

STOMATAL RESPONSE TO WATER VAPOR PRESSURE DEFICIT: AN UNSOLVED ISSUE

RESPOSTA ESTOMÁTICA AO DÉFICIT DE PRESSÃO DE VAPOR D'ÁGUA: UM ASSUNTO AINDA EM DEBATE

- A REVIEW -

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ABSTRACT

Leaf-to-air water vapor pressure deficit (VPD) is an important environmental factor that can affect stomatal functioning in higher plants. The objective of this review is to provide an overview on the stomatal response to VPD in higher plants and the possible mechanisms that have been proposed to explain such response. There are conflicting results about whether stomata respond to VPD or not. Soil water stress and leaf position are factors that may affect the stomatal response to VPD and can help to explain these conflicting results. When stomata do respond to VPD, the mechanism causing such response is not well understood, and two contrasting hypotheses have been proposed. The feedforward hypothesis states that stomatal conductance (Gs) decreases directly as VPD increases, with abscisic acid (ABA) in the leaves probably triggering the response. The feedback hypothesis states that Gs decreases as VPD increases because of an increase in transpiration (E) that lowers the leaf water potential. These two mechanisms have been the subject of vigorous debates as there are published results that support both hypotheses. The results of this review show that stomatal response to VPD is still a controversial issue and constitutes a good research rationale for the current generation of plant physiologists.

Key words: gas exchange, vapor pressure deficit, abscisic acid, drought.

INTRODUCTION

Exchange of water and CO₂ between leaves and the ambient air are important plant processes by which heat is dissipated (transpiration) and a primary substrate for photosynthesis is taken up, respectively. The exchange of these two gases is primarily by diffusion, but the concentration gradients and associated fluxes are in the opposite direction. The epidermis of leaves is covered by a waxy outer layer, the cuticle, which is an effective barrier to both water and CO₂ diffusion. Stomata are the openings at the leaf surface that enables the control of water efflux and CO₂ influx between the inside leaf and the ambient air (Figure 1).

Because the diffusion of water and CO₂ occurs through the same pathway (stomata), land plants are faced with a constant dilemma. Allowing the maximal influx of CO₂ for photosynthesis is advantageous but can dangerously lead to dehydration. Therefore, stomata must function in a way to optimize dry matter production by balancing photosynthesis and transpiration. In order to deal with this dilemma, stomata respond to internal and external (environmental) factors.

Internal factors that control stomata functioning are related to water potential of cells near the guard cells and chemicals, especially abscisic acid (ABA) and cytokinins (BLACKMAN &

DAVIES, 1983, 1985; DAVIES & ZHANG, 1991). With regard to external factors, stomata respond to many environmental factors such as light (quality and intensity), ambient [CO₂], leaf temperature, soil water status, leaf-to-air water vapor pressure deficit (VPD), and pollutants such as O₃, SO₂ and nitrogen oxides (SHIMAZAKI et al., 1986; APHALO & JARVIS, 1991; JONES, 1992). Among these environmental factors, the response to VPD is poorly understood and has been the subject of vigorous debates (MONTEITH, 1995; BUNCE, 1996). Not only the mechanism that causes stomata response to VPD is controversial, but also is it not clear if stomata always respond to VPD and how VPD interacts with other environmental factors. This review intends to provide an overview on what has been published in the scientific literature about the stomatal response to VPD in higher plants and the possible mechanisms that have been proposed to explain this response. It does not include the work of all plant physiologists of all countries of the Globe, but it certainly includes the main results from major scientific groups around the world.

Why should stomata respond to VPD?

Before going into details about stomatal response to VPD, it is important to understand the reason why stomata may respond to VPD. The VPD of interest here is defined as:

$$VPD = e_{\text{leaf}} - e_{\text{air}} \quad (1)$$

Where e_{leaf} is the saturation vapor pressure at the leaf temperature and e_{air} is the actual water vapor pressure at the outside air temperature. Units of SI in equation (1) can be Pa, kPa, Mpa, mol H₂O, among others (mmHg, bar, mbar). The assumption in equation (1) is that the air inside the stomatal cavity is saturated (ZEIGER et al., 1987).

