for crop production management and increase water use efficiency (Ahmed et al. 2018). In addition to their role in water capture, roots have been proposed 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 between aquaporin expression, diurnal variations in root hydraulic conductivity and transpiration that can be interpreted as a means for preventing a drop in water potential in the leaf when transpiration is high (Tsuda and Tyree, 2000). Transpiration restriction to high VPD has indeed been related to root conductance and its control by root and shoot aquaporins (Sadok and Sinclair, 2010; Reddy *et al.*, 2017, 2022; Sivasakthi *et al.*, 2020) but also leaf area (Choudhary *et al.*, 2020) or 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 reduction in xylem conductance has been associated with

increased TE in wheat (Richards and Passioura, 1989; Hendel *et al.*, 2021). In summary, there are two main benefits to restricting transpiration under high VPD (higher TE and more water for grain filling), on which several root traits and soil characteristics are likely to have a strong influence, and this would decrease the denominator term of Equation 4 (Box 2) and increase TE overall.

WUE at crop specie and crop agronomy level

This scale of assessment is the plot and is rather called water use efficiency (WUE) and the usual metrics is grain or biomass yield per millimeter of water used, i.e. $\text{kg ha}^{-1} \text{mm}^{-1}$ water used from either rainfall or irrigation (Box 3). For an easier connection to the other scales, this can also be expressed with the metrics from the previous section (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 (Equation 5 in Box 3). Equation 6 is then a daily integration over an entire crop cycle, following the integration developed in Box 2, where it comes out clearly that increasing WUE is about increasing TE (previous two sections) *and* minimizing soil evaporation and run-off.

[Please insert Box 3 about here, including the table below as part of Box 3]

Run-off occurs when rains (more rarely irrigation) are in excess of what the soil can absorb. The term of “precipitation use efficiency” (PUE) can be used and is an integration of the yield increments consecutive to any rainfall. Research on soil capacity to store more water has been a strategy to improve the efficiency of the precipitation in this rain fed conditions (Hatfield *et al.*, 2001). For example, over tilling of bare soil leads to a decrease in water and nutrient storage capacity that decreases the potential WUE of the future crop (Cresswell *et al.*, 1993). A scale up of the PUE is precipitation storage efficiency (PSE) that determines the capacity of a soil to be a more or less useful reserve for future crops. PSE is negatively affected by over tilling actions (Tanaka and Aase, 1987) and it was reported that PSE increased up to 40% from using herbicide to control weeds instead of conventional tillage (Wicks, 1968). Reasonable soil management showed then an avenue for increasing WUE as it has been demonstrated that PSE, PUE and WUE are related (Nielsen *et al.*, 2005) (Box 3). As far as soil evaporation is concerned, early vigor is a plant trait that has long been favored by breeders, ensuring a rapid cover of the ground, competing efficiently against weeds. A

faster soil coverage to reduce soil evaporation could also come from an increased sowing density, as this would reduce the evaporation component of the equation (Box 3). There are also promising avenues to decrease irrigation needs and improve WUE in semi-arid regions from advanced agronomic practices such as conservation tillage practices (DeLaune et al. 2012) or mulching practice (Igbadun et al., 2012; Liao et al., 2021), which are considered as an effective means to improve irrigation efficiency by reducing the fraction of water lost through non-beneficial soil evaporation. It also allows controlling weeds, reducing soil compaction, enhancing nutrient management and even incorporating additional nutrients (McCraw and Motes, 1991; Shaxson and Barber, 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, which will enhance water infiltration into soil, reduce runoff, and increase soil water storage (Li et al., 2013).

As far as the TE component of Equation 6 is concerned (Box 3), WUE of the crops can be affected by the management and optimized by the combination of the right genotype by management (GxM) interaction for a given E (environment) (Hsiao *et al.*, 2007; Messina *et al.*, 2009). In pearl millet, low soil P treatments were reported to decrease WUE (Beggi et al., 2015). An earlier report showed that both the intrinsic TE (A/T, Box 1) and the TE at the plant level (Gi/T, Box 2) were decreased about 10-fold by a low soil P treatment (Payne et al., 1992). This is to be related to the fact that low P nutrition also reduced plant hydraulic conductance (Radin, 1990). A number of reports also show an increased WUE as soil fertility increases (e.g. in wheat Fan et al., 2005; 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 increased WUE (French and Schultz, 1984; Hatfield *et al.*, 2001), and this was also interpreted as an effect of a limited leaf area index. In cotton, a higher sowing density affected the microclimate within the canopy when light transmission through the canopy increased light interception in some genotypes (Yang *et al.*, 2014). As an alternative interpretation, the benefit could also be the result of the combination with a decrease in VPD within the canopy (Box 2), allowing photosynthesis to continue at milder VPD, hence achieving higher intrinsic WUE gains (Box 1). Indeed, recent work on sorghum highlighted a significant increase in WUE when plants were grown under doubled sowing density, with a large genotypic variation in the response to the density treatment for WUE (Pilloni et al 2022). This may be contrasted with a lower WUE achieved in a skip-row planting and dry environment, and a higher WUE achieved in a skip-row planting and wetter

