

S34-005

Stomatal conductance regulates photosynthesis under progressive drought: from grapevines to a generalised pattern

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Keywords: stomatal conductance, photosynthesis, drought, chlorophyll fluorescence, non-stomatal limitations

Introduction

Whether drought mainly limits photosynthesis through stomatal closure or by metabolic impairment has been a long-lasting controversy (Lawlor, 1995; Cornic and Massacci, 1996). At least a part of this controversy may arise from difficulties to compare results from different experiments. For instance, important inter-specific differences in the response of stomatal conductance and photosynthesis to leaf water potential and/or relative water content, the most used parameters to assess the degree of drought, have been recognised (Lawlor, 1995; Cornic and Massacci, 1996). It is clear that stomata close progressively as drought progresses, followed by parallel decreases of net photosynthesis. However, stomatal conductance is controlled not only by soil water availability, but also by a complex interaction of factors internal and external to the leaf. Moreover, many times, stomata close in response to drought before any change is detectable in leaf water potential and/or leaf water content.

This complex regulation of stomatal conductance is related to important differences among species and genotypes in the response of stomata to leaf water potential, relative water content, ABA and other parameters. Nevertheless, it must be emphasised that a high degree of co-regulation of stomatal conductance (g) and photosynthesis is usually found. Since g is responsive to all the external (soil water availability, VPD) and internal (ABA, xylem conductivity, leaf water status) factors related to drought, it represents a more integrative basis for the overall effects of drought than leaf water potential and relative water content. Therefore, searching for a generalised pattern of photosynthetic response to drought, we have attempted to use g as an integrative parameter reflecting the water stress condition of the plant.

Materials and methods

Gas exchange rates (Li-6400, Li-Cor Inc., USA) and chlorophyll fluorescence (PAM-2000, Walz, Germany) were measured at steady state and light saturation during a series of experiments in field-grown grapevines and evergreen Mediterranean sclerophyll species, in which well irrigated plants were compared to plants subjected to different degrees of drought stress. The measurements included light- and CO₂-response curves of photosynthesis. The degree of drought was usually assessed by determining leaf water potential (Pressure pump, Soilmoisture corp., USA) and/or leaf relative water content (RWC). Details of the experimental conditions are published elsewhere (Flexas et al., 1998; Flexas et al., 2001).

According to the described limitations of water relations parameters to compare the photosynthesis response to drought among different species and experimental conditions, we

attempted to use g as an integrative parameter reflecting the water stress condition of the plant. However, stomatal movements are very dynamic, due to its complex regulation by multiple factors. For this reason, mid-morning, light-saturated stomatal conductance (which is usually correlated with the average daily mean conductance) was taken as a representative value of g .

The present report reviews this series of studies, in which every measured photosynthetic parameter was referred to the mid-morning light-saturated stomatal conductance observed for that plants at the moment of measuring.

Results and discussion

Early studies of chlorophyll fluorescence in irrigated and non-irrigated grapevines growing in the field during summer (Flexas et al., 1998) showed that the rate of light-saturated electron transport (ETR), measured at midday, decreased some times in non-irrigated plants, but to a lesser extent than net CO_2 assimilation (A_N). This was understood as indicative of a relative increase of photorespiration and/or Mehler reaction, which was demonstrated lately (Flexas et al., 1999a). Although there was a certain tendency of ETR to decrease with decreasing pre-dawn leaf water potential (Ψ), a non-significant relationship was observed between these two parameters (Flexas et al., 1999b). These results contrasted with the highly significant linear

