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Assessment of physiological water use efficiency of citrus germplasm

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SUMMARY An account is given of the assessment of physiological water use efficiency for the complete characterization of citrus biodiversity is given. This approach may allow to link “genetic” and “field” issues thus inducing the farmers to take sounder actions. Leaf gas-exchange measurements are applied by a portable photosynthesis system, which needs to be used for a couple of days during two different growth stages for each single biotype. All leaves measured will also be analyzed for nitrogen content.

Key words - citrus, photosynthetic water use efficiency, vapour pressure deficit, biodiversity.

RESUME *Le but de ce travail est d'évaluer l'efficience d'utilisation de l'eau pour la caractérisation complète des ressources phytogénétiques des agrumes. Cette approche pourrait permettre de mieux relier les aspects génétiques et les problèmes rencontrés sur le terrain, en vue de promouvoir une agriculture plus raisonnée. Les mesures des échanges gazeux réalisées grâce à un systéme portable, utilisé pour quelques jours durant deux stades de croissance différents pour chaque biotype. Toutes les feuilles mesurées seront aussi analysées afin d'évaluer la teneur d'azote.*

Mots clés - *agrumes, efficience d'utilisation utilisation photosynthétique de l'eau, déficit de la vapeur de pression, biodiversité.*

Introduction

Water deficit represents the main environmental constraint for the production of citrus in the Mediterranean region. Although there is evidence on water scarcity in this area, citrus is the most widespread fruit crop in the Mediterranean Basin, indicating its adaptive behaviour to these critical climatic conditions. Nevertheless, as the most active growth occurs during spring and summer, a combination of water deficit associated to both high evaporative demand and high thermal and radioctive regimes of the environment, may cause a progressive reduction of photosynthesis, plant growth and, in turn, final yield. This response may differ among species and varieties, making some of these more suitable to the most extreme conditions.

In the literature there is evidence of declined assimilation rate induced by water stress in field-grown olive trees (Giorio *et al.*, 1999) and grapevines grown in both open-field (Escalona *et al.*, 1999) and outdoor potted conditions (Flexas *et al.*, 1999), while no information exists on citrus. In particular, interesting differences between cultivars, in terms of different resistance to drought, have been reported by Escalona *et al.* (1999). These authors have found that cv. more drought-resistant reduced water loss, especially under limited water availability, by increasing the water use efficiency (WUE). High WUE was due to the ability of this cv. to maintain, also in correspondence of a low stomatal conductance, a good photosynthetic capacity under water stress, rather than the ability for high or quick stomatal closure.

In order to understand the effect of water stress on the most important tree-water relationships and to evaluate the reason of decreases in photosynthesis induced by drought conditions, a physiological assessment in terms of water use efficiency (WUE) of the major citrus varieties may allow a strong link between "genetic" and "field" issues for a more complete description of the citrus biodiversity in the Mediterranean and a subsequent more sound decision-making process by farmers.

Research framework

At leaf scale, the photosynthetic WUE (WUE_{ph}) is defined as the ratio of net assimilation to transpiration:

$$WUE_{ph} = \frac{A}{T} \qquad (1)$$

It is well known that assimilation and transpiration fluxes are strictly linked each other during the gas-exchange between plant and atmosphere, occurring at the leaf surface. In fact, both CO_2 and water vapour gases share the same pathway between atmosphere and intercellular air spaces inside the leaves, as it is shown in Fig. 1.

