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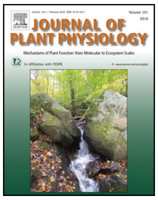

Review article

Improving stomatal functioning at elevated growth air humidity: A review

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ABSTRACT

Plants grown at high relative air humidity (RH ≥ 85%) are prone to lethal wilting upon transfer to conditions of high evaporative demand. The reduced survival of these plants is related to (i) increased cuticular permeability, (ii) changed anatomical features (i.e., longer pore length and higher stomatal density), (iii) reduced rehydration ability, (iv) impaired water potential sensitivity to leaf dehydration and, most importantly, (v) compromised stomatal closing ability. This review presents a critical analysis of the strategies which stimulate stomatal functioning during plant development at high RH. These include (a) breeding for tolerant cultivars, (b) interventions with respect to the belowground environment (i.e., water deficit, increased salinity, nutrient culture and grafting) as well as (c) manipulation of the aerial environment [i.e., increased proportion of blue light, increased air movement, temporal temperature rise, and spraying with abscisic acid (ABA)]. Root hypoxia, mechanical disturbance, as well as spraying with compounds mimicking ABA, lessening its inactivation or stimulating its within-leaf redistribution are also expected to improve stomatal functioning of leaves expanded in humid air. Available evidence leaves little doubt that genotypic and phenotypic differences in stomatal functioning following cultivation at high RH are realized through the intermediacy of ABA.

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1. Introduction

The ability of stomata to tune their aperture considerably affects plant survival, especially under conditions of water deprivation (Sellin et al., 2014; Papanatsiou et al., 2016). Since stomatal responsiveness to closing stimuli is set by the growth environment (Fanourakis et al., 2015b; van Meeteren and Aliniaeifard, 2016),

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Abbreviations: ABA, abscisic acid; RH, relative air humidity; VPD, vapour pressure deficit.

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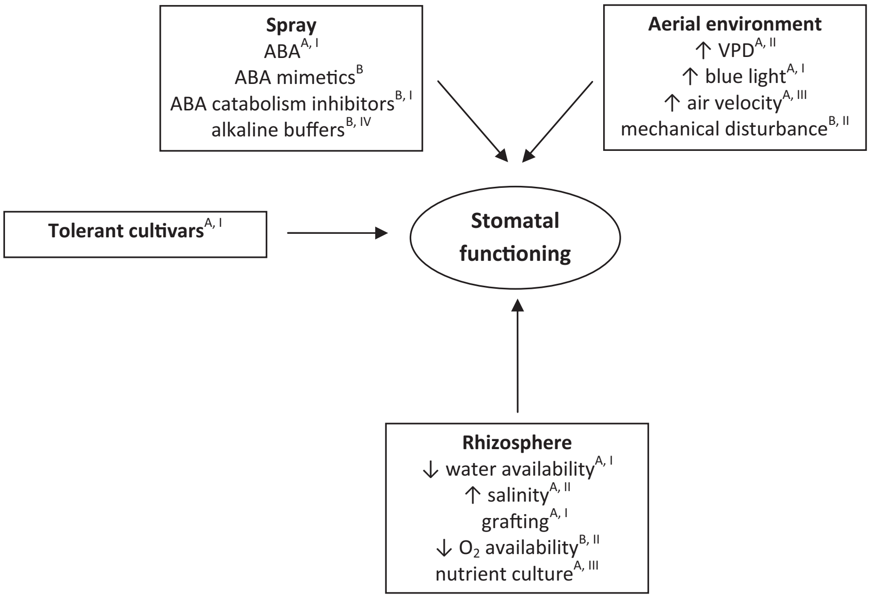

Fig. 1. Overview of the factors that have been reported (A) or expected (B) to improve stomatal functioning during growth at high relative air humidity (≥85%). I, increased leaf [ABA]; II, increased leaf [ABA] is expected, but not yet shown experimentally; III, increased sensitivity to ABA and/or within-leaf ABA re-distribution; IV, within-leaf ABA re-distribution. The effectiveness of the tested alleviating treatments is provided in Table 1.