Equation (1) indicates that VPD is the driving force for water movement from the inside leaf to the outside air, a process called transpiration (E). The greater the VPD the more water moves out of the leaf. If the diffusion increases up to a rate that cannot be supplied by the vascular structure of the plant, the leaf and the entire plant may go into a water stress situation. Therefore, and not surprisingly, stomata have to regulate their opening to avoid dehydration as VPD increases, especially at high VPD.

Do stomata respond to VPD?

Because high VPD can cause water stress in the plant, it would be reasonable to assume that stomata respond to VPD. This assumption, however, seems to be not always correct. The first controversy presented in this review is the conflicting results about whether stomata respond to VPD or not. Until the late 1960s, it was thought that stomata do not respond to

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VPD (MEIDNER & MANSFIELD, 1968). Studies in the 1970s, 1980s, and 1990s showed that stomata do respond to VPD (e.g. SCHULZE et al., 1972; TURNER et al., 1984; CONDON et al., 1992). However, reports of no stomatal response to VPD can still be found (e.g. RAWSON et al., 1977; INOUE et al., 1989). Some possible reasons for these conflicting results are presented in the following section.

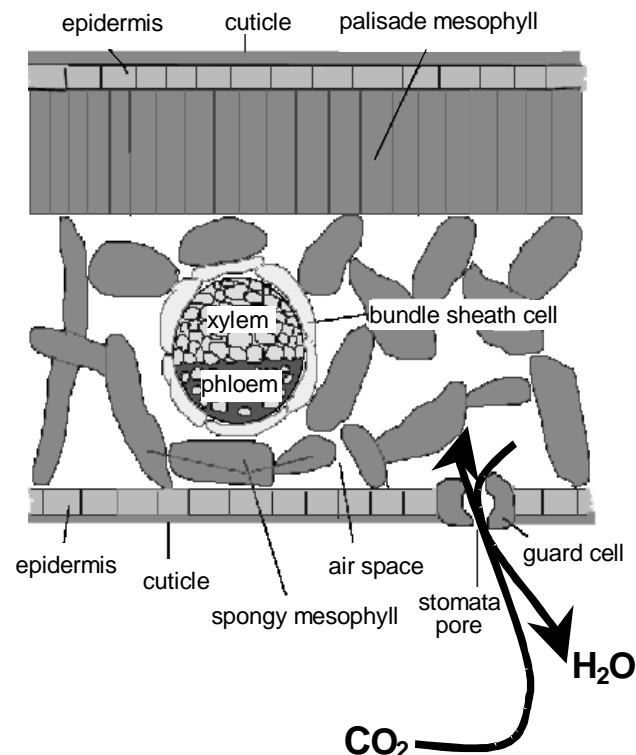


Figure 1 - The water vapor (H_2O) and CO_2 pathway through the leaf.

Factors that affect the stomatal response to VPD

There may be some factors that can confound the stomatal response to VPD and may help us to explain the different responses reported in the literature (or instead, to show our lack of understanding about the stomatal response to VPD). Soil water status is one of them. However, conflicting results have also been reported on the interaction between soil water and stomatal response to VPD. BLACK & SQUIRE (1979) and JOHNSON & FERREL (1983) found that stomatal response to VPD is reduced in dry compared to wet soil, while SCHULZE & KUPPERS (1979), OSONUBI & DAVIES (1980), and TURNER et al. (1985), reported that stomatal response to VPD is the same in dry and wet soil. SCHULZE et al. (1972) showed that stomatal response to VPD is higher in dry than in wet soil.

