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Opportunities for improving leaf water use efficiency under climate change conditions

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ABSTRACT

WUEi (intrinsic water use efficiency) is a complex (multi)-trait, that depends on several physiological processes, driving plant productivity and its relation with a changing environment. Climatic change predictions estimate increases in temperature and drought in the semi-arid regions, rendering improved water use efficiency is a mandatory objective to maintain the current global food supply. The aims of this review were (i) to identify through a meta-analysis the leaf traits mostly related to intrinsic water use efficiency (*WUEi*, the ratio between A – net photosynthesis and g_s – stomatal conductance), based on a newly compiled dataset covering more than 200 species/varieties and 106 genus of C_3 plants (ii) to describe the main potential targets for *WUEi* improvement via biotechnological manipulations and (iii) to introduce emergent and innovative technologies including UAVs (Unmanned Aerial Vehicles) to scale up levels from leaf to whole plant water status. We confirmed that increases in g_m/g_s and V_{cmax}/g_s ratios are systematically related with increases in *WUEi* maintained across species, habitats, and environmental conditions. Other emergent opportunities to improve *WUEi* are described such as the relationship between photosynthesis and respiration and their link with metabolomics. Finally, we outline our hypothesis that we are observing the advent of a “smart” agriculture, wherein new technologies, such as UAVs equipped with remote sensors will rapidly facilitate an efficient water use regulating the irrigation schedule and determination, under field conditions, of cultivars with improved water use efficiency. We, therefore, conclude that the multi-disciplinary challenge toward *WUE* has only just begun.

1. *WUE* in the era of climate change: the problem of water

The need for increasing food production driven by the exponential growth of the human population is clear from any perspective. The human water consume is mainly driven (around 70%) by its need for food production [1]. When combined an increased global water demand from agriculture and associated agro-industries can be anticipated. Water resources are already limited, however irrigated lands even though they represent only 18% of world cultivated areas produce around 45% of global food [2]. Indeed, the main increase in food production is coming more from expansion of irrigated lands rather than an increase of the total area of global agricultural land. It therefore follows that irrigated agriculture is of fundamental importance for global food supply. In addition, the last decade has observed the emergence of agricultural products dedicated to fuel production leading to additional pressures on arable areas, water and nutrient resources.

Climate change models also predict higher temperature and more erratic precipitation, which will further increase water demand in cropping areas but also the expansion of drought derived problems in most of the currently semi-arid areas [3,4]. Consequently, the combination of increasing food demand and an increasingly limited water availability leads to mandatory need of improving plant water use efficiency. This objective is supported from local politicians to UN-FAO organizations with the slogan of ‘more crop per drop’ calling for a blue revolution to follow the green revolution of the sixties [5]. The increasing necessity for a more

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sustainable use of available water is reflected in recent publications showing the interest in the improvement of *WUE* in a wide range of different crops [6–10]. However, it is important to note that, as discussed by Tallec and co-workers [11], there are several difficulties for the proper evaluation of the crop *WUE* under realistic field conditions. The increasing scientific literature concerned with *WUE* improvement can be classified to fit two major approaches: (i) by the improvement of crop *WUE* (via genetic breeding and other biotechnological approaches) and (ii) by the development of agronomic practices leading to maximize water storage in the root zone and to reduce the necessity of irrigation. The lack of immediate positive results has lead to some authors claiming that yield maintenance under limited watering has limited potential [12]. However, there is increasing evidence from both ecophysiological and breeding studies in support for the capacity for improvement of *WUE* via each of these strategies [9,13].

In this review we will focus on *WUE* at leaf level, indeed intrinsic water use efficiency *WUEi*, because there is an impressive amount of research published on this subject which largely contrast the paucity of studies at the whole plant or crop level. First, we analyzed literature data to search for the major leaf traits driving *WUE*. For this purpose, a dataset has been compiled comprising 106 genus covering more than 200 species/varieties, thus representing a considerably larger dataset than those previously analyzed in order to enhance understanding of *WUE* across the plant kingdom. Next, based on the analysis of this dataset, we discuss the possibility of manipulating leaf traits via biotechnological means in order to improve *WUE*. Then we propose two novel approaches based on the roles of respiration and metabolomics with respect to *WUE*. Finally, we briefly mention new technologies for adjusting *WUE* via irrigation scheduling, with particular emphasis on the emerging use of Unmanned Aerial Vehicles (UAVs).