environment (Abunyewa et al 2010). In the dense canopy condition, high WUE was achieved in genotypes with both a strong transpiration response to the evaporative demand, and to higher light penetration within the canopy (Pilloni et al. 2022). The benefit then came from the association of an agronomic management modification (density) and a genetic trait dealing with canopy architecture that allowed light penetration within the canopy. Plant architectural traits seem to be driving this 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 angle distribution and foliage spatial aggregation. Still, from a canopy perspective, the way leaves are spatially distributed and how biomass is allocated to them changes significantly. Unfortunately, leaf areas are still largely represented with a 2D metrics (m^2), and more work is needed to better understand and measure leaf areas in 3D and consequently to gauge the role they play in light distribution through the canopy and what are the potential implications for the microclimate within the canopy.

WUE can be linked to crop architecture, orientation and association - Previous section shows well that adapting the management of an annual crop can directly impact its water budget. In the case of a perennial crop, the choice in the management of the crop must also be taken into account and adapted to the landscape. A striking example is that of the vineyard, where rows orientation in space impacted how soil temperature and soil water content evolved with depth in vine crops (Hunter *et al.*, 2020) which may have an impact on the 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 canopies. A change in orientation in a Shiraz vineyard from North-South to East-West significantly reduced the transpiration, by up to 13%, without any significant reduction in yield and its component leading to an increase in WUE (Buesa *et al.*, 2017). It was suggested that the better distribution of radiation received by east-west orientated rows during the dry and hot season, and the low photosynthetic efficiency of the north-south vines during the afternoon contributed to the increased WUE.

These differences in canopy structure and the link to WUE can be also considered in the case of intercropping between annual crops or between perennial and annual species. For example, maize yield in a maize/coffee tree intercropping increased by 50 to 80%, depending on the crop/tree proximity, compared to sole maize. This was possibly due to lower direct radiation, milder microclimate effect due to tree transpiration and lower maize exposure to wind (Huxley *et al.*, 1994). In this case, reduced wind exposure would decrease the evaporative demand to the benefit of WUE and, *in fine*, yield (Chaves *et al.*, 2016; Hatfield and Dold, 2019). All above mentioned case studies show the importance to design the combination of

crops in an agroecosystem that smartly use the different resources and environmental constraints driving the pattern of water consumption (See landscape section below).

Increasing WUE from a better irrigation efficiency

Irrigation efficiency, 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 transpiration component, decreased by a component of soil evaporation and run-off (similar to Box 3) and percolation below the root zone (Box 4).

[Please insert Box 4 about here]

Improvement of irrigation efficiency at field level could also be achieved by reducing field evapotranspiration from weeds, or adopting practices such as optimizing irrigation timing, reducing waterlogging, or using advanced irrigation techniques to reduce the wetted area (Batchelor et al., 2014; Richter et al., 2017, Hatfield and Dold, 2019). A series of new irrigation practices and technologies based on physiological mechanisms of crop responding to water deficit has been developed to enhance WUE. These irrigation strategies encompass deficit irrigation (DI), regulated deficit irrigation (RDI) and partial root zone drying irrigation (PRD), and could be applied by surface, sprinkler or drip irrigation methods and possibly sub-surface to avoid soil evaporation (El-Hendawy et al., 2008; Jovanovic et al., 2020).

Deficit irrigation (DI) is a water-saving strategy that was proposed to permit a certain level of crop water stress while maintaining economically viable yields (Pereira et al., 2002; Manning et al., 2018). In sustained deficit irrigation, a certain water reduction is applied continuously throughout the season without compromising crop yield significantly. Regulated deficit irrigation (RDI) targets certain phenological stages during which plants are less sensitive to water stress while crop water needs are fully met at the critical growth stages (Romero et al., 2013). The partial root zone drying irrigation (PRD) is another technique that subjects one-half of the root system to a dry or drying phase while the other half is irrigated. PRD targets the plant physiological response through the production of the abscisic acid (ABA) by the dried roots, which reduces leaf expansion and stomatal conductance (then 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 improves WUE mainly through: (i) an enhanced

guard cell signal transduction network that reduces leaves transpiration (Schroeder et al. 2001); (ii) an optimized stomatal control that improves photosynthesis to transpiration ratio (Iqbal et al., 2020); and (iii) a reduced evaporative surface area (Xie et al., 2012). However, there is still debate about the importance of ABA signalling in regulating WUE of plants exposed to PRD (e.g. Perez-Perez et al. 2012) because ABA production in the dry-exposed part of the root may not be sustained over time (Dodd et al. 2008) which would actually maintain photosynthesis of PRD plants by attenuating stomatal limitations.

