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Induction of alternative respiratory pathway involves nitric oxide, hydrogen peroxide and ethylene under salt stress

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Key words: alternative respiratory pathway, ethylene, hydrogen peroxide, nitric oxide, salt stress, signaling molecule

Abbreviations: ACS, 1-aminocyclopropane-1-carboxylic acid synthase; AP, alternative respiratory pathway; AOX, alternative oxidase; CP, cytochrome pathway; H_2O_2, hydrogen peroxide; NO, nitric oxide; NOS, nitric oxide synthase; PM, plasma membrane; ROS, reactive oxygen species; WT, wild type

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Alternative respiratory pathway (AP) plays an important role in plant thermogenesis, fruit ripening and responses to environmental stresses. AP may participate in the adaptation to salt stress since salt stress increased the activity of the AP. Recently, new evidence revealed that ethylene and hydrogen peroxide (H_2O_2) are involved in the salt-induced increase of the AP, which plays an important role in salt tolerance in Arabidopsis callus, and ethylene may be acting downstream of H_2O_2. Recent observations also indicated both ethylene and nitric oxide (NO) act as signaling molecules in responses to salt stress, and ethylene may be a part of the downstream signal molecular in NO action. In this addendum, a hypothetical model for NO function in regulation of H_2O_2- and ethylene-mediated induction of AP under salt stress is presented.

Respiration plays a pivotal role in the metabolism of plants by providing adequate energy and carbon sources to drive the cellular metabolism and transport processes. In addition to the cytochrome pathway (CP), plant mitochondria have a cyanide-resistant respiration electron transport pathway, the alternative respiratory pathway (AP). Alternative oxidase (AOX) is used as the terminal oxidase in the AP and located in the inner membrane of mitochondria. It is well known that the AP plays an important role in plant thermogenesis, fruit ripening and responses to environmental stresses.[1-3] It is thought that the AP may play a role in preventing the formation of toxic reactive oxygen species (ROS) when the main CP is inhibited or restricted.[4] Salt stress can lead to an accumulation of high levels of ROS, such as superoxide ($O_2^{-}\cdot$), hydrogen peroxide (H_2O_2) and hydroxyl radicals ($OH\cdot$).[5,6] These may disturb cellular redox homeostasis, and then lead to oxidative damage. It has been shown that the AP may participate in the adaptation to salt stress since salt stress increased the activity of the AP.[7,8] However, whether respiration could be involved in the prevention of ROS formation under salt stress is not reported. Furthermore, the mechanism of AP regulation affected by salinity remains unknown.

Ethylene and H_2O_2 are both able to induce AP in plant cells.[3,9] The essential role of ethylene for AP induction was reported by Simons et al. (1999) in Arabidopsis, and it was shown that AP operation is ethylene dependent.[11] In several studies, H_2O_2 is considered as the second messenger to induce AOX activity by directly oxidizing transcription factors or by modulating phosphorylation processes.[9,11] Although ethylene and H_2O_2 have been found to be possibly involved in AP induction, the interaction between them in the induction of the AP during environmental stresses remains unclear.

Our results indicated that both H_2O_2 and ethylene induced AP activity in wild-type (WT) Arabidopsis but not in ethylene-insensitive mutant under salt stress, suggesting ethylene signaling is required for AP induction. Subsequently, we set out to investigate the relationship between H_2O_2 and ethylene under salt stress. It was found that H_2O_2 stimulated ethylene emission, while ethylene reduced H_2O_2 production under salt

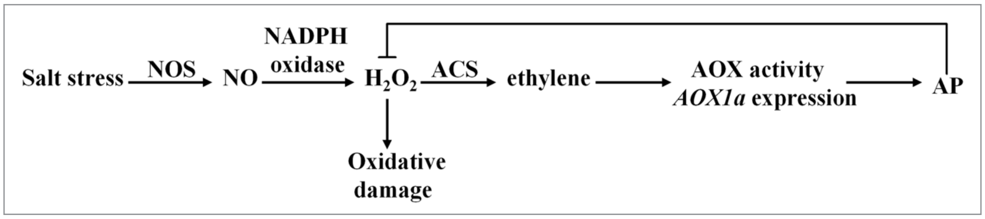

Figure 1. Hypothetical model for the potential function of NO, H_2O_2 and ethylene as signaling molecules in AP induction under salt stress in Arabidopsis. Salt stress activates a signal transduction cascade that leads to the increased activity of AOX, whose expression leads to enhanced AP activity. NO is generated by NOS, H_2O_2 is likely generated by PM NADPH oxidase attributed to NO, and ethylene emission is stimulated by ACS attributed to H_2O_2. The AP activity is regulated by ethylene directly under salt stress.

stress. Further results indicated H_2O_2 and ethylene modulated salt-induced AOX gene (*AOX1a*) expression and the increase in pyruvate content. These results suggest ethylene and H_2O_2 are involved in the salt-induced increase of the AP, which plays an important role in salt tolerance in WT calluses, and ethylene may be acting downstream of H_2O_2. There are reports that nitric oxide (NO) greatly induces *AOX1a* expression in Arabidopsis cell cultures and in tobacco plants.[11,12] Our previous work demonstrated that salt possibly induced NO accumulation resulting from stimulating nitric oxide synthase (NOS) in Arabidopsis callus, and NO stimulated ethylene emission by increasing 1-aminocyclopropane-1-carboxylic acid synthase (ACS) activity under salt stress,[13] suggesting ethylene may be a part of the downstream signal molecular in NO action in response to salt stress. These observations imply that NO may also be involved in AP induction under salt stress. In addition, salt-induced NO production was involved in H_2O_2 generation by stimulating plasma membrane (PM) NADPH oxidase activity.[14] Growing evidences suggest that PM NADPH oxidase is responsible for H_2O_2 accumulation under stresses.[14,15] In addition to functioning as an endogenous oxidant, H_2O_2 has been suggested as a diffusible signal for selective induction of defense mechanisms in plant cells.[16,17] Summing up these observations that allows us to speculate NO maybe regulate H_2O_2- and ethylene-dependent AP induction under salt stress.

Based on the results obtained so far, a model for the function of NO, H_2O_2 and ethylene in AP induction under salt stress is proposed (**Fig. 1**). According to our model, the increased NO accumulation under salt stress is involved in ethylene-dependent AP induction. Under salt stress, NO generated from NOS acts as a signal molecule to activate PM NADPH oxidase activity to stimulate H_2O_2 generation. The accumulated H_2O_2 activates ACS activity to induce ethylene emission. The increased ethylene emission induces *AOX1a* expression and pyruvate content, thus resulting in enhanced AP activity. Eventually, the enhanced AP can dampen H_2O_2 generation in excess to avoid ROS damage in plant cells. The model we have proposed here should provide further insights into the mechanism of AP induction regulated by NO, H_2O_2 and ethylene signal molecules under salt stress.

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