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Research article

Magnesium decreases leaf scald symptoms on rice leaves and preserves their photosynthetic performance

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ABSTRACT

The aim of this study was to investigate the effect of magnesium (Mg) on the photosynthetic gas exchange parameters ([net CO_2 assimilation rate (A), stomatal conductance (g_s), and internal CO_2 concentration (C_i)], chlorophyll (Chl) fluorescence *a* parameters {minimal fluorescence (F_0), maximum fluorescence (F_m), maximum quantum yield of photosystem II (F_v/F_m), photochemical quenching coefficient (q_p), yield of photochemistry [Y(II)], yield of regulated energy dissipation [Y(NPQ)] and yield of non-regulated dissipation losses [Y(NO)]} as well as on the concentrations of chloroplastidic pigments in rice plants grown in a nutrient solution containing 0.5 or 1.5 mM of Mg (-Mg or + Mg plants, respectively) and non-inoculated or inoculated with *Monographella albescens*. A higher Mg supply decreased the leaf scald symptoms in addition to partially preserving the photosynthetic performance of rice leaves challenged with *M. albescens*. Photosynthetic impairments were associated with photochemical and biochemical dysfunctions at the chloroplast level. The images of Chl *a* fluorescence evidenced increases in both the Y(II) and q_p coupled with decreases in Y(NPQ) associated with a higher Mg supply regardless of inoculation, suggesting increased electron transport rates and lower energy dissipation as heat. Notably, as the leaf scald developed, the use of light energy through photochemical reactions was continuously lost, especially for the inoculated -Mg plants. Interestingly, the lower values for F_0, F_m, and F_v/F_m for -Mg plants were associated with greater photochemical dysfunctions and a progressive loss of photosynthetic pigments during the infection process of *M. albescens*. The underlying mechanism through which Mg can affect rice resistance against *M. albescens* remains to be fully elucidated.

1. Introduction

Among the diseases affecting rice production worldwide, leaf scald, caused by the fungus *Monographella albescens* [(Hashiola and Yokogi) Samuels and I. C. Hallet = *Rhynchosporium oryzae* Hashiola and Yokogi], is one of the greatest importance (Filippi et al., 2005). On leaves, leaf scald symptoms appear as zonate or oblong colored olive lesions with light brown halos without well-defined margins (Filippi et al., 2005). As the disease develops, large part of the leaf blades become blight and dry out very quickly giving the leaf a scalded appearance (Ou, 1985; Nunes et al., 2004; Filippi et al., 2005).

Magnesium (Mg) is the central atom in the tetrapyrrole ring of both chlorophyll (Chl) *a* and Chl *b* molecules in the chloroplasts in order to make effective at gathering light for photosynthetic carbon reduction reactions (Taiz and Zeiger, 2009). The Mg per se is also involved in CO_2 assimilation reactions (Hannaway et al., 1980) as the photophosphorylation reactions that occur in the chloroplasts are affected by the Mg ions (Marschner, 1995). Furthermore, a large proportion (i.e., 75%) of the Mg in the leaf cells is associated either directly or indirectly with the protein synthesis, via its roles in ribosomal structure and function, for the stability of ribosomal particles (Bould et al., 1984; Marschner, 1995). The Mg is also required for RNA polymerase activity and thus for the formation of RNA in the nucleus (Marschner, 1995). Also, mitochondria in plant cells undergo structural degeneration without adequate amounts of Mg (Marinos, 1963). This may occur because many respiratory enzymes such as the phosphatases, ATPases and carboxylases require Mg (Marschner, 1995). Thus, Mg plays a central role in ATP and energy metabolism. Considering that Mg is preferentially bound to phosphoryl groups, it forms an Mg-ATP complex, which can be used by the active sites of ATPases for transferring energy-rich phosphoryl

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groups (Marschner, 1995). Finally, besides being required for the activation of several enzymes involved in lipid metabolism (e.g., acetic thiokinase and various phospholipid-synthesizing enzymes), Mg is also involved in the biosynthesis of phospholipids, and therefore, in the formation of functional cell membranes (Marschner, 1995).

