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Peroxidase activity in ethylene-, ABA-, or MeJA-treated rice (*Oryza sativa* L.) roots

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Abstract. Changes of peroxidase (EC 1.11.1.7) activity in ethylene-, ABA- or methyl jasmonate (MeJA)-treated rice (*Oryza sativa* L. cv. Taichung Native 1) roots were investigated. Guaiacol and syringaldazine were used as substrates for peroxidase activity determination. On a protein or fresh weight basis, activity of wall-bound guaiacol and syringaldazine peroxidase in air-grown roots decreased as growth advanced. In air-grown roots, soluble peroxidase activity on a fresh weight basis also decreased, but activity on a protein basis remained constant. In response to 10 μl/l ethylene, root growth was strongly inhibited while, in contrast, activity of cell wall-bound guaiacol and syringaldazine peroxidase on a protein or fresh weight basis increased. Activity of soluble peroxidase on a fresh weight basis in ethylene-treated roots also increased, although soluble peroxidase activity per mg protein did not change. ABA (10 μM) or MeJA (50 μM) also resulted in an inhibition of root growth but an increase of wall-bound guaiacol and syringaldazine peroxidase activity. Thus, activity of wall-bound peroxidase is inversely related to plant hormone-mediated growth inhibition of rice roots.

Keywords: *Oryza sativa* L.; Root; Ethylene; ABA; Methyl jasmonate; Cell wall-bound peroxidase.

Abbreviations: ABA, abscisic acid; **FW**, fresh weight; **MeJA**, methyl jasmonate.

Introduction

It is known that peroxidase (EC 1.11.1.7) influences several reactions involved in cell wall formation. The ferulic acid is esterified to the arabinoxylans and the peroxidase is believed to catalyze the formation of the diferuloyl cross-links between arabinoxylan chains. Peroxidase is involved with the assembly of lignin and may be involved in linking protein and lignin in the wall (Fry, 1986; Van Huystee, 1987; Whitmore, 1978) subsequently decreasing wall extensibility (Fry, 1979). In peanut hypocotyls (Zheng and Van Huystee, 1992), mung bean hypocotyl (Goldberg et al., 1987) and dwarf sorghum (Schertz et al., 1971), an elevated peroxidase activity is associated with the decrease of plant growth. Studies on two genotypes of tall fescue (*Festuca arundinacea* Schreb.) with different lengths of leaf elongation zones also showed that the cessation of elongation is closely related to the increase of wall-bound peroxidase activity (MacAdam et al., 1992). Wall-bound peroxidase is involved in the ethylene-regulated growth of higher plants. In the case of *Pharbitis*, ethylene, which caused the inversion-induced growth inhibition of shoots, is suggested to stiffen the wall by increasing activity of wall-bound peroxidase (Prasad and Cline, 1987). The ethylene-mediated inhibition of pea epicotyl elongation is accompanied by increasing of peroxidase activity (Ridge and Osborne, 1970). In *Ranunculus sceleratus* L., ethylene that promotes petiole growth results in decreasing of peroxidase activity (Horton, 1993).

The growth of rice roots is regulated by several plant growth regulators. Ethylene at high concentrations inhibits root growth in etiolated rice seedlings (Jackson, 1982). ABA inhibits rice root growth (Horton, 1991; Lee et al., 1994) and methyl jasmonate (MeJA) also inhibit the growth of rice seedlings (Yamane et al., 1981),

At present, the metabolic processes involved in plant growth regulator-mediated growth inhibitions of rice roots are still unknown. To obtain further information as to whether peroxidase is associated with growth of rice roots, the activities of soluble and cell wall-bound (NaCl extractable) peroxidase were determined in this study. The H^+ donor, guaiacol, was used for peroxidase activity determination. Since syringaldazine is thought to be oxidized by peroxidase bound to cell walls that have undergone lignification (Goldberg et al., 1983), it was also used for peroxidase activity determination.