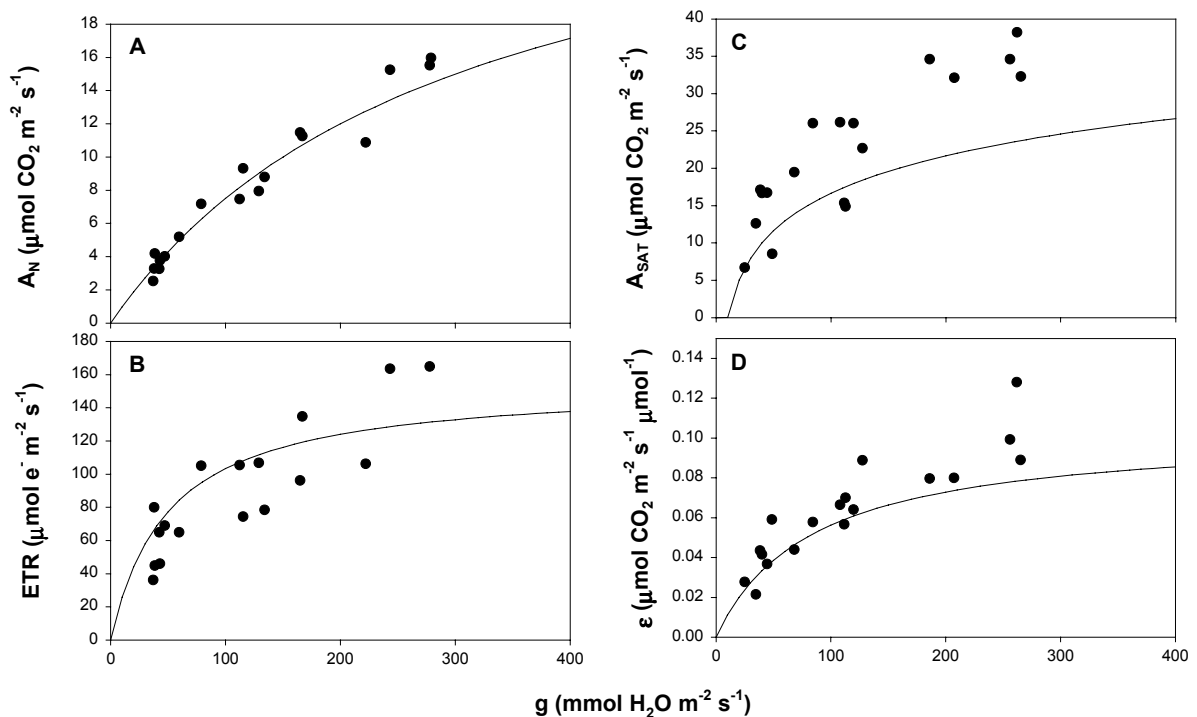


Fig.1. The relationships between stomatal conductance (g) and: (A.) net CO_2 assimilation (A_N), (B.) photosynthetic electron transport rate (ETR), (C.) light- and CO_2 -saturated net CO_2 assimilation (A_{SAT}), and (D.) apparent carboxylation efficiency, estimated as the initial slope of A_N - C_i curves (ϵ). Solid lines correspond to the best-fitting correlation curves obtained with field-grown grapevines, all them being hyperbolic and highly significant. In each plot, data on six different Mediterranean sclerophyll shrubs (solid circles) have been added.

relationship that was lately observed between ETR and Ψ in two year old grapevines of the same cultivar maintained on large pots and growing as well under field conditions (Flexas et

al., 1999b). Again, these discrepancies questioned the reliability of Ψ as an indicative parameter of drought when comparing different studies, even with the same species and cultivar. A very similar conclusion was reached when using leaf relative water content (RWC) as a reference parameter. By contrast, when referring A_N or ETR directly to g , a single curvilinear correlation was observed for all the data belonging to different experiments and different cultivars.

To further test the reliability of g as a unifying reference parameter, several photosynthetic parameters were plotted against g for grapevines and other species (Figure 1).

Figure 1 shows that both grapevines and the six sclerophyll evergreen species share a common pattern of response to g for A_N , ETR and ϵ . This was surprising, since the analysed species represent a substantial variability of life forms, photosynthetic characteristics and patterns of response to drought. In particular, three of these species (*Quercus ilex*, *Rhamnus alaternus* and *Rhamnus ludovici-salvatoris*) showed proportional decreases of g and RWC in response to soil drying. The other three species (*Quercus pubescens*, *Pistacia lentiscus* and *Pistacia terebinthus*), by contrast, showed similar decreases of g but maintaining RWC almost constant, as occurs in grapevines. The most unfitting data were those of A_{SAT} , which could be reflecting a higher mesophyll resistance in the sclerophyll species.

From the present data, it is concluded that, although there is wide variability among species and genotypes in the maximum values of photosynthesis and stomatal conductance, the photosynthesis to conductance ratio is largely maintained (see also Farquhar et al., 1987). Even when the relationships between different photosynthetic parameters and g depend on the species as well (Schulze and Hall, 1982; Farquhar et al., 1987), such a dependence seems to be much lower than those between photosynthesis and RWC or Ψ .

These generalised photosynthetic responses to g reveal a pattern of gradual response of photosynthesis to water stress that is similar to that proposed by Lawlor (1995). After an early effect of drought consisting in partial stomatal closure, a metabolic adjustment takes place through limited RuBP-regeneration (possibly due to an impaired ATP synthesis). Further reductions of g as drought progresses lead to reduced photochemistry and carboxylation efficiency. Photoinhibition eventually occurs under conditions of very severe drought and almost complete stomata closure.

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