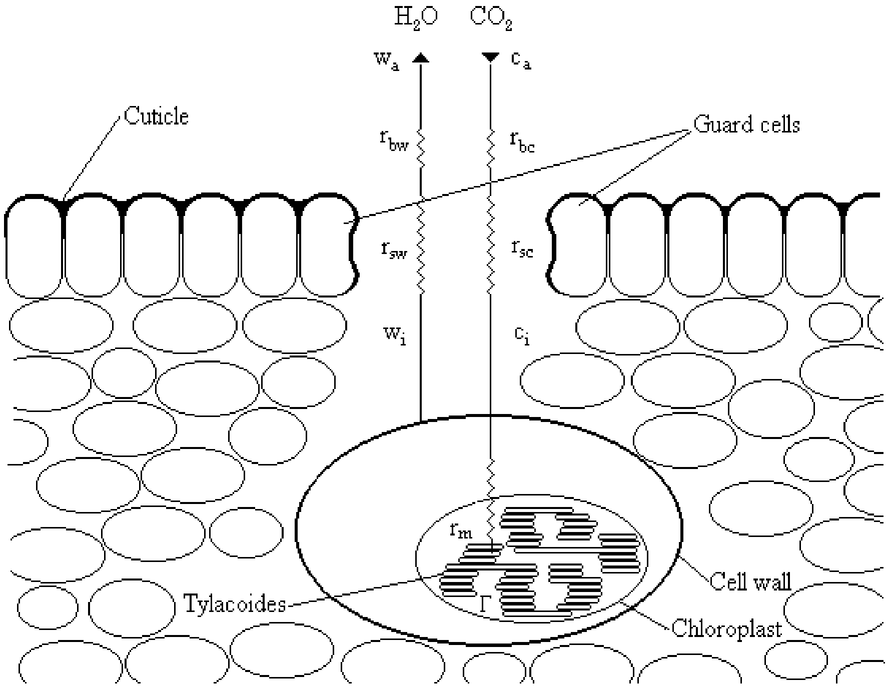

Fig 1 Scheme of the gas-exchanges pathway (water vapor and CO_2) between the leaf and the atmosphere. r_{bw} and r_{sw} are boundary layer and stomatal resistances for water vapor, respectively; w_a and w_i are the water vapor partial pressure in the bulk atmosphere and in the intercellular spaces, respectively; r_{bc}, r_{sc}, and r_m are the boundary layer, the stomatal and the mesophyll or metabolic resistances for CO_2, respectively; c_a and c_i are the CO_2 partial pressure in the bulk atmosphere and in the intercellular air spaces, respectively;   is the CO_2 partial pressure at the sites of carboxylation.

When water vapour moves from the cell wall up to bulk air it crosses the stomatal resistance (r_{sw}), and the boundary layer resistance (r_{bw}). A gradient in water vapor pressure (w) between intercellular air spaces (w_i) and bulk atmosphere (w_a), that represents the driving force for water vapour transport, is then established. When CO_2 moves from bulk atmosphere down to the cell wall, it crosses the same resistances to gas transport (r_{bc} and r_{sc}) as in transpiration, although the different values between r_{sw} and r_{sc} and between r_{bw} and r_{bc} are due to differences in binary diffusivity of water vapor and CO_2 in the bulk air ($r_{sc} = 1.6\ r_{sw}$) and in boundary layer ($r_{bc} = 1.37\ r_{bw}$), (von Caemmerer and Farquhar, 1981). A gradient in CO_2 partial pressure (c) between bulk atmosphere (c_a) and intercellular air spaces (c_i), that represents the driving force for CO_2 transport, is also in this case established. But when CO_2 moves in liquid phase from the cell wall toward the carboxylation sites, it crosses an additional resistance (r_m), corresponding to the liquid phase pathway itself jointly to the biochemical carboxylation capacity of the leaf, that is specific for assimilation only. By assuming steady state conditions, the gas-exchange fluxes of T and A, over the pathway shared by CO_2 and water vapor, can be formalized as follows:

$$T = \frac{w_i - w_a}{r_{bw} + r_{sw}} \qquad (2)$$

$$A = \frac{c_a - c_i}{r_{bc} \quad r_{sc}} \qquad (3)$$

where all symbols have been already defined.

