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Controlling stomatal aperture in semi-arid regions—The dilemma of saving water or being cool?

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ABSTRACT

Stomatal regulation of leaf gas exchange with the atmosphere is a key process in plant adaptation to the environment, particularly in semi-arid regions with high atmospheric evaporative demand. Development of stomata, integrating internal signaling and environmental cues sets the limit for maximum diffusive capacity of stomata, through size and density and is under a complex genetic control, thus providing multiple levels of regulation. Operational stomatal conductance to water vapor and CO₂ results from feed-back and/or feed-forward mechanisms and is the end-result of a plethora of signals originated in leaves and/or in roots at each moment. CO₂ assimilation *versus* water vapor loss, proposed to be the subject of optimal regulation, is species dependent and defines the water use efficiency (WUE). WUE has been a topic of intense research involving areas from genetics to physiology. In crop plants, especially in semi-arid regions, the question that arises is how the compromise of reducing transpiration to save water will impact on plant performance through leaf temperature. Indeed, plant transpiration by providing evaporative cooling, is a major component of the leaf energy balance. In this paper we discuss the dilemma of 'saving water or being cool' bringing about recent findings from molecular genetics, to development and physiology of stomata. The question of 'how relevant is screening for high/low WUE in crops for semi-arid regions, where drought and heat co-occur' is discussed.

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1. Introduction

Under semi-arid climates (receiving precipitation below potential evapotranspiration) plants are often subjected to periods of water deficits, with high impact on plant functioning and production. The effects depend on stress duration, intensity and rate of progression, as well as on genotype, developmental stage of plants and the interaction with other stresses [1–3]. In Mediterranean and some semi-arid sub-tropical climates, terminal drought (that occurs late in the crop cycle) is common, due to scarce seasonal rain-

fall or to limited pre-seasonal stored soil moisture. Often, terminal drought co-occurs with high air temperature and high air vapor pressure deficit (VPD) [4]. The great variability of the weather that characterizes semi-arid climates amplifies the potential of stress that plants may be subjected to. The situation is likely to be exacerbated by an enhanced frequency of extreme events induced by climate change, as is the case of heat waves [5].

Most crops cultivated today have been selected for optimal performance under the current climatic conditions and have progressed towards the yield potential with the green revolution [6]. Yield potential determines crop production in the absence of drought. However, with the increased risk of water shortage, sustainable production systems are being developed (selection of genotypes and agronomic management tools), where irrigation water and nutrients are used with parsimony [7]. Under these circumstances, the basic drought mechanisms – drought escape, avoidance or tolerance – become vital for crop production. Drought escape through changing phenology or sowing/planting date is desirable in the case of predictable drought. Avoidance and tolerance traits are important under both predictable and unpredictable drought scenarios.

Abbreviations: A_{max} , maximum net photosynthesis; A, net leaf carbon assimilation; VPD, air vapor pressure deficit; E, transpiration; E_{night} , Night-time transpiration; g_s , conductance for H₂O vapor and CO₂; g_{smax} , maximum leaf diffusive conductance; g_s , conductance for H₂O vapor and CO₂; g_{smax} , maximum leaf diffusive conductance; g_{snight} , Night-time conductance for H₂O vapor; RV, resident vegetation; S, pore size; SD, stomatal density; ST, soil tillage; WUE, water use efficiency; WUE_i, intrinsic water use efficiency; WUE_i, instantaneous water use efficiency; WUE_c, season-long crop water use efficiency; $\partial E/\partial A$, marginal unit water cost of plant carbon gain.

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Matching crop water demand with season supply of water will enable crops to escape terminal water stress [3]. Increased crop water use efficiency (WUE), defined as the ratio of leaf carbon assimilation (A) to transpiration (E), may be important to save water for the crucial periods of plant development [8], but has to be equated in terms of the balance between water savings and yield penalty [2]. Moreover, when drought and heat co-occur stomatal closure and decreased transpiration, associated with high WUE, may lead to a dramatic increase in leaf temperature (up to 7 °C above air temperature) [4]. If this situation stands for long periods leaf photo-damage and/or xylem embolism may occur, leading to severe defoliation and plant death.

Stomata play a central role in the pathways for both carbon uptake and water loss by plants. Regulation of stomatal aperture, estimated by stomatal conductance, is a complex process with operational limits set during leaf development, namely the pattern of stomata in epidermis that include distribution, size and density (number per unit area of leaf) [9]. Recent advances in molecular genetics of stomatal development together with the physical diffusion model of stomatal conductance revealed a direct relation between the physiology of stomata and the role of genes regulating stomatal pattern [10]. This regulation is dependent on several environmental stimuli [11], signaled via internal factors such as hormones and hydraulics [12–15]. Under high atmospheric evaporative demand, stomatal response to VPD is an important mechanism to save water, showing genotypic differences, even between closely related species [16] that can be explored by plant breeders. Similarly, the sensitivity of stomata to dehydrating soil is variable, explaining the isohydric or ‘pessimistic’ response as compared to the anisohydric or ‘optimistic’ (but riskier) response. Isohydric species are likely more susceptible to xylem cavitation and therefore tend to have stricter control of transpiration, whereas anisohydric tend to use available water in a less conservative way and have presumably a lower risk of xylem embolism [17].