Another factor that may affect stomatal response to VPD is leaf position (i.e. leaf number). Leaves at different positions within the stem develop under different environmental conditions in field grown crops, may have different functions, and have different anatomical structure. Earlier leaves synthesize carbohydrates that are used mostly for vegetative growth whereas later leaves, especially the flag leaf in monocots, are responsible for providing carbohydrates for grain growth (EVANS, 1983; LAWLOR et al., 1989;

FREDERICK, 1997). Stomatal density increases in leaves at higher positions on the stem in several species (DUNSTONE et al., 1973; TICHÁ, 1982; ARAUS et al., 1986). Therefore, stomatal response to VPD may be different for leaves at different positions.

WARRIT et al. (1980) measured the stomatal response to VPD of three groups of apple (*Malus domestica* Borkh.) leaves located on three different types of shoots (spurs carrying fruits, spurs without fruits, and extension shoots). The stomatal response to VPD was lower in the leaves that were on spurs without fruits compared to the other two shoots. STRECK (2002) measured the stomatal response to VPD in winter wheat (*Triticum aestivum* L.) leaves at two different positions on the stem, the one located four leaves below the flag leaf (FL-4) and the flag leaf (FL). The FL-4 showed no evidence of stomatal response to VPD whereas the FL consistently showed stomatal closure as VPD increased under different levels of soil water.

The results by STRECK (2002) may help to explain the results reported in some studies that stomata did not respond to VPD in wheat [the greenhouse study by RAWSON et al. (1977) and the field study by INOUE et al. (1989)]. In these two previous studies, gas exchange parameters were measured on leaves other than the flag leaf during the entire period of measurements (RAWSON et al., 1977) or at least in part of the period of measurements (INOUE et al., 1989). On the other hand, studies that indicate a stomatal response to VPD in wheat were taken on flag leaves (e.g. BUNCE, 1998; XUE, 2000).

STRECK (2002) hypothesized three reasons for the different response to VPD of the FL-4 and FL in wheat. Firstly, it might be an adaptation to different environmental conditions during the lifetime of each leaf. In a field grown winter wheat crop, the FL-4 emerges at least one month earlier than the FL in the spring of temperate climates. Consequently, environmental conditions are less favorable for transpiration (lower temperatures, lower daily incident solar radiation, and lower evaporative demand) during the lifetime of the FL-4 than during the lifetime of the FL. Therefore, the FL-4 may not need to respond to VPD as the FL does. Secondly, the anatomical structure of these two groups of leaves is different. Leaves located at lower levels in the plant have been reported to have lower stomatal density than those located in upper levels (DUNSTONE et al., 1973; TICHÁ, 1982). In wheat, the FL-3 had a stomatal density 29-41% less than the FL (TEARE et al., 1971; FRANK et al., 1973). Also in wheat, ARAUS et al. (1986) reported that stomatal density increased by 87%, G_s increased by 42%, and transpiration increased by 74% from the FL-5 to the FL. Thirdly, it is certainly advantageous for the plant that the FL has sufficient plasticity to respond to environmental factors, including VPD, in an attempt to maintain its photosynthetic activity as high as possible compared to leaves at lower positions. The FL in monocots is the last leaf to senesce, and produces the majority of the carbohydrates for grain growth (EVANS, 1983; LAWLOR et al., 1989; FREDERICK, 1997). Closing stomata in response to VPD helps to maintain high total water potential in the FL cells, which maintains the photosynthetic capacity of the mesophyll (JONES, 1973; ANTOLIN & SANCHEZ-DIAZ, 1993; XU et al., 1994). During the period the FL-4 is photosynthesizing, there are usually four to five other leaves that are actively photosynthesizing (McMASTER et al., 1991), so that in situations where environmental conditions are limiting, there are more leaves photosynthesizing.

The mechanism of stomatal response to VPD

In this section of the review, let us assume that stomata respond to VPD and the focus is on the mechanism that causes stomatal closure as VPD increases. The mechanism causing stomatal response to VPD is not well understood (MONTEITH, 1995; BUNCE, 1996; MATZNER & COMSTOCK, 2001), and two contrasting hypotheses have been proposed to explain this mechanism (Figure 2).