The understanding of physiological changes that occur in a certain host during the infection process of a pathogen allows us to predict the effects of the disease on both crop growth and yield (Boote et al., 1980; Bastiaans, 1993). Plant growth and photosynthesis are negatively impacted due to the infection of pathogens associated with irreversible damages to the photosynthetic apparatus (Bassanezi et al., 2002; Berger et al., 2004; Dan Gao et al., 2011; Iqbal et al., 2012; Resende et al., 2012; Aucique-Pérez et al., 2014; Debona et al., 2014). Therefore, the proper assessment of the photosynthetic performance of plants infected by pathogens through the simultaneous measurement of leaf gas exchange and Chl *a* fluorescence parameters can provide crucial insights into the mechanisms underlying their intrinsic interaction with the potential to obtain new control strategies for the disease (Berger et al., 2007; Rolfe and Scholes, 2010). A decrease in the net carbon assimilation rate as well as limitations on stomatal and mesophyll conductance are the primary effects caused by pathogens infection (Berger et al., 2007; Barón et al., 2012). Taking this into consideration, non-invasive methods such as Chl *a* fluorescence imaging, particularly when combined with leaf gas exchange measurements, can provide a detailed spatio-temporal analysis of how an infected leaf may respond to a certain pathogen infection (Baker et al., 2001; Rolfe and Scholes, 2010; Iqbal et al., 2012; Rousseau et al., 2013; Tatagiba et al., 2015). Indeed, the Chl *a* fluorescence imaging technique has successfully been used in a range of studies to assess the interactions between plants and fungal pathogens (Rolfe and Scholes, 2010). This technique provides images that map the changes in single parameters associated with photosynthesis onto the leaves (Rousseau et al., 2013). Among the various Chl *a* fluorescence parameters that can be measured, the maximum photosystem (PS) II photochemical quantum efficiency, often assessed by the variable-to-maximum Chl *a* fluorescence ratio (F_v/F_m), has widely been used to compare non-infected and infected host tissues (Rousseau et al., 2013; Tatagiba et al., 2015). This ratio is close to or slightly above 0.8 in non-infected leaf tissue and progressively decreases as the damages to the PS II reaction centers are exacerbated (Krause and Weis, 1991). By comparison, the energy absorbed by PS II reaction centers can be divided between the fraction used in photochemistry [Y(II)] and that lost non-photochemically, which can be further divided into two competing non-photochemical pathways: the yield induced by down-regulatory processes [Y(NPQ)] associated with controlled thermal dissipation and the yield for other energy losses [Y(NO)] (Kramer et al., 2004). The measurement of the Y(NPQ) parameter give us an estimate of the level of photon flux density shows, therefore, that the leaf has retained the physiological means to protect itself by regulation (Kramer et al., 2004). On the other hand, the Y(NO) parameter indicates that both photochemical energy conversion and protective regulatory mechanisms are inefficient (Kramer et al., 2004). In general, during the infection process of the most aggressive pathogens in the absence of the appearance fo disease symptoms, the values of the parameters Y(II), Y(NPQ) and F_v/F_m decrease while the values of Y(NO) increase (Rolfe and Scholes, 2010; Resende et al., 2012; Aucique-Pérez et al., 2014; Debona et al., 2014; Tatagiba et al., 2015; Jiao et al., 2016). Depending on the host-pathogen interaction, the concentration of Mg on the plant tissue can decrease or increase the resistance to diseases (Huber, 1981). For example, a high foliar concentration of Mg exacerbated disease symptoms on the leaves of tomato and green pepper infected with *Xanthomonas campestris* pv. *vesicatoria* (Woltz and Jones, 1979). In sharp contrast, a high concentration of Mg on rice leaf sheaths was associated with reduced size of the lesions of sheath blight caused by *Rhizoctonia solani* (Schurt et al., 2014). Moreira et al. (2013) also reported that high foliar Mg concentration reduced the severity of brown spot on rice and increased the activities of polyphenoloxidases, peroxidases and phenylalanine ammonia-lyases. From the above, whether and how a proper Mg concentration on leaf blades can alter host resistance to diseases remains to be fully resolved (Jones and Huber, 2007).