plant survival largely depends on the prevailing environmental conditions during growth (Fanourakis et al., 2013b; Aliniaeifard and van Meeteren, 2013). Among the environmental factors that can disrupt stomatal functioning (i.e., continuous light, ozone, hydrogen sulfide and sulfur dioxide), long-term high relative air humidity (RH ≥ 85%) was found to be the most detrimental (reviewed by Aliniaeifard and van Meeteren, 2013). Although only partially resolved, it is clear that abscisic acid (ABA) plays an important regulatory role in stomatal (mal)functioning at high growth RH (Rezaei Nejad and van Meeteren, 2007; Fanourakis et al., 2011; Arve et al., 2013).

RH is the ratio of the amount of water vapour in the air, as compared to the amount that air holds at saturation. Since the saturation value increases as air temperature rises, RH is related to both the available amount of water vapour and temperature. The vapour pressure deficit (VPD) combines the effect of both RH and temperature, and is the difference between saturation vapour pressure and actual air vapour pressure. The VPD in combination with air velocity define the evaporative demand of a given environment, and these together with radiation are the driving forces of transpiration. Higher VPD (i.e., drier air), increased air velocity (i.e. higher boundary layer conductance), and higher radiation all tend to accelerate transpiration and stomatal regulation represents the key process to limit the loss.

In vitro culture vessels or propagation benches for rooting of leafy cuttings are typical examples of artificial environments where RH is set at very high levels (close to 100%) to prevent wilting of plant material during rooting (Xiao et al., 2010; Fei and Weathers, 2016). However, *in vitro* plantlets and leafy cuttings frequently show lethal wilting symptoms, when further exposed to moderate RH environments (Santamaria et al., 1993; Dias et al., 2014). The rapid wilting of these plants has been related to their inability to control water loss (Xiao et al., 2010; Dias et al., 2014). Plantlets grown in vessels set at lower RHs showed improved control of water loss, as a result of more functional stomata, as compared to plantlets exposed to typical RH levels close to 100% (Xiao et al., 2010).

High levels of RH (≈90%) also arise in greenhouse horticulture, especially during the winter (Fanourakis et al., 2012a,b, 2015b). Similarly to *in vitro* plantlets, stomatal malfunctioning has been reported in plants grown in protected cultivation, where RH was high for prolonged periods (Mortensen and Gislerød, 1999; Fanourakis et al., 2012a,b). As a consequence, cut flowers grown at high RH show poorer keeping quality than plants cultivated at moderate RH (reviewed by Fanourakis et al., 2013b, 2015b).

Interest on methods that stimulate stomatal functioning under high RH conditions is driven from both fundamental and practical point of view. Unraveling the amelioration mechanism is of significant interest to understand the reasons underlying the loss of stomatal functioning (Aliniaeifard and van Meeteren, 2013). This knowledge also lays the foundation for practical applications (Fanourakis et al., 2013b, 2015b), since it enables the production of plants with adequate regulation of water loss at high RH, which in turn will substantially improve the survival rates of these plants following exposure to environments of increased evaporative demand.

In this review, we survey the techniques that have been reported to partly or fully mitigate the high RH-induced stomatal malfunction (Fig. 1). Special attention is paid to observed genotypic variation (Mortensen and Gislerød, 1999; Fanourakis et al., 2013a; Giday et al., 2013b), together with the mechanism underlying these differences. We also suggest concepts that are expected to stimulate stomatal function under high RH conditions. The critical role of ABA in mediating genotypic and phenotypic differences in stomatal functioning following cultivation at high RH is addressed. In addition, scattered information in the literature about traits that undermine plant survival following growth at high RH is collectively examined. Finally, the role of changed stomatal anatomy on determining closing ability following leaf expansion in humid air is briefly evaluated. The cases (and references) presented in this review mostly refer to *Rosa hybrida*, which has been studied most extensively. When a reference to other species takes place, this is indicated.

2. Procedures alleviating the high RH-induced stomatal malfunction

To date, several strategies have been reported to circumvent the high RH-induced stomatal malfunction (Fig. 1). We have grouped