In rain-fed agriculture of semi-arid regions, supplemental irrigation (SI) has emerged as a promising climate-resilient practice. It consists in 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 and Hachum, 2012). Several studies reported substantial increases in crop yields. For example, Oweis et al. (2000) showed that WUE of rainfed wheat can be substantially improved by adopting a level of SI to satisfy up to 2/3 of irrigation requirements, along with early sowing and appropriate levels of nitrogen. Timely SI at jointing and anthesis growth stages of wheat resulted in high grain yields and nitrogen use efficiency while achieving higher WUE as suggested by Wu et al. (2018). Chickpea yield were increased 30% by applying 40mm irrigation at the beginning of seed growth (Vadez et al., 2011) (Box 4).

Finally, combining both crop management and irrigation techniques are also an avenue to increase irrigation efficiency. In a review study that analyses the combined effect of mulching and drip irrigation, Zhang et al. (2022) found that combining film-mulching and drip irrigation improves significantly the crop yield and WUE compared to no mulch, and the improvements were affected by climatic and soil conditions, crop type and water consumption. This technique was more effective in planting areas with rainfall or water consumption less than 400 mm and areas with medium soil texture. Field crops showed a more sensitive WUE than vegetables under film-mulching drip irrigation, mainly due to the increased soil temperature that promote photosynthesis in vegetable crops and subsequently increased irrigation requirement.

Maximizing WUE at farm system level

Water efficiency at farm level is often calculated as the ratio of total farm production to the total amount of irrigation water used. If in economic terms the word production usually means the gross margin of a farm (revenue minus production costs), this efficiency may also be expressed in terms of the number of calories produced by the crops grown on the farm, or

by the negative or positive externalities that a farm can produce, e.g. the quantity of water used, nitrogen leached, organic matter, erosion, drainage, etc.

This efficiency is often considered on a per-hectare basis for easy comparison to regional level. To better understand this global 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 farm level is rarely used for rainfed crops. Finally, the concept of irrigation efficiency at farm level is often used to i) characterise and analyse the performance of farms with regard to the quantities of irrigation water involved, ii) to put forward and test the effect of technical (new varieties, new rotation, tillage) and socio-economic (water pricing, subsidies for more efficient irrigation systems) alternatives meant to improve water efficiency and consequently the overall performance of the farm, or (iii) to better understand the determinants that affect overall water efficiency (soil effects, rotation, irrigation systems).

The concept of water efficiency at farm level - The stochastic frontier production approach is the most widely used method to analyse technical efficiency (TE_i) in production (Battese and Coelli, 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 the effect of all other factors impacting efficiency (Yigezu et al., 2017). IWTE is calculated following Karagiannis et al., (2003) (Box 5). This efficiency formulation is based on three strong simplifications: all production factors other than water are less limiting, all these factors act in the same way on production, all these production factors are substitutable. For this reason, these factors are often expressed in monetary terms such as production costs, and not in quantitative terms for easier aggregation. In this case, we speak of ITCE: irrigation technical cost efficiency (Akridge, 1989) (see Equation 10 in Box 5). This formulation implies that improving farm efficiency could 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 (labour, access to resources and the market) and where several production objectives are targeted (food, economic, social, environmental). In this context, comparing and especially understanding the inefficiency 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 to be analysed. Here, the main issue in calculating efficiency is

not the mathematical formulation of efficiency, but the availability and quality of data (Appendix S1 for more details).

[Please insert Box 5 about here]

Water efficiency, production and resilience in arid areas - It is often assumed that better efficiency in the use of irrigation water would make it possible to safeguard water resources, improve crop production per hectare, reduce production costs by reducing irrigation doses, potentially reduce nitrate leaching, and finally, more globally, to improve farmer income. This type of conclusion must be handled with great caution when the analysis is carried out at farm level. Indeed, several dryland countries have implemented support policies to promote sprinkler and drip irrigation instead of submersion, which has led to higher productivity per hectare. However, intervening only on the water component has only allowed a modest improvement of irrigation efficiency, because several other production factors remained limiting (labour availability, adapted and certified seeds, fertility). In addition, access to water is often not available at the right time for the crop (e.g. grain filling time). In the efficiency equation, this leads to a reduction in the denominator (quantity of irrigation water) but a fairly small increase in the numerator, mostly expressed by the gross margin on the farm (Eq10, Box 5). One possible side effect even an increase in leaching (El Ansari et al., 2020), since irrigation rates are calculated for optimal yields and not yields limited by other factors.