The advantage of considering only the gaseous phase for CO_2 is that complex metabolic changes in the liquid phase, and thus in r_m, associated with changes in environmental conditions are reflected in the c_i value, relatively to c_a. Since only physical processes are involved in the gaseous phase, all terms in equations (2) and (3) are well defined and can be experimentally determined (Hsiao, 1993). Combining equations (2) and (3), WUE_{ph} will be proportional to the ratio of CO_2 to water vapor concentration differences between inside and bulk atmosphere according to the following equation:

$$WUE_{ph} = \frac{A}{T} = \frac{(r_{bw} \quad r_{sw})}{(r_{bc} \quad r_{sc})} \frac{(c_a \quad c_i)}{(w_i \quad w_a)} \qquad (4)$$

However, because CO_2 resistance differs from water vapor resistance only by the binary diffusivity, equation (4) suggests that any change in the boundary layer and stomatal resistances will have similar impact on both assimilation and transpiration. It also shows the importance of knowing c and w and of referring to a constant atmospheric CO_2 partial pressure and to the same w, in order to compare WUE_{ph} of different species leaves. When w is normalized for the evaporative demand of the atmosphere, namely vapour pressure deficit (VPD), only the degree of c_i determines the degree of WUE_{ph}.

That is:

$$\mathrm{WUE}^{*}_{ph} = K\frac{(c_a - c_i)}{(w_i - w_a)}\mathrm{VPD} = K'(c_a - c_i) = K'' - K'c_i \qquad (5)$$

where:

$\mathrm{WUE}^{*}_{ph} = \mathrm{WUE}_{ph}$ normalized for VPD;

$$K = \frac{(r_{bw} + r_{sw})}{(r_{bc} + r_{sc})}\,;$$

$$K' = \frac{K}{(w_i - w_a)}\mathrm{VPD}\,;$$

and $K'' = K'c_a$ with c_a constant. The terms K, K' and K'' are constants.

Eq. (5) indicates the strict proportionality between WUE^{*}_{ph} and c_i. Consequently, if c_i remains constant for single leaves, as it has largely reported for many species (Hsiao, 1993), and, in turn, also WUE^{*}_{ph}, the optimization theory in resources use by plants (Cowan, 1982) will be supported. In this case, a strict and linear relationship will be established between net assimilation (A) and stomatal conductance (g_s), independently from variations in the environmental or plant-internal conditions.

Thus WUE^{*}_{ph} *versus* g_s, along with A *versus* g_s, represent a powerful tool to investigate whether stomata tend to optimize stomatal conductance, through a concerted action between assimilation and transpiration, and then to establish differences, in terms of drought resistance, among cultivars. As an example, if cv. 1 shows to be more spread out in hostile environments and, then, more resistant to water stress conditions as compared to cv. 2, it may due to its higher WUE^{*}_{ph} (Fig. 2a), or to its higher A (Fig. 2b), for the same stomatal conductance value.