In this paper we discuss how stomata are regulated under a variable environment, how the type of stomatal responses influences crop WUE and leaf/canopy temperature and ultimately how plant breeding and management can improve crop performance under hot and dry conditions to resolve the dilemma between saving water or being cool. We use examples from our own work in grapevine, a species with high genotypic diversity, including varieties exhibiting iso- and aniso-hydric stomatal control and which is cultivated under rainfed and irrigated conditions. This perennial crop is a recognized model to study plant water relations [18].

2. Stomatal regulation of water loss

2.1. The carbon compromise

Stomatal regulation of carbon uptake and water loss under a changing environment was a key step in the colonization of land by plants [19]. The evolutionary pathway of this regulation is still largely unknown [20], but may have been an incremental one, over more than 450 million years since stomata first evolved [21]. It implied a ‘carbon compromise’: to fix CO₂ from the atmosphere while avoiding lethal dehydration of the photosynthetic leaf tissues. An impermeable cuticle on leaf epidermis would prevent water vapor loss to the atmosphere, but would not allow CO₂ uptake as well. Stomata are the microscopic pores that provide a variable porosity in the epidermis. They were described for the first time over three centuries ago and begun to be studied with modern methods in the last years of the 19th century. Francis Darwin (Charles Darwin’s son) for example, recognized that stomata closed in response to plant water deficits [22]. Since then, there was vast progress in our understanding of stomatal functioning, from the

mechanics of opening and closing to the behavior of stomata in the field. In plants with adequate water supply stomata may regulate leaf temperature close to the optimum for metabolic processes, including photosynthesis [23] or prevent tissue heat damage under excessive radiation or temperature. A remarkable example of the cooling effect of leaf transpiration was shown by O.L. Lange [24] in the hot and dry environments of the Mauritania Sahara, where large leaved species (*Citrullus colocynthis*) were able to keep leaf temperature below the upper temperature limits for survival. Because large leaves have a low convective heat exchange with the air they would not survive without transpiration cooling. This apparently paradox phenomenon (existence of large-leaf species in deserts, instead of small-leaved ones that intercept less radiation) was also observed by Smith [25] in the Sonoran desert of southern California. He recorded leaf temperatures of large leaved desert perennials 20 °C below air temperature (40 °C or above). This was explained by very high rates of transpiration made possible by plants taking advantage of sporadic rainfall events.

Stomatal aperture, measured as the conductance (g_s) for CO₂ or water vapor, varies continuously with changes in the environment (light intensity, atmospheric CO₂ concentration, air temperature, air humidity, wind) as well as with time of day and plant water status [11]. Therefore, the term of reference will be the maximum leaf diffusive conductance (g_{smax}), which depends on pore size (S) and the number of stomatal pores per unit leaf area (stomatal density, SD). Other characteristics (mainly anatomical) such as the position of guard cells relative to the epidermal cells (e.g. sunken stomata as in *Pinus* and other conifers, or *Nerium* or deposition of waxes on the stomata) may reduce g_{smax} . There is a set of conditions that induce changes in stomatal size and density of stomata. For example, the increase in CO₂ concentration in the atmosphere stimulates the production of leaves with less number of stomata per unit leaf area and vice-versa in lower CO₂ environment [26]. The impact, however, may not be large as there is experimental evidence that density is negatively correlated with stomata size [27].

2.2. Water use efficiency

Plants differ in the amount of carbon assimilated per unit of mass of water lost, i.e. their *instantaneous water use efficiency* (WUE_i) that can be estimated as the ratio of leaf net carbon assimilation (A) to transpiration (E), i.e. A/E (in mmol CO₂ mol⁻¹ H₂O). The ratio A/E is highly variable with environmental conditions, namely vapor pressure deficit (VPD) that determines the transpiration rate. That means that comparison of plants under different climatic conditions cannot be done. In order to avoid ambiguity associated with the effects of VPD, we may use instead the ratio of carbon assimilation to stomatal conductance A/ g_s referred to as *intrinsic water use efficiency* (WUE_i) [28,29]. However, often we want to know the WUE encompassing a growing season of a crop. A *season-long crop water use efficiency* (WUE_c, g DM kg⁻¹ H₂O) can then be defined as the ratio of the net gain of plant biomass (dry matter) over a given period, by the water lost over the same time.

When comparing C₃ and C₄ species it is apparent that C₄ plants exhibit higher WUE due to higher A_{max} and lower g_{smax} . In warm regions, where C₄ species evolved, photorespiration was stimulated considerably, as well as transpiration demand [30]. By increasing CO₂ concentration nearby RuBisCO C₄ plants greatly enhanced carboxylation efficiency and were able to inhibit photorespiration. By producing smaller stomata (for a given stomatal density) or reducing stomatal aperture plants will function at low g_{smax} . Lower g_s will improve plant water status and mitigate hydraulic demands on the conducting pathway in the xylem, therefore preventing hydraulic failure [31].

In general, stomatal regulation of gas exchange at the leaf level operates in a way that maximizes carbon assimilated per water

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