One of these hypothesized mechanisms is the feedforward hypothesis, which states that stomatal conductance (G_s) decreases directly as VPD increases as a result of stomata somehow being able "to sense" an increasing VPD (FARQUHAR, 1978). How stomata "sense" the increased VPD is not clear, but strong evidence suggests that ABA controls this response (DODD et al., 1996; BUNCE, 1998; TARDIEU & SIMONNEAU, 1998). One possible mechanism to explain the role of ABA in controlling G_s under high VPD would be that there is a change in the rate of delivery of ABA to the guard cells in the transpiration stream caused by changes in the peristomatal transpiration (transpiration in the area surrounding stomata) in response to VPD (BUNCE, 1996).

The other hypothesis is a feedback response, where a decrease in G_s as VPD increases is caused by a direct increase in E (MONTEITH, 1995; MATZNER & COMSTOCK, 2001). The feedback mechanism is based on evidence that stomata respond to changes in the humidity of the ambient air by sensing E rather than VPD (MOTT & PARKHURST, 1991). A high E would be responsible for stomatal closure by increasing the water potential gradient between guard cells and other epidermal cells or by lowering bulk leaf water potential (STEWART & DWYER, 1983; FRIEND, 1991; MONTEITH, 1995).

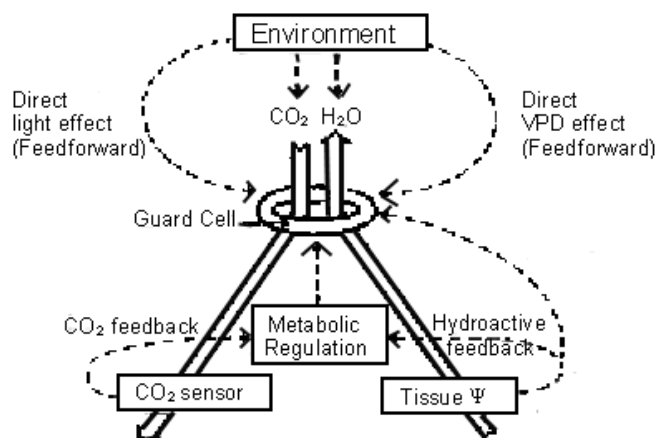


Figure 2 - Simplified diagram illustrating the feedforward and the feedback mechanisms of the stomatal response to environmental factors (after JONES, 1992).

BUNCE (1996) criticized the feedback hypothesis because of the lack of response of G_s to VPD observed in three species, *Glycine max* (L.) Merr., *Abutilon theophrasti* (L.), and *Chenopodium album* (L.), exposed to low atmospheric CO_2 concentration ($[\text{CO}_2]$ ($0\text{--}50 \mu\text{mol mol}^{-1}$)). In this low $[\text{CO}_2]$ environment, stomatal conductance was at a maximum and an increase in VPD of 0.5 kPa caused a two-fold increase in the evaporation rate without causing significant change in stomatal conductance. A further criticism of the feedback mechanism is the evidence that stomata closed in response to low soil water

treatments even when bulk leaf water potential and turgor were maintained the same as in well watered plants, either by pressurizing the roots (GOLLAN et al., 1986; MUNNS, 1987; PASSIOURA, 1988) or applying a drought treatment in only part of the root system (BLACKMAN & DAVIES, 1985; ZHANG et al., 1987; SAAD & SHARP, 1989). In these experiments, if leaf water potential controls stomata (i.e. a feedback response), then stomata should have been maintained open in plants under soil water stress.