Materials and Methods

Plant Cultivation and Plant Growth Regulator Treatment

Rice (*Oryza sativa* L. cv. Taichung Native 1) seeds were sterilized with 5% sodium hypochlorite for 10 min. After

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being washed with distilled H_2O, seeds were incubated in Petri dishes at 30°C in darkness as previously reported (Lee and Chu, 1992). After 3 d, etiolated rice seedlings with 4 mm roots were used in all experiments. All treatments were carried out in darkness. For air controls, ten seedlings were placed in a Petri dish (8 cm width, 1 cm depth) containing 5 ml distilled H_2O such that seedlings were not submerged. For ethylene treatment, ten seedlings were placed in a 25 ml vial and humidified ethylene gas (10 μl/l) was passed through at a flow rate of 10 ml/min. Ethylene gas was filtered through a 0.45 μm filter. For ABA (10 μm) or MeJA (50 μm) treatment, ten seedlings were also placed in a Petri dish (8 cm width, 1 cm depth) containing 5 ml distilled H_2O and ABA or MeJA. Forty seedlings were used for root length determination. Ten seedlings from one Petri dish were used for the peroxidase activity assay, and there were 4 replicated samples. Seedlings were ground under liquid N_2 in a mortar. No significant level of peroxidase was found in the culture fluid from the seedlings.

Sample Preparation and Determination of Peroxidase Activity

Air-grown or ethylene-treated roots (about 0.5 g fresh weight) were frozen in liquid nitrogen and then stored at -70°C. For enzyme extraction, plant samples were homogenized in liquid nitrogen and 3 volumes (tissue fresh weight [g] : extraction buffer volume [ml] = 1 : 3) of 10 mM phosphate buffer (pH 6.4) were added. After centrifuging at 1,000 g at 4°C for 10 min, the supernatant was used for the determination of soluble peroxidase activity. The pellet was resuspended in the same volume of extraction buffer, and the suspension was centrifuged at 1,000 g at 4°C for 10 min. The washing step was repeated at least four times until no peroxidase activity was found in the supernatant. The washed pellet was then shaken with 3 volumes of 1 M NaCl in extraction buffer for 2 h at 30°C with continuous shaking and centrifuged at 1,000 g at 4°C for 10 min. The activity in the supernatant was used as a measure of wall-bound peroxidase activity. The extracts were assayed within 1 h of preparation to avoid loss of activity. In each treatment, there were four replicated samples.

Guaiacol peroxidase activity was analyzed in 10 mM phosphate buffer (pH 6.4) containing 8 mM guaiacol and 2.75 mM H_2O_2 (Chance and Maehley, 1955). The increase of absorbance at 470 nm was recorded within 30 sec after adding 2.75 mM H_2O_2. Syringaldazine peroxidase activity was determined by a modification of the method of Pandolfini et al., 1992. A sample was incubated in 100 mM sodium-phosphate buffer (pH 6.0) containing 1.5 mM H_2O_2 and 0.04 mM syringaldazine (dissolved in methanol-dioxane, 1:1, v/v). The increase of absorbance at 530 nm was recorded within 1 min. The specific activity of peroxidase was expressed on the basis of mg soluble protein content or gram fresh weight. Peroxidase activity values pooled are the average of four replicates (mean +/- SE, n=4).

Protein Content Determination and Chemicals

Soluble or NaCl-extracted protein content was determined according to Bradford (1976) using bovine serum albumin as a standard. All chemicals were from Sigma (U.S.A.) or Merck (Germany).

Results

Changes of root length and fresh weight are shown in Figure 1. In air, roots elongated rapidly as growth advanced. After exposure to ethylene (10 μl/l), root elongation was markedly inhibited. The length of ethylene-treated roots was only 57.5% that of air controls 4 d after treatment. In air-grown seedlings, the fresh weight per root also increased gradually as growth advanced. The increase in root fresh weight was also substantially inhibited by ethylene treatment. After 4 d, the fresh weight of ethylene-treated roots was only 58.3% that of air controls. When transferred to ethylene-free conditions, ethylene-treated roots resumed growth. Ethylene below 10 μl/l had less effects on root growth (data not shown).