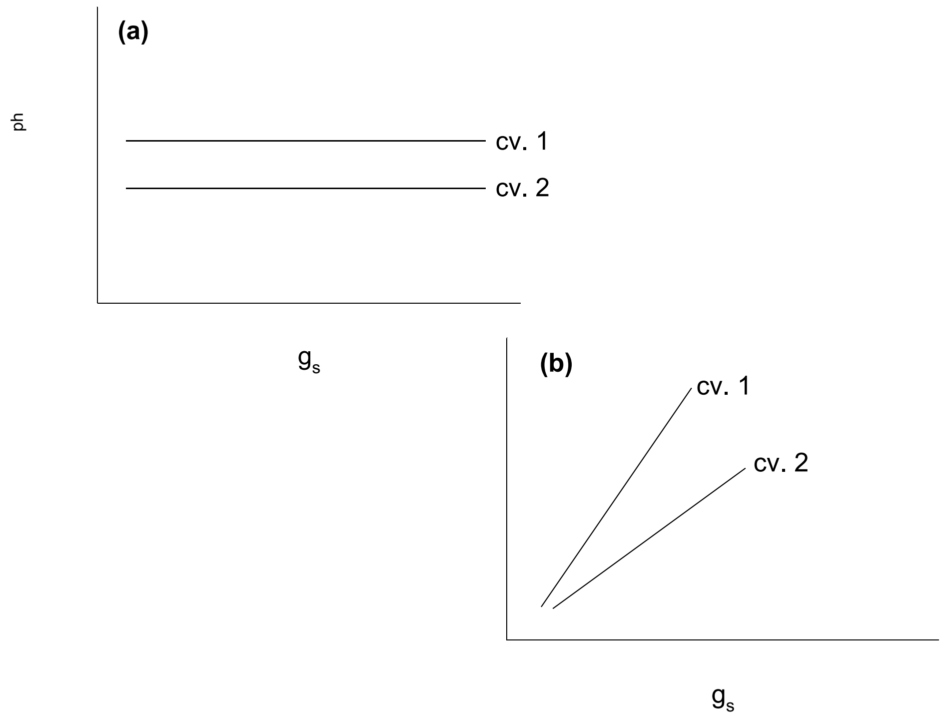

Fig. 2 Theoretical relationships between **(a)** normalized photosynthetic WUE (WUE^*_{ph}) and stomatal conductance (g_s), and **(b)** net CO_2 assimilation rate (A) and g_s of two different cultivars of citrus.

Nevertheless, differences in WUE^*_{ph} and A among cultivars may also be due to different nitrogen leaf content, as nitrogen content is strictly related to the carboxylation process. In order to avoid this risk, leaf nitrogen content would be determined on the same leaf where gas-exchange is measured and WUE^*_{ph} plotted in relation to the nitrogen content. If unique relationship is found for different cultivars, it indicates that leaf nitrogen variation is not the cause of differences in both WUE^*_{ph} and A *versus* g_s relationships, and then a real difference, in terms of standing water stress conditions, exists among cultivars.

A furthermore step for the characterization of physiological water use efficiency of biotypes might require a set of CO_2 assimilation rate to CO_2 partial pressure in the intercellular leaf spaces (A/c_i response curve) determinations.

The A/c_i curve is a valuable measure for comparing and characterizing the performance of photosynthetic apparatus subjected to different conditions. It allows the separation of the stomatal and non-stomatal limitations to photosynthesis for evaluating whether the decline in photosynthesis under water stress is due to stomatal closure or to a decrease in carboxylation efficiency. A detailed description of the A/c_i curve is reported by Albrizio (1997) and Steduto *et al.*, 2000.

Leaf gas-exchange measurements

The determination of leaf gas-exchange parameters will be measured by a portable photosynthesis system (model Li-6400; LiCor Inc., Lincoln, Nebraska, USA), operating as an open gas-exchange steady-state system. It consists of two main components: the system console and the sensor head. The first component allows the setting of measurement parameters and data logging, the second contains a leaf chamber in which all microclimate variables (temperature, vapour pressure deficit, CO_2 partial pressure, irradiance) are controlled. The total control of all the micro-environmental variables, within the chamber enclosing the leaf, permits the normalization of the results when compared with each other, making these measurements extremely reliable.

A picture of the two components of LICOR-6400 is reported in Fig. 3.

Fig. 3 Portable photosynthetic system LICOR 6400 for measuring leaf gas-exchange: system console and leaf chamber with a tree leaf clamped into.

The leaf chamber is climbed on a tripod to hold proper position and orientation of leaves during the measurement period. Calibration of the zero offset, the span of CO_2 and H_2O, and zero flow meter are usually made before starting every measurement with know CO_2 and water vapour concentration sources.

Leaf gas exchange measurements will be taken around noon on well-exposed leaves. Generally, 1-2 days for each biotype will be needed to collect repeated sets of gas-exchange measurements (on different leaves and/or different plants). Furthermore, it is suggested to repeat sets of measurement in two developmental stages, for instance one at full development, though before flowering, and one during fruits ripening. All leaves subjected to measurements will be harvested for nitrogen content. The different gas-exchange data-sets collected in this way will be then easily compared with each other through simple computer graphics.

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