Based on this observation, it is essential to combine the irrigation efficiency indicator with indicators that express all the ecosystem services (see also Section 6 and Box 6), aiming at 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 today in the drylands are those that are poor, with very limited access to the resource (low numerator and denominator in the efficiency equation).

The limits of water efficiency - By massively subsidising the renewal of irrigation systems, dryland countries sought to improve irrigation efficiency, increase farmer incomes, and preserve water resources. However, two unexpected effects occurred: (i) saving water per hectare also increased irrigated areas, hence total water use; (ii) the improvement of irrigation efficiency either led to a simplification of their cropping system, or partial/total replacement of traditional cropping systems based on cereals and legumes with more profitable crops. While this has led to a significant increase in farmer income per hectare, it also decreased the

diversity of cropping systems on the farm, and increased crop protection treatments. This quest for greater irrigation efficiency via the simplification of cropping systems has also been followed by a reduction in the diversity of farm households' food intake, as most or all of the production is now marketed, and leading to unbalanced diets (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 became either too dependent on water (Nasrallah et al., 2018), or the simplification of cropping systems that has followed this 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 tradeoffs between various and possibly antagonist water user needs (see more details in Box 6). Beyond satisfying the aforementioned needs, modulating water levels within different compartments (root zone, aquifers, surface reservoirs) is critical for the sustainability of systems that depend on rainfall directly (infiltration for rainfed crops) or indirectly (irrigation from aquifer or surface reservoir).

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 paper 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 several 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, as this is where the choice can be made between water efficient and inefficient crops (Box 6).

Analyzing and controlling the crop WUE at the landscape level 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), or preservation of aquatic environments (e.g., lakes, rivers, wetlands). In doing so, the analysis of water availability and uses leads to delineating landscapes in accordance to watershed, a hydrological spatial unit that permits to address the

drivers of soil water availability such as hydrological fluxes (infiltration, runoff, evaporation, transpiration, groundwater recharge) and their interactions within the hydrological cycle (Vereecken et al., 2015). Then, increasing crops WUE may have a negative impact on other water uses that have therefore to be both taken into account and quantified. In other words, at the landscape level, the challenge is to establish trade-offs between (1) one or more ecosystem functions of soil water supply that we seek to modulate in time and space to increase crops WUE, and (2) other ecosystem functions, such as stream flow variations, that we also seek to modulate. The landscape approach in 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 plant and animal organisms. This approach therefore requires involving a diversity of stakeholders and social groups with diverse and possibly antagonistic interests (national and local authorities, water production and distribution companies, fishermen, environmental no governmental organizations), a diversity that goes far beyond the circle of farmers or groups of farmers (Koontz and Newig, 2014).

[Please insert Box 6 about here]

The landscape-specific levers for steering and optimizing WUE are twofold (Box 6). The first lever is the choice of landscape composition (Stroosnijder et al., 2012). This involves (1) determining crops species and varieties adapted to climatic conditions and soil water availability, (2) specifying agricultural practices (e.g., type plowing date, seeding density and date, grassing, mulching) to be implemented for modulating rainwater infiltration or limiting evaporation, and (3) determining effective man-made infrastructures to appropriately distribute rainwater between landscape compartments (see Eq12 in Box 6). The main landscape infrastructures, are rainwater harvesting systems such as water reservoirs, terraces, and contour trenches or ridges that follow the topographic levels (Habets et al., 2018; Lasage and Verburg, 2015). The second lever for controlling WUE consists of reasoning the landscape configuration, namely (1) the spatial allocation of crops and practices, at the scales of subfield and field patchwork (Colin et al., 2012), and (2) the implementation of landscape infrastructures in specific areas related to pedological substrate and hydrographic network. This reasoning relies on scientific or expert knowledge about environment, climate and hydrology across the whole landscape (Laudon and Sponseller, 2018). Beyond water resource

management, reasoning landscape composition and configuration is the basis of landscape agroecology (Jeanneret et al., 2021) (eq12, Box 6).