The activities of soluble and wall-bound peroxidase in air-grown roots are shown in Figures 2 and 3. On the protein basis, the activity of soluble guaiacol (Figure 2A) or syringaldazine (Figure 3A) peroxidase in air-grown roots remained almost constant as growth advanced. While on

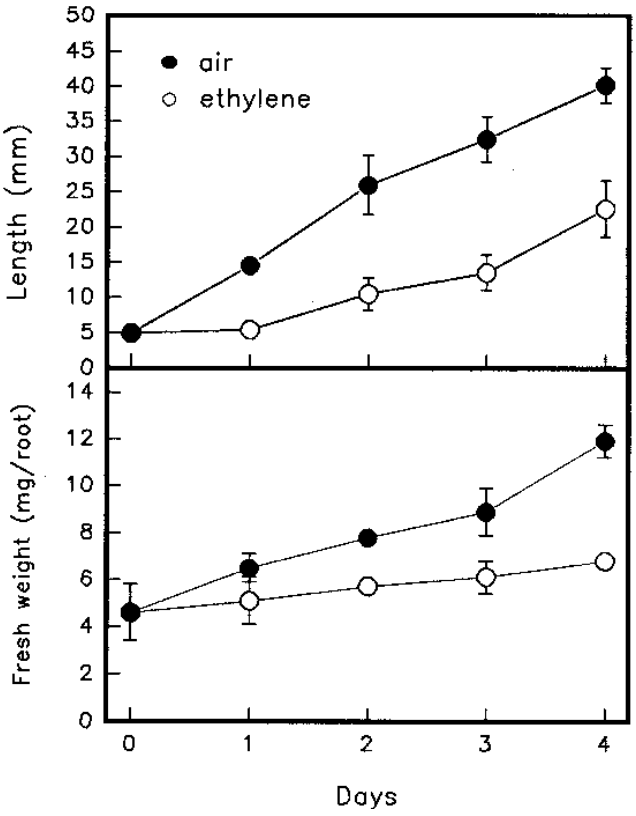

Figure 1. Changes of length of air-grown or ethylene-treated rice seedling roots. Ethylene concentration is 10 μl/l. Bars indicate the standard errors (Mean ± SE, n=40).

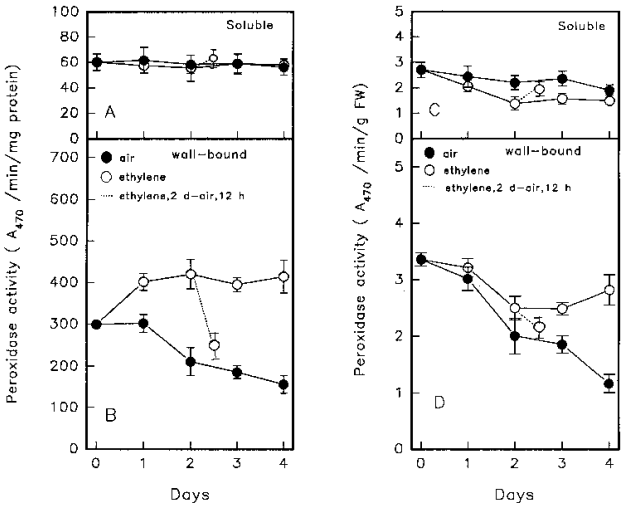

Figure 2. Guaiacol peroxidase activity in air-grown or ethylene-treated rice seedling roots. Ethylene concentration is 10 μl/l. After 2 d of ethylene treatment, ethylene-treated rice seedlings were transferred to ambient air conditions. Bars indicate the standard errors (Mean ± SE, n=4). A and C, soluble peroxidase; B and D, wall-bound peroxidase.

