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From leaf to whole-plant water use efficiency (WUE) in complex canopies: Limitations of leaf WUE as a selection target

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ABSTRACT

Plant water use efficiency (WUE) is becoming a key issue in semiarid areas, where crop production relies on the use of large volumes of water. Improving WUE is necessary for securing environmental sustainability of food production in these areas. Given that climate change predictions include increases in temperature and drought in semiarid regions, improving crop WUE is mandatory for global food production. WUE is commonly measured at the leaf level, because portable equipment for measuring leaf gas exchange rates facilitates the simultaneous measurement of photosynthesis and transpiration. However, when those measurements are compared with daily integrals or whole-plant estimates of WUE, the two sometimes do not agree. Scaling up from single-leaf to whole-plant WUE was tested in grapevines in different experiments by comparison of daily integrals of instantaneous water use efficiency [ratio between CO_2 assimilation (A_N) and transpiration (E); A_N/E] with midday A_N/E measurements, showing a low correlation, being worse with increasing water stress. We sought to evaluate the importance of spatial and temporal variation in carbon and water balances at the leaf and plant levels. The leaf position (governing average light interception) in the canopy showed a marked effect on instantaneous and daily integrals of leaf WUE. Night transpiration and respiration rates were also evaluated, as well as respiration contributions to total carbon balance. Two main components were identified as filling the gap between leaf and whole plant WUE: the large effect of leaf position on daily carbon gain and water loss and the large flux of carbon losses by dark respiration. These results show that WUE evaluation among genotypes or treatments needs to be revised.

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1. Introduction

Water use efficiency (WUE) is an important subject in agriculture in semiarid regions, because of the increasing areas under irrigation and the high water requirements of crops (which consume around 70% of water available to humans). The scarcity of water resources is leading to increasing controversy about the use of water resources by agriculture and industry, for direct human consumption, and for other purposes. Such controversy could be alleviated by increasing crop water use efficiency, so that improving WUE of crops is becoming a main goal for agriculture and food security goals [1–5]. Moreover, climate change predictions show clear increases in temperatures (and concomitant increase in potential evapotranspiration) and more frequent episodes of climatic anomalies, such as droughts and heat waves [6,7]. All of these climate change phenomena are prevalent in most semiarid areas [8]. Consequently, the optimization of water use for crops by improvement of WUE is a challenge for securing agricultural sustainability in semiarid areas. In response to this challenge, a large volume of applied and fundamental research has been focused on optimization of crop water use.

The water issue is crucial for environmental sustainability of viticulture, because 60% of vineyards are located in semiarid areas and regular water applications are necessary to complete the growth cycle of grapevines. Grapes growth and mature during the driest months, making irrigation scheduling and timing critical [9–11]. Consequently, scientific interest in research on grapevine WUE has focused on the evaluation of new irrigation techniques [12–15] and on genetic variation in WUE in grapevine rootstocks or cultivars [16–18] and reflect the social interest and necessity of optimizing water use in viticulture. Fortunately, in most winegrowing regions, the main concern for farmers is not high grape yield but quality. Fruit quality is negatively correlated with high yield [19,20], so that it can be said that high quality yield is generally achieved under suboptimal crop conditions. For this reason, water stress has become a management target to secure high fruit quality, increasing the sustainability of water use by favoring crop quality over quantity.

WUE can be measured at different scales, ranging from instantaneous measurements on the leaf to more integrative ones at the plant and crop levels (Fig. 1). The pros and cons of those different ways to estimate WUE have been discussed elsewhere [21,22], and the decision on the most appropriate way depends on the capacity, facilities, and scale of the specific study. Most studies of WUE are performed on the basis of instantaneous measurements of leaf photosynthesis and transpiration, on the assumption that they are representative of whole-plant WUE, although only a few reports have evaluated WUE at the whole-plant level [18,23–25]. Comparison between instantaneous and whole-plant values sometimes reveals a clear relationship [10], but often does not. This lack of correspondence is an important limitation to the applicability of the research conducted in this field. Its causes need to be clarified for scaling from single to whole-plant estimates of WUE.

In the present work we analyze data from multiple experiments identifying sources of environmentally induced leaf WUE variations, showing the importance of both the light environment and dark respiration, often neglected, to whole-plant carbon balance and in turn to whole-plant WUE.

2. Materials and methods

2.1. Plant material and treatments

2.1.1. Field-grown plants

A field experiment was conducted in the experimental field of the University of Balearic Islands (Majorca, Spain) on grapevines of the cultivars Tempranillo and Grenache during

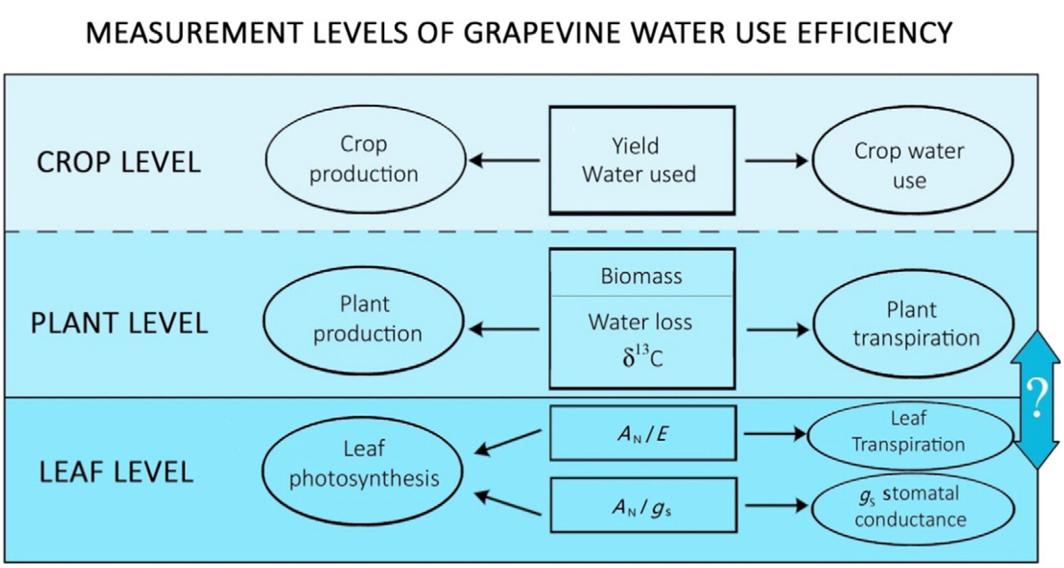

Fig. 1 – Different complexity levels for water use efficiency measurements. From leaf to crop level, as from instantaneous to growth-season measurements, there is a progressive integration of different crop production processes and water expenses with different measurement techniques. The double arrows indicate the difficulties in scaling up from leaf to plant level.