WUE at the landscape level: biophysical metrics, scales - At the landscape level WUE can be quantified in relation to the water pathways at the scale of a local watershed with a few km² size to regional watershed with a few tens of km² size (Wilson et al., 2022) (Box 6). Because WUE at the landscape level is aggregating WUE from the many crops / vegetation from the landscape, the aggregation is both at a time scale (as in Boxes 1-2-3) and at the space scale. Small space scale aggregation includes previous ratios (Box 3-4) and expand to gross / net primary productivity to plant transpiration or crop evapotranspiration, at the spatial scale of an agricultural field, and over time scales that range from day to crop cycle (Box 6). Larger space scale aggregation would include a mix of rainfed and irrigated crops within any spatial extent, and rely on a variety of hydric indicators such as rainfall, watershed wetting (difference between rainfall and runoff and include watershed-scale infiltration for crop and underlying aquifers), root zone water content for crop only, or withdrawals within dams to be used for irrigation (Du et al., 2018; Abeshu and Li, 2021). These large-scale aggregations are spatially distributed and allow measuring efficiency at different scales (land use classes, watershed, aquifer). These large-scale metrics are also defined across various timescales, from daily timescale to the whole crop cycle, including specific periods related to phenological stages with critical balance between water needs and water availability, as was shown in Section 3 above (i.e., grain filling period at the beginning of spring for rainfed crops under semi-arid climate, or summer period for irrigated perimeters) (see Box 3).

Current research paths - WUE can be evaluated using (1) ex-post approaches, by monitoring the implementation and subsequent impacts of new cropping systems or landscape infrastructures, or (2) ex-ante approaches, by evaluating impacts of forecast scenarios about possible changes in landscape composition / configuration. Ex-post evaluation allows changes to be assessed experimentally in real conditions with non-academic stakeholders. Ex-ante approach allows to guide the latter, in the context of long-term adaptation linked to global changes. Both approaches have to be simultaneously considered 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 (1) from an integrated view across the watershed of interest that is the analysis / decision level for decision-makers, and (2) from a local viewpoint at the spatial grain of the agricultural field, which is the analysis / decision level for farmers. This scientific challenge determines several current research avenues (see Eq 12 in Box 6). The first avenue is the development of spatialized observation

methods for characterizing (1) landscape composition and configuration, including classes, delineations, geometries and functional properties; (2) the forementioned variables related to WUE indicators, namely rainfall, evapotranspiration, runoff and soil moisture - Current research focus on several limitations and innovations related to remotely sensed imagery to assess these variables (Jacob et Weiss, 2014; Weiss et al, 2020; Deliry and Avdan, 2021; Chen et al., 2022). The second avenue is the design of agro-hydrological models that simulate both crop functioning and water fluxes within landscape in a coupled manner (e.g., Lebon et al., 2022). Agro-hydrological models are potential tools for ex-ante assessment of WUE at the landscape scale when evaluating possible choices of cropping systems or landscape management modes in accordance to climate scenarios (Krysanova and Srinivasan, 2015). The third avenue is the formulation of evolution scenarios about landscape composition and configuration. Such scenarios, to 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 to account for drivers of stakeholder strategies (de Girolamo and Porto, 2012).

Conclusion

There is a long way from intrinsic water use efficiency at the leaf level to improve water efficiency at farm system / landscape level. This review attempted to draw a path and show connections, but also trade-offs, between biological, physical, hydrological and increasingly human scales. While additive efficiency gains can be made at each of these different scales, overall water use efficiency gains can only be made if these scales are connected and numerous trade-offs along the way are meaningfully addressed. In this context, human decisions, often moulded by societal/policy influence, represents very likely the main level of influence on landscape WUE, i.e. the choice of a water efficient crop specie or a water efficient irrigation system or a landscape allocation/design that would maximize return on water. Yet, once these choices are made, there remains a lot of room for WUE improvement from the plant/crop point of view, following agronomic levers from Box 3, and using water efficient cultivars developed from plant traits described in Box 1 and 2. Equation 12 of Box 6 is an attempt to put together (i) the levers to increase WUE from a organ/plant/crop/field angle (Box 1-4) and (ii) the human and society dimension aspects that only 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.

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Author contribution

All authors participated in the design of the paper and in the write up of different sections – VV aggregated the sections and developed a full version of the paper on which all authors commented - VV developed the boxes and received comments from all authors.

Conflict of interest

Authors declare they have no conflicts of interest.

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Captions

Box 1. TE at the leaf scale.

At the leaf level, TE is rather called “intrinsic transpiration efficiency” (TE_{int}) defined as A/G_s where A is the CO_2 assimilation by photosynthetic biochemistry and G_s is the stomatal conductance. Two equations describing the basic framework of A/T are proposed by Condon *et al.* (2004) and updated by Condon (2020) as follows, where G_{SC} and G_{SW} are the stomatal conductance for CO_2 and water, C_a and C_i are the CO_2 concentration in the air and in the stomatal chamber, and W_a and W_i are the vapour pressure in the air and in the stomatal chamber. Text boxes and arrows indicate possible levers affecting different terms of the equations.

[insert box 1 figure followed by table]

	Scale / model type	Notes – References – Web links
Time Frame	< seconds	
Scale	Cell - Leaf spot - Organ	
Models	Gs models	Tardieu <i>et al.</i> (2015) Buckley <i>et al.</i> (2017) and Blatt <i>et al.</i> (2022) reviewed different approaches of modelling stomatal conductance.

