

Role of rice heme oxygenase in lateral root formation

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Lateral roots (LRs) play important roles in increasing the absorptive capacity of roots as well as to anchor the plant in the soil. In rice, exposure to auxin, methyl jasmonate (MJ), apocynin, and CoCl_2 has been shown to increase LR formation. This review provides evidence showing a close link between rice heme oxygenase (HO) and LR formation. The effect of auxin and MJ is nitric oxide (NO) dependent, whereas that of apocynin requires H_2O_2 . The effect of CoCl_2 on the LR formation could be by some other pathway unrelated to NO and H_2O_2 . This review also highlights future lines of research that should increase our knowledge of HO-involved LR formation in rice.

In recent years, root development has emerged as a central focus of research in many laboratories across the world. Lateral roots (LRs) play important roles in water and nutrient acquisition and anchorage. Root architecture, including LR, has been suggested to be one of the promising feature of crops in a new green revolution.¹ Thus, understanding the regulation LR development is of agronomic importance.

Heme oxygenase (HO; EC1.14.99.3) catabolizes heme into carbon monoxide (CO), biliverdin (BV), and free iron. Three isoforms of HO (HO-1, HO-2, and HO-3) have been identified, which are products of distinct genes.² HO-1 is highly inducible, whereas HO-2 and HO-3 are constitutively expressed. In plants, HO-1 has been shown to be associated with LR formation.^{3,4} Plant HO-1 also plays roles in phytochrome chromophore synthesis and protection against oxidative cell damage.^{5,6} The expression of HO-1 has been shown to be induced by nitric oxide (NO)⁷ and H_2O_2 .⁸⁻¹⁰ In this mini-review, which is not intended to be comprehensive, we shall be concerned strictly with the role of rice HO in LR formation, and mostly with the work from our laboratory.

HO and LR Formation Caused by Auxin and Methyl Jasmonate

A large body of work has indicated that auxin, a plant hormone that influences many aspects of plant development, is a primary regulator of LR formation. Plants that are treated with auxin

or that overproduce it form more LRs, whereas plants that are impaired in auxin signaling form fewer.¹¹ Nitric oxide (NO), a free radical active gas, is now recognized as an ubiquitous signal involved in diverse physiological process in plants.¹² Correa-Aragunde et al.¹³ provided the first evidence about the interplays between auxin and NO during LR formation in tomato. In rice, NO-donor sodium nitroprusside (SNP) and indole-3-butyric acid (IBA, a naturally occurring auxin) were able to induce LR formation.¹⁴ This effect is specific for NO because the NO scavenger 2-(4-carboxyphenyl)-4,4,5,5-tetramethylimidazolin-1-oxyl-3-oxide (cPTIO) blocked the action of SNP and IBA.¹⁴ Moreover, SNP and IBA-induced NO production were localized in root area corresponding to emergence of LRs.¹⁴ In another recent report, we demonstrated that SNP and IBA could induce *OsHO1* mRNA expression.¹⁵ LR formation and HO activity induced by SNP and IBA was reduced by cPTIO and Zn protoporphyrin (ZnPPIX, the specific inhibitor of HO).¹⁵ It seems that HO is required for auxin- and NO-induced LR formation in rice (Fig. 1).

Jasmonic acid (JA) and methyl jasmonate (MJ), originally identified as the major component of jasmine scent, play a universal role in the plant kingdom and are involved in the regulation of diverse aspects of plant biology, including growth, development, metabolism, and interaction with the environment.¹⁶ Application of MJ to rice seedlings induced LR formation, *OsHO1* mRNA expression, and HO activity.^{17,18} Using NO scavenger cPTIO and HO inhibitor ZnPPIX, we were able to show that LR formation caused by MJ is NO dependent and that HO participates in MJ-promoted LR formation in rice roots.^{17,18} Sun et al.¹⁹ demonstrated that JA-mediated auxin biosynthesis in the Arabidopsis roots is critical for LR formation. Whether auxin biosynthesis is required for MJ-induced LR formation in rice remains to be examined (Fig. 1).

To study the contribution of the NO sources in LR formation in rice, pharmacological approaches using both nitrate reductase (NR) and nitric oxide synthase inhibitors have been employed. Application of NR inhibitor sodium tungstate completely inhibited IBA- and MJ-induced NO production and LR formation.^{14,17} Our results support the participation of NR-catalyzed NO synthesis in IBA- and MJ-induced LR formation in rice.