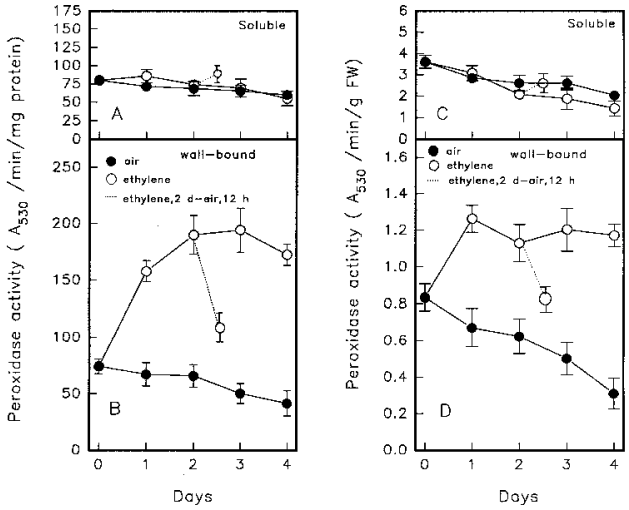

Figure 3. Syringaldazine peroxidase activity in air-grown or ethylene-treated rice seedling roots. Ethylene concentration is 10 μl/l. Bars indicate the standard errors (Mean ± SE, n=4). A and C, soluble peroxidase; B and D, wall-bound peroxidase.

the fresh weight basis, both soluble guaiacol (Figure 2C) and syringaldazine (Figure 3C) peroxidase activities in air-grown roots decreased slightly. Activity of wall-bound guaiacol (Figure 2B and 2D) or syringaldazine (Figure 3B and 3D) peroxidase, based on protein or fresh weight, decreased progressively in air-grown roots as growth advanced.

Changes of soluble and wall-bound peroxidase activity in ethylene-treated roots are also shown in Figures 2 and 3. On the protein basis, neither soluble guaiacol (Figure 2A) nor syringaldazine (Figure 3A) peroxidase activities were affected by 10 μl/l ethylene. However, on the fresh weight basis, both soluble guaiacol (Figure 2C) and syringaldazine (Figure 3C) peroxidase activities in ethylene-treated roots decreased, especially 3 d after treatment. In contrast to the soluble peroxidase, the activity of wall-bound guaiacol or syringaldazine peroxidases expressed on a protein basis increased significantly in the 24 h following exposure to 10 μl/l ethylene (Figures 2B and 3B). If expressed on a fresh weight basis, wall-bound guaiacol peroxidase in ethylene-treated roots decreased during the first 2 d in parallel with the air controls, but remained unchanged afterward (Figure 2D). In contrast, cell wall-bound syringaldazine peroxidase expressed on a protein basis increased and reached a plateau 3 d after ethylene treatment (Figure 3C), while on the fresh weight basis cell wall-bound syringaldazine peroxidase increased and reached a plateau 1 d after ethylene treatment (Figure 3D). When transferred to air (ethylene-free conditions), the activity of soluble or wall-bound, respectively, guaiacol and syringaldazine peroxidases either on a protein or fresh weight basis increased or decreased, respectively, almost to the level of air controls 12 h after transfer (Figures 2 and 3).

Our preliminary experiments have shown that ABA above 1 μM or MeJA above 25 μM could inhibit the growth of both shoots and roots of etiolated rice seedlings. Thus, we also tested the effects of ABA at 10 μM or MeJA at 50 μM on peroxidase activity. Figure 4 shows that treatment of ABA at 10 μM for 2 d inhibited both root elongation and fresh weight accumulation. On either protein or fresh weight basis, the activity of soluble or wall-bound peroxidases increased significantly after ABA treatment.

MeJA applied at 50 μM for 2 d, caused a small inhibition of both root elongation and fresh weight accumulation (Figure 4). The results are not similar to ABA treatment. Thus for soluble or wall-bound guaiacol peroxidase there was an increase in activity as expressed both on the protein and fresh weight basis, but this was not, especially in the latter case, as large as for ABA. The situation is quite different for the syringaldazine peroxidase where the difference from the controls is probably not significant. The comparison between ABA and MeJA treatments shows that effects of ABA on root growth and peroxidase activity were much stronger than MeJA.

Discussion

The activity of wall-bound peroxidase, especially the syringaldazine enzyme, is inversely correlated with elongation of rice seedlings roots both in air (Figures 2 and 3) and in the presence of ethylene, where root elongation is reduced (Figures 2 and 3). A similar inhibitory role of wall-bound peroxidase in ethylene-mediated growth was observed in pea epicotyl cells (Ridge and Osborne, 1970) and the inhibition of elongation induced by inversion induced gravity stress of *Pharbitis nil* shoots (Prasad and Cline, 1987).