Considering the importance of Mg in plant metabolism and the lack of information about the effect of Mg on the rice-*M. albescens* interaction, especially at the photosynthesis level, the present study was carried out to perform an in-depth analysis of the photosynthetic performance of rice leaves challenged with *Monographella albencens* by combining leaf gas exchanges, Chl *a* fluorescence images and photosynthetic pigment analyses.

2. Materials and methods

2.1. Nutrient solution preparation and plant growth

Rice plants were grown in nutrient solutions prepared based on Hoagland and Arnon (1950) with some modifications and consisted of: 1.0 mM KNO_3, 0.25 mM $NH_4H_2PO_4$, 0.1 mM NH_4Cl, 1.0 mM $Ca(NO_3)_2$, 0.30 μM $CuSO_4.5H_2O$, 0.33 μM $ZnSO_4.7H_2O$, 11.5 μM H_3BO_3, 3.5 μM $MnCl_2.4H_2O$, 0.1 μM $(NH_4)_6Mo_7O_{24}.4H_2O$, 25 μM $FeSO_4.7H_2O$ and 25 μM EDTA disodium. The Mg doses were 0.5 mM (using $MgSO_4.7H_2O$) or 1.5 mM (0.5 mM in the form of $MgSO_4.7H_2O$ and 1.0 mM in the form of $MgCl_2$). These two Mg doses were chosen based on previous studies (Moreira et al., 2013, 2015) to obtain low and high foliar Mg levels but within the adequate range of Mg concentrations for rice leaves (Malavolta et al., 1997).

Rice seeds from the 'Primavera' cultivar, which is susceptible to leaf scald, were surface-sterilized in 10% (v/v) NaOCl for 2 min, rinsed in sterilized water for 3 min and germinated on distilled water-soaked germitest paper in a germination chamber (MA-835/2106UR; Marconi, São Paulo, Brazil) at 25 °C for six days. The seedlings were then transferred to 5-L plastic pots (30 cm diameter) with one-half-strength nutrient solution for two days. After this period, the plants were transferred to new plastic pots with nutrient solutions that were prepared with the two Mg doses as described above. The nutrient solution, without aeration, was changed every four days. The pH was checked daily and maintained at approximately 5.5 using NaOH or HCl (1 M) when needed.

2.2. Plant inoculation with M. albescens

An isolate of *M. albescens* (UFV/DFP-022) that was obtained from the symptomatic leaves of rice plants of the 'Bonança' cultivar was used to inoculate the plants (Tatagiba et al., 2014). This isolate was preserved in glass vials containing potato-dextrose-agar (PDA), covered with mineral oil and maintained at 4 °C. Plugs of PDA with fungal mycelia were transferred to Petri dishes containing PDA. After three days, the PDA plugs containing the fungal mycelia were transferred to new Petri dishes that also contained PDA. The Petri dishes were maintained in a growth chamber (MA-835/2106UR; Marconi, São Paulo, Brazil) at 25 °C with a 12-h photoperiod for 15 days. Five plants per replication of each treatment were inoculated with *M. albescens* after growing for 45 days (the emergence of the tenth leaf from the main tiller (Matsuo and Hoshikama, 1993) in a hydroponic culture containing 0.5 or 1.5 mM of Mg. Three PDA discs (0.3 cm^2) containing *M. albescens* mycelia were equidistantly placed on the adaxial side of the 7th, 8th and 9th leaves, from the base to the apex, of each plant and gently pressed onto the surface with an