2. Leaf traits involved in *WUE*: a meta-analysis across different plant species

2.1. Definition of WUE at different spatial and time scales

The term water use efficiency (*WUE*) reflects the balance between carbon gains and the associated costs in water. This balance can be measured at different spatial and temporal scales [8,9,14]. The different spatial scales depend if carbon and water fluxes are considered from the leaf scale, whole plant, the canopy or crop parcel and finally at the biome or the ecosystem. Each scale involves specific methods and approaches that comprise satellites or aircraft imaging, eddy-covariance stations or portable gas exchange analyzers. Time scales of these measurements can vary greatly from instantaneous (seconds) to months/years integrations, also based on various methods such as gas exchange or isotopic tools such as ^{13}C discrimination. When using instantaneous leaf gas exchange measurements, it is easy to directly estimate *WUE* by relating net CO$_2$ assimilation rate (A_N) to stomatal conductance (g_s) – i.e. the so-called intrinsic water use efficiency (*WUEi*) –, or A_N to leaf transpiration rate (E) – defined as instantaneous water use efficiency (WUE_{inst}) [15]. These two parameters, A_N/g_s and A_N/E, are mostly used to characterize genetic and environmental effects, respectively [8,16–18]. Here we focus on the A_N/g_s ratio, the intrinsic *WUE* (*WUEi*), estimated at the leaf level and the instantaneous scale. Finally, we focussed the meta-analysis of C$_3$ plants only, but discuss the differences of mechanism used to fix CO$_2$ between C$_3$ and C$_4$ plants, and thus the processes regulating the *WUE*.

Fig. 1 shows the key processes involved in the regulation of the intrinsic water use efficiency (*WUEi*) in a C$_3$ plant. Stomata are a common regulation point in the exchange fluxes of water and carbon dioxide between the leaf and the surrounding atmosphere. This is illustrated by application of Fick's First Law for the transpiration (E) and the CO$_2$ assimilation rates (A):

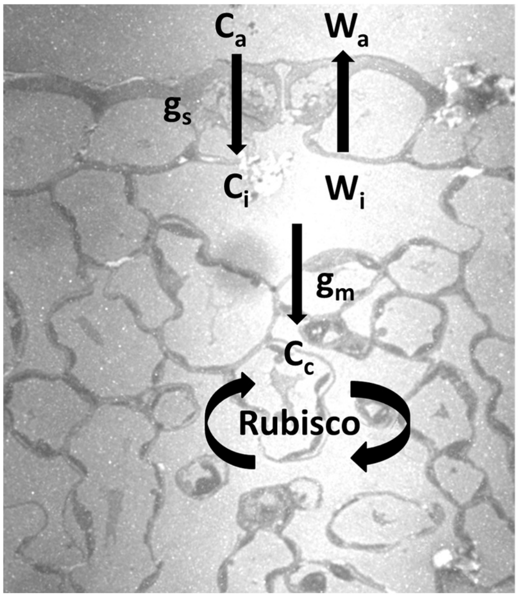

Fig. 1. CO$_2$ and H$_2$O diffusion pathways along a fully expanded leaf. C_a (ambient CO$_2$ concentration), C_i (CO$_2$ sub-stomatal cavity concentration), C_c (CO$_2$ concentration at the site of Rubisco carboxylation within the chloroplastic stroma), g_s (stomatal conductance), g_m (mesophyll conductance), W_i and W_a are the concentrations of water vapour in the substomatal cavity and the atmosphere, respectively.

$$E = g_{sw} \cdot (W_i - W_a) \quad (1)$$

$$A = g_{sc} \cdot (C_a - C_i) \quad (2)$$

where g_{sw} and g_{sc} are the stomatal conductances for water vapour and CO$_2$, respectively, W_i and W_a are the concentrations of vapour water in the substomatal cavity and the atmosphere, respectively, and C_a and C_i are the concentrations of CO$_2$ in the atmosphere and the substomatal cavity, respectively. Given that, $g_{sc} = g_{sw}/1.6$, it is evident that decreasing E through stomatal closening has the drawback of lowering g_{sc}. This should in principle decrease A, at an extent depending on which part of the relationship A vs. g_{sc} is affected by the decreased stomatal conductance (see Flexas et al. [19] for a complete description).

Carbon dioxide flux inside the leaf is dependent on two other processes (Fig. 1). The first process comprises a complex set of consecutive barriers to CO$_2$ flux within the leaf mesophyll, commonly integrated within the term mesophyll conductance (g_m). Applying Fick's First Law, under steady-state A can be given as:

$$A = g_m \cdot (C_i - C_c) \quad (3)$$

where C_c is the CO$_2$ concentration at the site of Rubisco carboxylation within the chloroplastic stroma. It is noticeable that C_c depends not only on the CO$_2$ supply (i.e. g_s and g_m), but also on the velocity at which carbon is consumed inside the chloroplast, which basically depends on the velocity of Rubisco and photosynthetic metabolism. Therefore, considering this later point and looking at Eqs. (1)–(3) it is clear that, besides g_s, the two principal mechanisms to regulate *WUEi* are g_m and any factor governing the velocity of C_c consumption. Among the latter factors is the maximum capacity of carboxylation by Rubisco (V_{cmax}), which is determined in turn by the Rubisco amount, catalytic rate and activation. Other alternatives to improve the 'demand' side of photosynthesis and, hence, *WUE* would be to decrease photorespiration by means of increasing Rubisco efficiency for CO$_2$ [20,21], short-circuiting the photorespiratory CO$_2$ release by inserting alternative metabolic pathways into leaves [22] or converting typical C$_3$ crops into C$_4$ [23]. As these goals