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Box 2. TE at the plant scale.

A definition of TE (Sinclair et al., 1984), gives a daily TE value such as $TE = G_d/T = k_d / (e_a^* - e)_d$, where G_d is the daily biomass accumulation, and T the plant transpiration. 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 Eq2 in Box 1, whereas $(e_a^* - e)_d$ is a term that represents the gradients of water vapor pressure deficit (VPD). The term k_d is akin to the numerator term of the previous definition in Eq2 of Box 1 (Condon et al., 2002). In the equations below, both terms were integrated at the time scale of a period 'n', where 'n' is in hours or days, so that TE was represented as the average of TE value over one such period (1 to n hours or days). Text boxes and arrows indicate possible levers affecting directly or indirectly the terms of the equations.

[insert box 2 figure followed by table]

	Scale / model type	Notes – References – Web links
Time Frame	Day(s)-Months	Up to a crop cycle
Scale	Plant-Crop	
Models	Functional–structural plant models (FSPM) - Crop models in Box3	https://www.quantitative-plant.org/model/cplantbox CPlantBox (Zhou <i>et al.</i> , 2020)

Box 3. WUE at the crop/field scale.

At this scale TE is rather called WUE (water use efficiency) and is the ratio of grain yield to water used, coming either from rainfall or irrigation (Eq 5), which can be disaggregated in an equation ($\text{Yield} = T \times \text{TE} \times \text{HI}$, Passioura, 1977) bringing T and TE from Box 2 and where HI is the harvest index. In equation 6, this ratio is reduced into a sum of daily ratios of TE to the proportions of transpiration that evaporate or run-off, and that are integrated over a season of 'n' days. This equation 6 indicates that soil evaporation and run-off need to be minimized to maximize WUE. Text boxes and arrows indicate possible levers affecting directly the terms of the equations.

[insert box 3 figure followed by table]

	Scale / model type	Notes – References – Web links
Time Frame	Months	Crop cycle
Scale	Field	
Models	Process-based crop simulation models like APSIM – DSSAT – WOFOST – DAISY – CROPSYST - AQUACROP - SSM	https://daisy.ku.dk/ - http://ssm-crop-models.net/ 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 http://sites.bsyse.wsu.edu/cs_suite/cropsyst/ https://www.fao.org/aquacrop/en/

Box 4 Figure – Increasing WUE with a better irrigation efficiency (IE). IE represents the proportion of irrigated water that will eventually be used for plant transpiration and then for growth. Equations 7 and 8 only focus here on the ‘T’ component from previous box 1-2-3. The integration is also done over a season of ‘n’ days. Equation 7 brings a component of water percolation (Perc.) below the root zone. Water losses can also occur during transfer of water from the source to the field, or during irrigation application. This can be measured by the conveyance efficiency, defined as the ratio of water diverted from the source (reservoir, river, or pumping station) to the water reaching the field (Howell, 2003; Rogers et al., 1997), and the field application efficiency, defined as the ratio of water needed by the crops to the amount of water available at the field inlet (Bos and Nugteren, 1990). These are not represented below. Text boxes and arrows indicate possible levers affecting directly the terms of the equations.

[insert box 4 figure followed by table]

	Scale / model type	Notes – References – Web links
Time Frame	Months	Crop cycle - Years
Scale	Field – Irrigation basin	
Models	Crop models of Box 3 Irrigation management models like HYDRUS and CROPWAT Agrohydrology models like Soil Water Atmosphere Plant (SWAP)	https://www.pc-progress.com/en/default.aspx https://www.fao.org/land-water/databases-and-software/cropwat/en/ https://www.swap.alterra.nl/

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Box 5 Figure – WUE at farm scale. Irrigation water technical efficiency ($IWTE_i$) (Eq9) determines for X_1 units of other inputs than water and the minimum needed feasible water use W_2 for the optimal C units of output. A : represents the quantity of non-optimal units of the output obtained from the combination of the same (X_1) level of all other inputs and W_1 as a non-optimal quantity of irrigation water. The ratio W_1/W_2 expresses the percentage of irrigation water loss or to save ($1-(W_1/W_2)$). It also enables the determination of the maximum possible reduction in water use ($W_1 - W_2$). ITCE: irrigation technical cost efficiency is defined in Eq10, where SW_i is the observed cost share of irrigation water (W) in the total input cost (C) of the i th studied farm, and $S_{j,i}$ is the corresponding cost share of the j th input. By definition, cost shares of all inputs must add up to 1 (i.e., $SW_i + \sum_{j=1}^n S_{j,i} = 1$ for all i and j and $j \neq w$) and as mentioned above, $IWTE_i$ takes values between zero and one. This implies: $0 < ITCE_i < 1$.