The feedback mechanism, however, has received considerable support in recent years as the mechanism to explain rapid diurnal responses to VPD (MONTEITH, 1995; MATZNER & COMSTOCK, 2001) for several reasons. Firstly, it has been recognized for some time (more than 50 years ago) that stomatal closure is an effective mechanism to increase the resistance of water flow out of the plant (VAN DER HONERT, 1948), and a possible negative feedback loop between stomatal conductance and leaf water potential was proposed almost 40 years ago (COWAN, 1965). Secondly, leaf water potential is usually the lowest water potential in the plant (compared to the other plant parts), and therefore is more likely to be the signal for sensing a drying environment (i.e., high VPD) than a chemical signal (KRAMER, 1988). Thirdly, studies showed that leaf water status could indeed explain stomatal closure in response to soil drying and VPD (SALIENDRA et al., 1995; FUCHS & LIVINGSTON, 1996; COMSTOCK & MENCUCINI, 1998). These studies used a root pressurizing technique to manipulate leaf and shoot water potential and showed that stomatal closure due to water stress (low soil water potential, low shoot and leaf hydraulic conductance, and high VPD) could be reversed by applying pressure to the roots. Fourthly, while it is evident that ABA plays an important role as a regulator of long-term stomatal response to soil water stress, the feedback mechanism is more appropriate for short-term (diurnal) responses to VPD, as an ABA signal is unlikely to respond in such a quick fashion (KRAMER, 1988; COMSTOCK & MENCUCINI, 1998).

STRECK (2002), in a field study where rain was prevented by a plastic cover system, observed that the stomatal response to VPD of the flag leaf of two winter wheat cultivars was a feedback response. These results, however, do not agree with those found by XUE (2000), who worked with the same cultivars in a two-year rain fed field experiment at the same location (Lincoln, NE, USA). In both high and low soil water status, XUE (2000) found a feedforward response of G_s to VPD in the flag leaf. Soil water status during the gas exchange measurements was unlikely to account for such different stomatal response to VPD in the two studies. The difference between these two studies was the soil water status prior to and at the beginning of the gas exchange measurements period. In STRECK (2002), plants were well watered except during the period of the gas exchange measurements, when soil water started high and depleted naturally during a single drying cycle until the last gas exchange measurement date. XUE (2000) had a rain fed experiment, and plants were exposed to intermittent drying periods before and during the gas exchange measurements. Therefore, the prior history of soil water status may account for the different mechanism of stomatal response to VPD of the flag leaf between STRECK (2002) and XUE (2000). Plants exposed to drought show an increase in [ABA] in the xylem and in the leaves (NEALES et al., 1989; DAVIES & ZHANG, 1991; ALI et al., 1999a,b), and stomatal closure in drought-stressed plants is well related to xylem and leaf [ABA] (DAVIES et al., 1994; LIANG et al., 1997; ALI et al., 1999a,b). However, stomata respond to leaf

[ABA] only at concentrations above a threshold value (DAVIES & ZHANG, 1991; DAVIES et al., 1994; ALI et al., 1999a,b). This threshold is believed to exist because ABA is naturally produced in the leaves, and there must be a differentiation between ABA produced in the leaf and drought-related ABA produced in the roots (DAVIES & ZHANG, 1991). The ABA produced in the roots that induces stomata closure in response to drought is transported in the transpiration stream (xylem) and deposited in the epidermal cell walls adjacent to guard cells (MEIDNER, 1975), which is believed to be the site of action for ABA on the guard cells (HARTUNG, 1983). Wheat plants in XUE (2000) might have had their leaf [ABA] at high levels and above the threshold when gas exchange measurements began. Plants in the STRECK (2002) study were exposed to soil water stress about one week after the beginning of the gas exchange measurements on the flag leaf. Consequently, it is reasonable to assume that leaf [ABA] of plants in the study by STRECK (2002) was low and below the threshold most if not all the time. Even if plants in the STRECK (2002) study would have produced some drought-related ABA during the first drying period, this ABA would have been metabolized during the 13-day period until the next soil drying cycle was applied, because after two days of rewatering, leaf [ABA] is close to the content before the drying cycle started (LIANG et al., 1997).