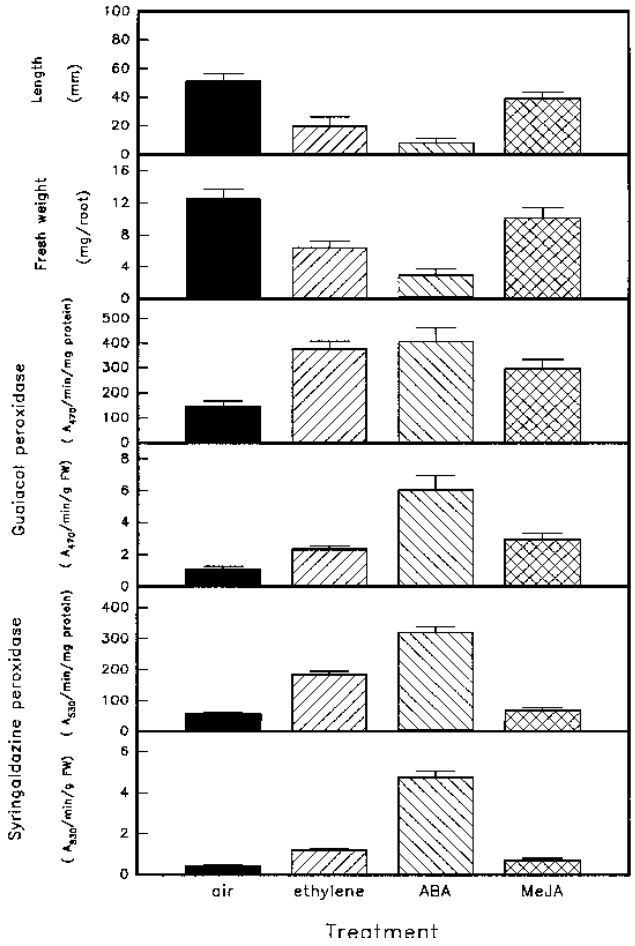

Figure 4. Effects of ethylene (10 μl/l), ABA (1 μM), or MeJA (5 μM) on rice seedling root growth and wall-bound peroxidase activity. After 2 d of plant growth regulator treatment, roots were harvested. Root length, fresh weight (n=40), and peroxidase activities (n=4) were determined. Bars indicate the standard errors (Mean ± SE).

In contrast, a number of plants such as sweet potato (Bueschner, 1975; Gahagan, 1968), cucumber (Abeles et al., 1988; Retig and Rudich, 1972; Stermer and Hammerschmidt, 1985), and tobacco (Van Loon and Antoniw, 1982), also show an increase of peroxidase activity in response to ethylene. In these cases, the increased peroxidase activity is associated with defence systems (Levine et al., 1994) or senescence-related chlorophyll degradation. Since our seedlings are grown in sterile conditions in the dark, peroxidases related to defence or chlorophyll removal are probably not involved in the changes shown here.

According to the present study, wall-bound guaiacol or syringaldazine peroxidase activity is also inversely related to ABA- or MeJA-regulated root growth of rice seedlings. In tomato petioles (Sherf et al., 1993), potato and tomato callus culture (Roberts and Kolattukudy, 1989) and duckweed *Spirodela polyrrhiza* L. (Chaloupkova and Smart, 1994) ABA has been reported to affect peroxidase gene expression. However, we still do not know whether ABA regulates wall-bound peroxidase activity of rice roots at the transcriptional or translational level. It is known that MeJA has biochemical and physiological effects similar to ABA (Parthier, 1991). As compared with ABA, however at a higher concentration (50 μM), MeJA results in a slight inhibition of rice root growth and an increase of wall-bound guaiacol peroxidase activity. The weaker effects of MeJA compared with ABA may be due to a gradual decrease of MeJA concentration in solution through MeJA evaporation.

Recently, peroxidase activity was also shown to increase in ABA- or MeJA-treated rice leaves (Yeh and Kao, 1994). The ABA- or MeJA-induced peroxidase activity in detached rice leaves was suggested to be correlated with senescence processes such as chlorophyll degradation (Yeh and Kao, 1994).