[insert box 5 figure followed by table]

	Scale / model type	Notes – References – Web links
Time Frame	Crop cycle	
Scale	Farm – several fields	
Models	Bio-Economic models or simulator like IMPACT model and DAHBSIM	https://www.ifpri.org/publication/dynamic-agricultural-household-bio-economic-simulator-dahbsim-model-description https://www.ifpri.org/publication/international-model-policy-analysis-agricultural-commodities-and-trade-impact-model-0

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Box 6 Figure – WUE at landscape scale.

The WUE metrics (WUE_{land}) in Equation 11 is a ratio of several possible metrics, which include also GPP or NPP (gross or net primary productivity). WUE at landscape scale (WUE_{land}) can also be expressed as an interaction function between the crop distribution in the landscape ('Environment', Env_t), the management (Mgt, e.g. rainfed or irrigation), and the crops / species chosen by farmers, divided by water. 'Water' includes several hydric indicators such as rainfall, watershed wetting (rainfall–runoff = infiltration for crop and aquifers), root zone water content, withdrawals within dams, and is akin to the denominator of Eq5 (Box 3). The major difference with earlier boxes 1-4 is that since WUE is considered here for the many crops of a landscape, WUE in Equation 12 needs to be aggregated both in time ('i') as seen in boxes 1-4, and in space ('j') according to land use classes (agricultural statistics), watershed or aquifer (water resource management), and then weighted by the area covered by each crop/specie/management combination. The bold arrows also show unavoidable interactions / trade-offs, for instance with WUE of other landscapes (WUE_{land1} vs WUE_{land2}), or between the landscape design and non-farming stakeholders or the need for ecosystem services such as river flow.

[insert box 6 figure followed by table]

	Scale / model type	Notes – References – Web links
Time Frame	Day(s)-phenological stages – one to several crop cycles	Up to decades
Scale	Field, land use class, watershed, aquifer	
Models	Hydrological, agrohydrological, models like SWAT, ParFlow and APEX Coupled hydrologic and crop growth models Integrated models (SWAT, MHYDAS-Small-Reservoirs) Watershed and land management models like WEAP	https://swat.tamu.edu/ https://parflow.org/ https://epicapex.tamu.edu/ https://doi.org/10.1016/j.envsoft.2022.105409

• Hasten G_s response to light
↓

$$TE_{\text{int}} = \frac{A}{G_s} = \frac{G_{\text{sc}} * (C_a - C_i)}{G_{\text{sw}} * (W_i - W_a)} \quad \leftarrow \quad \begin{array}{l} \cdot \nearrow \text{mesophyll conductance to } \text{CO}_2 \\ \cdot \text{ Play with ABA sensitivity} \\ \cdot \searrow \text{Stomata leakiness at night} \end{array} \quad (\text{Eq1})$$

$$TE = \frac{0.6C_a * (1 - C_i / C_a)}{(W_i - W_a)} \quad \leftarrow \quad \begin{array}{l} \cdot \nearrow \text{Photosynthetic efficiency} \\ \cdot \searrow \text{Stomatal conductance} \\ \cdot \text{ Switch from C3 to C4 crop} \\ \cdot \text{ Act on Calvin-Benson cycle} \\ \cdot \text{ Synchronize G}_s \text{ and A better} \\ \cdot \text{ Use optimal plant nutrition} \end{array} \quad (\text{Eq2})$$

Accept

Box 2

$$TE = \frac{G_n}{T} = \frac{k_n}{(e_a^* - e)_n} = \left[\sum_{i=1}^n \frac{G_i}{T_i} \right] / n \quad (\text{Eq3})$$

- Genetics (species / cultivars)
- Agronomic management

• Levers from Box 1 Eq1&2

$$= \left[\sum_{i=1}^n \frac{k_i}{(e_a^* - e)_i} \right] / n \quad (\text{Eq4})$$

- Root hydraulics
- Rhizosphere
- Xylem vessels
- Soil hydraulics/ water fluxes in soil

Transpiration restriction

- Daily
- Monthly

- Shift sowing date
- Sowing density

Accepted

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

- Levers from Box 2

- ↗ Sowing density
- Orientate rows North-South
- Use adequate plant nutrition
- ↗ Light penetration in canopy

$$= \left[\sum_{i=1}^n \frac{TE_i}{1 + \text{Evap}_i/T_i + \text{Run-off}_i/T_i} \right] * HI / n \quad (\text{Eq6})$$

- Irrigation at key times
- ↗ Soil storage capacity
- ↗ Sowing density
- Use North-South row orientation