STRECK (2002) hypothesized that, if ABA is responsible for stomatal closure in the feedforward mechanism (BUNCE, 1996, 1998), then stomata of plants that are exposed to previous soil drying cycles are potentially more suitable to respond to VPD through a feedforward mechanism (the plants in XUE, 2000) than those plants under water stress but that did not have a previous history of drought (e.g. the plants in STRECK, 2002). In plants that did not have a drought-stressed history, stomatal closure in response to increasing VPD may more likely be a feedback response. The hypothesis of previous drought history as a factor that affects stomatal response to VPD explains the feedforward response in both years and a stronger positive G_s and E relationship in the driest compared to the wettest year observed in XUE (2000).

FINAL REMARKS AND CONCLUSION

Despite years of intense and fruitful study, stomatal response to VPD is still a controversial issue. There are some reports of no stomatal response to VPD and many reports that stomata do respond to VPD. Soil water status and leaf position are factors that may affect stomatal response to VPD. If stomata do respond to VPD, the mechanism that causes stomatal closure at high VPD is not well understood. The controversy about the possible mechanism involving stomatal response to VPD (feedback or feedforward) is ultimately the same controversy about the mechanism that causes stomata to respond to soil water stress (KRAMER, 1988; PASSIOURA, 1988). The traditional view of leaf water potential as a measure of water stress in plants (RASCHKE, 1975; ZEIGER, 1983; KRAMER, 1988) has been negated (SINCLAIR & LUDLOW, 1985; PASSIOURA, 1988), because of the evidence that soil water instead of leaf water status governs stomatal function under drought conditions through chemical signals (among them ABA) that originate in the root system (DAVIES & ZHANG, 1991; LIANG et al., 1997; FROMM & FEI, 1998). The feedback hypothesis as the mechanism that stomata respond to VPD was proposed based on the assumption that leaf water status was responsible for stomatal control (MONTEITH,

1995). The feedforward hypothesis assumed that if chemical signals are responsible for the stomatal response to soil water stress, then similar signals (e.g., ABA) would also be produced in the leaves in response to VPD (FARQUHAR, 1978; BUNCE, 1998). In the field, drought history of the crop may define the type of mechanism that causes stomatal response to VPD (STRECK, 2002).

In conclusion, stomatal response to VPD is still a good research rationale for the current generation of plant physiologists. However, to be able to move a step further in knowledge and improve our understanding about stomata functioning in response to VPD, we probably need new hypotheses on how plants deal with soil water shortage. Thus, improving understanding in this area may be quite far away in the horizon, since coming up with new hypotheses usually takes time because, as always in life, the devil is in the details.

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RESUMO

O déficit de pressão de vapor d'água entre o interior da folha e o ar externo (VPD) é um importante fator ambiental que afeta o funcionamento estomático. Esta revisão analisa a resposta estomática ao VPD em plantas superiores e os possíveis mecanismos propostos para explicar esta resposta. Os resultados são conflitantes se os estômatos respondem ao VPD ou não. Estresse hídrico no solo e a posição da folha no dossel vegetal são fatores que podem afetar a resposta estomática ao VPD e ajudam a explicar estes resultados conflitantes na literatura. Quando existe resposta estomática ao VPD, o mecanismo que causa esta resposta também não é bem entendido, sendo duas hipóteses propostas para este mecanismo. A hipótese de "feedforward" é de que a condutância estomática (G_s) diminui diretamente com o aumento do VPD, com o ácido abscísico sendo o sinal para a resposta. Na hipótese de "feedback" ou retroalimentação, G_s diminui com o aumento do VPD devido ao aumento na transpiração foliar, o que abaixa o potencial de água na folha. Estes dois mecanismos têm sido objeto de debates na comunidade científica pois existem resultados publicados na literatura que suportam ambas as hipóteses. Os resultados desta revisão de literatura mostraram que a resposta estomática ao VPD ainda é um assunto não resolvido, o que justifica a continuação da pesquisa nesta área para a atual geração de fitofisiologistas.

Palavras-chave: trocas gasosas, déficit de pressão de vapor, ácido abscísico, seca.

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