



The participation of hydrogen peroxide in methyl jasmonate-induced NH_4^+ accumulation in rice leaves

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Summary

Ammonium is a central intermediate in the nitrogen metabolism of plants. We have previously shown that methyl jasmonate (MJ) not only increases the content of H_2O_2 , but also causes NH_4^+ accumulation in rice leaves. More recently, H_2O_2 is thought to constitute a general signal molecule participating in the recognition of and the response to stress factors. In this study, we examined the role of H_2O_2 as a link between MJ and subsequent NH_4^+ accumulation in detached rice leaves. MJ treatment resulted in an accumulation of NH_4^+ in detached rice leaves, which was preceded by a decrease in the activity of glutamine synthetase (GS) and an increase in the specific activities of protease and phenylalanine ammonia-lyase (PAL). GS, PAL, and protease appear to be the enzymes responsible for the accumulation of NH_4^+ in MJ-treated detached rice leaves. Dimethylthiourea (DMTU), a chemical trap for H_2O_2 , was observed to be effective in inhibiting MJ-induced NH_4^+ accumulation in detached rice leaves. Scavengers of free radicals (sodium benzoate, SB, and glutathione, GSH), nitric oxide donor (*N-tert*-butyl- α -phenylnitron, PBN), the inhibitors of NADPH oxidase (diphenyleneiodonium chloride, DPI, and imidazole, IMD), and inhibitors of phosphatidylinositol 3-kinase (wortmannin, WM, and LY 294002, LY), which have previously been shown to prevent MJ-induced H_2O_2 production in detached rice leaves, inhibited MJ-induced NH_4^+ accumulation. Similarly, changes in enzymes responsible for NH_4^+ accumulation induced by MJ were observed to be inhibited by DMTU, SB, GSH, PBN, DPI, IMD, WM, or LY. Seedlings of rice cultivar Taichung Native 1 (TN1) are jasmonic acid (JA)-sensitive and those of cultivar Tainung 67 (TNG67) are JA-insensitive. On treatment with JA, H_2O_2 accumulated in the leaves of TN1 seedlings but not in the leaves of TNG67. Ethylene action inhibitor, silver thiosulfate, was observed to inhibit MJ- and abscisic

Abbreviations: ABA, abscisic acid; DMTU, dimethylthiourea; DPI, diphenyleneiodonium chloride; FW, initial fresh weight; GS, glutamine synthetase; IMD, imidazole; JA, jasmonic acid; LY, LY 294002; MJ, methyl jasmonate; PAL, phenylalanine ammonia-lyase; PI3K, phosphatidylinositol 3-kinase; PI3P, phosphatidylinositol 3-phosphate; ROS, reactive oxygen species; STS, silver thiosulfate; TN1, Taichung Native 1; TNG67, Tainung 67; WM, wortmannin

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acid-induced accumulation of NH_4^+ and changes in enzymes responsible for NH_4^+ accumulation in detached rice leaves, suggesting that the action of MJ and ABA is ethylene dependent.

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Introduction

Ammonium is a central intermediate in the nitrogen metabolism of plants. Glutamine synthetase (GS) is a key enzyme in NH_4^+ assimilation and catalyzes the ATP-dependent condensation of NH_4^+ with glutamate to produce glutamine (Mifflin and Lea, 1976). Phenylalanine ammonia-lyase (PAL) catalyzes the elimination of NH_4^+ from phenylalanine producing *trans*-cinnamic acid (Hahlbrock and Grisebach, 1979). NH_4^+ , released from the PAL reaction, is known to be incorporated into glutamine by the action of GS (Razel et al., 1996; van Heerden et al., 1996). Sakurai et al. (2001) provided evidence to show that GS is partly coupled to the reaction of PAL in developing rice leaves. Cd-induced NH_4^+ accumulation in rice leaves is associated with decreases in GS activity and increases in PAL specific activity (Hsu and Kao, 2004).

GS activity in plants is known to be regulated at the levels of transcription and turnover. Oxidative modification of GS has been implicated as the first step in the turnover of GS in bacteria (Levine, 1983; Rivett and Levine, 1990). Stieger and Feller (1997) have shown that GS degradation in illuminated chloroplasts requires the photosynthetic electron transport chain. Chloroplastic GS of wheat seedlings has been reported to be particularly prone to degradation under oxidative stress conditions (Palatnik et al., 1999). By incubating soybean root extracts enriched in GS in a metal-catalyzed oxidation system to produce the hydroxyl radical, Ortega et al. (1999) have shown that GS is oxidized and that the oxidized GS is inactive and more susceptible to proteolysis than nonoxidized GS. It is clear that GS degradation requires the participation of reactive oxygen species (ROS). We also demonstrated that paraquat, which is known to produce ROS, decreased GS activity and increased NH_4^+ content in rice leaves in the light (Chien et al., 2002). It has been shown that protease specific activity (or proteolysis) increased under photooxidative environmental conditions and treatment with a hydroxyl radical generating system or H_2O_2 (Casano and Trippi, 1992; Casano et al., 1990, 1994). Kumar and Knowles (2003) demonstrated that PAL specific activity induced by wounding in potato tubers is related to the ability to produce superoxide radicals.

Recently, researchers have focused on the functional aspects of H_2O_2 . H_2O_2 is a constituent of oxidative metabolism and is itself a ROS. Because H_2O_2 is a small, diffusible, and ubiquitous molecule that can be synthesized, as a stimulus, it fulfills the important criteria for an intracellular messenger (Neill et al., 2002; Foyer and Noctor, 2005). Thermoprotection obtained by spraying salicylic acid or by heat acclimation was suggested to be achieved by a common signal transduction pathway involving very early increases in H_2O_2 content (Dat et al., 1998). In tomato plants, H_2O_2 has been shown to act as a second messenger for induction of defense genes in response to wounding and systemin (Orozco-Cárdenas et al., 2001). It has been demonstrated that H_2O_2 is required for the induction of cytosolic ascorbate peroxidase mRNA by oxidative stress (Morita et al., 1999). H_2O_2 has now also been shown to be a critical component of abscisic acid (ABA)-induced stomatal closure (Pei et al., 2000; Zhang et al., 2001; Kwak et al., 2003) and ABA-induced rice leaf senescence (Hung and Kao, 2004b), ABA-induced activities of ascorbate peroxidase and glutathione reductase in rice roots (Tsai and Kao, 2004), and gibberellic acid-induced programmed cell death in barley aleurone cells (Fath et al., 2001).

Methyl jasmonate (MJ) was first considered to be secondary metabolite with a possible application in the perfume industry (Demole et al., 1962). It is now evident that jasmonates are a class of plant hormones, which mediate various aspects of developmental and stress responses (Creelman and Mullet, 1997). MJ has been shown to cause H_2O_2 production in parsley suspension-cultured cells (Kauss et al., 1994) and to act as a signal molecule for the induction of defense genes in tomato plants (Orozco-Cárdenas et al., 2001). We have previously shown that MJ not only increases the content of H_2O_2 (Hung and Kao, 2004a), but also causes NH_4^+ accumulation (Chen and Kao, 1998) in rice leaves. In this paper, we have examined the possible involvement of H_2O_2 in MJ-induced NH_4^+ accumulation in rice leaves.

Materials and methods

Plant materials and treatments

Rice (*Oryza sativa* L., cv. Taichung Native 1, TN1, or Tainung 67, TNG 67) seeds were sterilized with 2.5%

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