- Use mulching
- ↗ Sowing density

- Use terracing, levelling
- Do contour bunds

Accepted

Box 4

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

- ↘ Weeds
- Use supplemental irrigation
- Play with DI - RDI - PRD

$$= \left[\sum_{i=1}^n \frac{1}{1 + \underbrace{\text{Evap}_i/T_i + \text{Run-off}_i/T_i}_{\text{See levers from Box 3}} + \text{Perc}_i/T_i} \right] / n \quad (\text{Eq8})$$

- See levers from Box 3
- Use mulch + drip irrigation
- Optimize irrigation timing & duration
- ↗ Soil storage capacity

Accepted

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

$$IWTE_i = X_1 C / X_1 A = W_1 / W_2; \quad 0 < IWTE_i < 1 \quad (\text{Eq9})$$

$$ITCE_i = SW_i \cdot IWTE_i + \sum_{j=1}^j S_{ji} \quad \text{for } J \neq W \quad (\text{Eq10})$$

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

Accepted

$$WUE_{\text{land}} = \frac{\text{Biomass; yield; GPP; NPP}}{\text{Rainfall + Irrigation}} = \frac{\text{Envt} * \text{Mgt} * (\text{Crop or Specie})}{\text{Water}} \quad (\text{Eq11})$$

- Policy maker decisions
- Landscape design
- Farmer decisions
- All levers from Box1-3

$$WUE_{\text{Land1}} = \left[\sum_{j=1}^m \frac{\text{Envt}_j * \text{Mgt}_j * \text{Area}_j}{\sum_{j=1}^m \text{Area}_j} * \left[\sum_{i=1}^n \frac{TE_i}{1 + \text{Evap}_i/T_i + \text{Run-off}_i/T_i} \right] * \text{HI} / n \right] \quad (\text{Eq12})$$

- **Need for ecosystem services**
- **Effects of man-made infrastructures**
- **Decisions from non-farming stakeholders**
- All levers from Box 3-4

WUE_{Land2}

Accepted

Appendix S1.

Data, an important limiting factor in the efficiency analysis when using multi-criteria and multi-scale approaches

The databases used for the calculation of water efficiency are related to the purpose, domain and spatial scale of the study. Two scales/domains are often cited in the literature but often separately: i) the field as a base element where soil-plant processes (water and nutrient budgets, yield formation...), influenced by climate and management, occur, and ii) the farm as the level where field decisions are made, where production is related to labour availability, the market, natural resource use and family food consumption, and where policies influence decisions (subsidies, penalties, etc.). In most of the above studies, the proposed methods do not take into account the possible interactions between the biophysical characteristics of the farm and the socio-economic resources and strategies that determine the productive potential and efficiency of the system at field and farm levels (Belhouchette *et al.*, 2012). In fact, every decision made at a particular level of this complex hierarchical system (field, farm) potentially affects the functioning of the other levels negatively and/or positively (Souissi *et al.*, 2018) and the efficiency of the whole system may arise following a specific combination of diversity at the different levels (plant diversity in the fields and activity diversity on a farm) (El Ansari *et al.*, 2020).

For a multi-domain and multi-scale efficiency analysis, Hammouda *et al.*, 2018 suggested building the efficiency related-database by combining a list of interconnected socio-economic (labour availability, crop contracts, etc.), agronomic, as well as technical (rotation, irrigation, soil, etc.) components/variables, using a system approach. To do so, the concept of Agricultural Activity, which is based on an approach known as "primal", is suggested (Flichman *et al.*, 2011; Hammouda *et al.*, 2018). This approach makes it possible to establish a direct relationship between the choice of inputs (in terms of quantity or timing) and their effects on production and externalities/services, for every cropping system used. This approach differs from the conventional economic approach within which the Agricultural Activity is represented by a production or a cost, without taking into account the way in which this activity is carried out, and without specifying the biophysical context (soil, climate) in which it takes place (Louhichi *et al.*, 2010). This conventional approach therefore implies that all the Agricultural Activities which have the same production level and/or production costs are not only substitutable, but they present the same crop management practices, as well as the same externalities, potentially (Harper and Zilberman, 1989). Similarly, this implies that the production and externalities produced are directly correlated with the cost of production, and not with their production process (Flichman and Jacquet, 2003).

In order to define each Agricultural activity, it is important to have quantifiable data on the inputs used for each activity, as well as on its outputs (production and externalities). These data can come from different sources: experimentation, experts, farmer surveys, regional statistics. However, this often seems insufficient for the multi-criteria and multi-scale analysis of efficiency. For this reason, Belhouchette *et al.*, 2011 suggest the use of biophysical modelling (in particular by using summary models) and bio-economic modelling to generate data in order to better understand the link between

biophysical data and technical and economic data.

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