It has been reported recently that an increase of endogenous ABA levels is closely associated with the ethylene-mediated growth inhibition of rice roots (Lee et al., 1994). Since the present study shows that ABA treatment could promote wall-bound peroxidase activity in rice roots, it is possible that change of internal ABA is involved in the regulation of wall-bound peroxidase activity in ethylene-treated rice roots. However, interactions among ethylene, ABA, and MeJA in peroxidase activity regulation still need to be elucidated.

Wall-bound peroxidase plays an important role in lignification and cross-linking between extensin molecules and between feruloylated polysaccharides (Castillo, 1984; Fry, 1986; Van Huystee, 1987; Taiz, 1984). It has been proposed (Fry, 1986) that the peroxidase-mediated conversion of ferulic acid to diferulic acid on polysaccharide is correlated with wall extensibility. In the case of rice, ferulic acid and diferulic acid do exist in endosperms (Shibuya, 1984) and coleoptiles (Tan et al., 1992), but an equal ratio of ferulic and diferulic acid between air-grown and submerged rice coleoptiles suggests that the increase of feruloylation of arabinoxylans and not the peroxidation of ferulic to diferulic acid plays a role in the wall stiffening of air-grown coleoptiles (Kutschera et al., 1993; Tan et al., 1992). However, the possible connection between a peroxidase-catalyzed conversion of ferulic acid esters to diferulic acid esters in ethylene-, ABA-, or MeJA-treated rice seedlings and the inhibited growth of rice roots has not been explored.

Another possibility of peroxidase's effect on ethylene-, ABA- or MeJA-inhibited rice roots is that it catalyzes the cross-linking of isodityrosine or lignification in the cell wall. The extent to which these events are occurring in the duration of the experiments has not been determined, but needs to be in the future. Several studies have established that cell wall-bound peroxidase catalyzes the insolubilization of hydroxyproline-rich glycoprotein in the wall via cross-linkage of isodityrosine. Cooper and Varner (1983), for example, used root slices (7 mm diameter by 1.5 mm thick) from phloem parenchyma tissue of carrot a dicot; Fry (1979) examined the primary cell wall of growth spinach a dicot; Iiyama et al. (1994) re-

viewed many plant tissues used; Waffenschmidt et al. (1993) used *Chlamydomonas,* a single-cell alga. Also established is that levels of insoluble hydroxyproline-rich glycoprotein are inversely related to wall extensibility. Sadava and Chrispeels (1973) used epicotyls of pea a dicot. In the case of 19–22 d old *Pharbitis nil* seedlings under continuous light, the ethylene-mediated cross-linkings of hydroxyproline-rich glycoprotein and lignin are considered to be an important factor in the elongation cessation of inverted shoots (Prasad and Cline, 1987). Finally, Marigo and Boudet (1980) using 20–35 d old seedlings of tomato a dicot established that ethylene mediates the peroxidase-induced lignification which makes cell walls more rigid and limits cell growth. In the present study, activity of syringaldazine peroxidase increased as root elongation was inhibited by ethylene, ABA, or MeJA. This strongly indicates that the peroxidase-mediated lignification could be involved in ethylene-, ABA-, or MeJA-regulated inhibition of root growth and that the enzyme activity may belong to a lignin forming anionic peroxidase (Lagrimini et al., 1987). However, we are not sure if the same gene or different genes are turned on by the growth regulators we used. Levels of lignin and hydroxyproline-rich glycoprotein contents in ethylene-, ABA-, or MeJA-treated rice roots are under study to determine whether the cross-linkage between extensin and lignin is involved in the peroxidase-related control of cell elongation in rice roots.

In summary, the activity of peroxidase in the form of wall-bound (1M NaCl extractable enzyme) is inversely related to air-grown rice root growth and with the growth regulator-mediated growth inhibition of rice roots. The significant increase of wall-bound peroxidase activity may at least explain part of the inhibitory effects of ethylene, ABA, or MeJA on the growth of rice roots. Since syringaldazine is an unnatural substrate, changes of different isoforms of peroxidase will be determined using true substrates e.g. cinnamyl alcolhos (Lagrimini et al., 1987) to specify the difference among ethylene, ABA, and MeJA action on the wall-bound peroxidase activity increase in rice roots in the near future.

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