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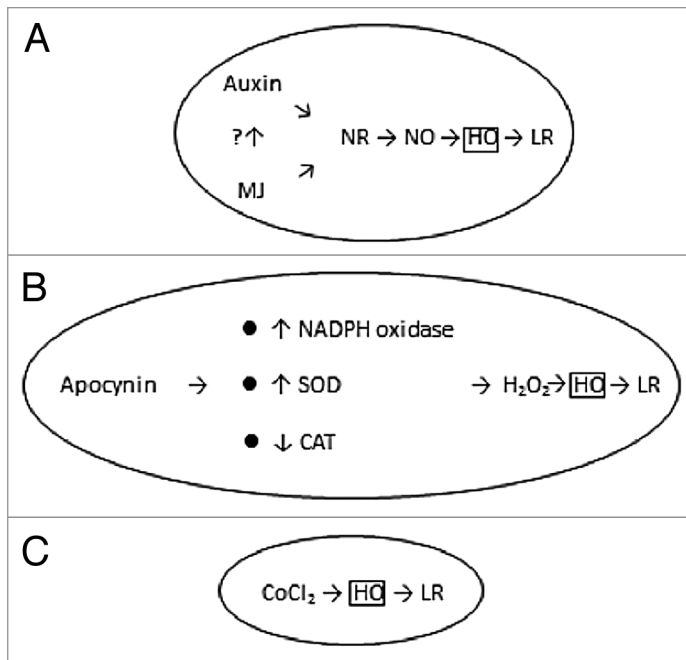


Figure 1. Diagram showing the pathways by which auxin and MJ (A), apocynin (B), and CoCl₂ (C) might induce LR formation in rice.

HO and LR Formation Caused by Apocynin

Apocynin (acetovanillone) is a compound originally isolated from the medicinal plant *Picrorhiza kurroa*, a small perennial herb that grows in Himalayas. In animal system, apocynin induces NO synthesis.²⁰ Tossi et al.²¹ also demonstrated that apocynin increases NO production in maize leaves. This is the only work showing that apocynin increases NO production in plants. The effect of apocynin on LR formation in rice has been examined.²² Our data suggest that both H₂O₂ and HO are required for apocynin-induced LR formation in rice (Fig. 1). Our conclusion is supported by the observations that (1) treatment with apocynin induced LR formation and increased H₂O₂ production, but had no effect on NO production; (2) H₂O₂ production caused by H₂O₂ and apocynin was localized in the root area corresponding to the LR emergence; (3) treatment with H₂O₂ and apocynin also increased *OsHO1* mRNA expression and HO activity; and (4) LR formation and HO activity induced by H₂O₂ and apocynin were reduced by ZnPPIX (the specific inhibitor of HO).

Plasma-membrane NADPH oxidase is a protein that transfers electrons from cytoplasmic NADPH to an O₂ to form O₂⁻, followed by dimutation of O₂⁻ to H₂O₂.²³ Diphenyleiiodonium chloride, an inhibitor of NADPH oxidase, was effective in reducing apocynin-induced H₂O₂ production and LR formation.²² This indicates that apocynin-dependent H₂O₂ production in rice originated at least in part, from plasma-membrane NADPH oxidase. The increase in superoxide dismutase (SOD) activity and the decrease in catalase (CAT) activity could result in

H₂O₂ accumulation. Apocynin was also observed to increase SOD activity and decreased CAT activity in rice roots.²² These results suggest that apocynin may exert other effects besides its ability to induce NADPH oxidase, for instance, it increase SOD activity and decrease CAT activity.

HO and LR Formation Caused by CoCl₂

Cobalt is usually considered as a non-essential element. Gad and Atta-Aly²⁴ provided the first evidence showing that cobalt induces adventitious root formation in cucumber and tomato. Later work by Xu et al.²⁵ demonstrated that CoCl₂ induces LR formation in tomato. Recently, the effect of CoCl₂ on LR formation in rice has been examined.²⁶ CoCl₂ has been shown to increase the number of LRs in rice, induce the expression of *OsHO1* gene and the activity of HO. Moreover, ZnPPIX reduced LR formation, *OsHO1* mRNA expression, and HO activity caused by CoCl₂. Our data support the importance of HO in regulating CoCl₂-increased LR formation (Fig. 1). Moreover, CoCl₂ had no effect on H₂O₂ content and NO production. Therefore, the effect of CoCl₂ could be mediated by some other pathway unrelated to H₂O₂ and NO. Exposure of plants to mild chronic stress can cause induction of specific, stress-induced morphogenic responses (SIMRs) characterized by an inhibition of root elongation, and enhanced formation of LRs.²⁷ CoCl₂ treatment causes a typical SIMR in rice.²⁶ It is most likely that rice HO is involved in SIMR caused by CoCl₂.

Conclusions and Perspectives

Overall, the data summarized here indicate a close link between rice HO and LR formation. *OsHO1* mRNA expression and HO activity could be mediated by NO, H₂O₂ or pathway unrelated to NO and H₂O₂. A critical issue to be further explored is the detailed function of *OsHO1*, a rice HO-1 gene in LR formation. Evaluation of overexpression of *OsHO1* in transgenic rice plants will uncover the detailed function in LR formation. There are still important aspects related to LR formation that require characterization. It is well established that cell cycle regulatory genes are the regulatory genes of LR formation. It is of great interest to know whether cell cycle regulatory genes might be target for HO-involved LR formation in rice induced by auxin, MJ, NO, H₂O₂ or CoCl₂.

Disclosure of Potential Conflicts of Interest

No potential conflicts of interest were disclosed.

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