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ARTICLE ADDENDUM

Are avoidance and acclimation responses during hypoxic stress modulated by distinct cell-specific mechanisms?

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ABSTRACT

Plants respond to hypoxic stress through either acclimation to the stress or avoidance of it, as they do to most environmental stresses. The hypothesis that has general consensus among the community is that ethylene response factors (ERFs) are central elements that control both types of responses to hypoxia. Recent studies suggest that this may not be the case for all cells experiencing hypoxic stress. Mature maize root cells undergoing hypoxic stress were found to undergo acclimation and avoidance mechanisms involving ERFs, whereas meristematic root cells and cells still undergoing differentiation acclimated to the response without the involvement of ethylene synthesis or ERFs. Phytoglobins (PGBs) and NO were demonstrated to be components critical to the acclimation response. These findings are discussed relative to the possibility that PGBs may be acting as molecular switches controlling cellular stress responses and hormonal changes and responses in cells.

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Introduction

Plants respond to hypoxic stress, as they do to with most environmental stresses, by altering their metabolism and growth to avoid the stress and/or acclimate to it.[1,2] Avoidance mechanisms generally involve altering growth patterns or sacrificing cells and/or tissues that are not critical to the survival of the organism to gain access to non-stress environments, or to await a more hospitable environment. Acclimation comes into play to ensure that cells and/or organs survive the hostile environment.

These concepts are best exemplified during freezing stress, when plants enter a day length driven growth cessation and dormancy period to avoid the stress [3] and further acclimate to it through a low temperature-driven process that reduces the potential for ice crystal formation in vital cells and organs.[4] While the 2 triggering processes, light and temperature have interacting effects, the processes that affect growth cessation and dormancy are distinct from those that influence survival to ice crystal formation.

One of the more studied hypoxia-avoidance mechanisms used by some plants is the formation of aerenchyma that permits oxygen movement within hypoxic roots.[5] After prolonged exposure to low oxygen levels, cortical cells within the mature region of the root initiate program cell death (PCD), a process that leads to the formation of aerenchyma. The death program is precluded in the root apical meristem (RAM) harboring the "stem" cells. Retention of a functional (RAM) is an acclimation mechanism that allows hypoxic roots to grow and escape conditions of low oxygen levels, and to produce vigorous root systems upon the re-establishment of normoxic conditions. Decision on whether a cell dies, as is the case for aerenchyma-forming cortical cells, or survive, as is the case for meristematic cells, appears to be controlled by cell and tissue-specific mechanisms managing ethylene synthesis and response.[6]

Ethylene: A common denominator in avoidance or acclimation to hypoxic stress

There is strong evidence that processes associated with ethylene are critical in the plant's capability to tolerate hypoxic stress.[1,2] Of the myriad of physiologic responses resulting from low oxygen stress, most have ethylene as a common denominator.[2] Thus, ethylene has long been recognized as a factor during hypoxic avoidance strategies including adventitious rooting and aerenchyma formation in maize,[7] hyponastic growth and petiole elongation in Rumex,[8,9] and in stem elongation in deep-water rice.[10]

Ground-breaking studies have demonstrated the importance of the Sub1A and Sub1C alleles of the Sub1 locus in affecting submergence survival of lowland rice,[11] while the same locus has been shown to be involved in internode elongation during submergence of deep-water rice.[12] Ethylene response factors (ERFs) are the central elements within the Sub1 locus regulating these events, resulting in considerable attention to the role of these factors in the hypoxic response. The involvement of the N-end rule pathway in the turnover of ERFs,[13,14] has resulted in proposals that N-cysteine oxidase, a main component of the N-end rule pathway, may act as an oxygen sensor [14] and/or a nitric oxide (NO) sensor [15] in regulating the hypoxic response. The N-end rule pathway is likely one of several mechanisms regulating the hypoxic response,[16] but it only possesses the ability to control the ethylene response pathway by regulating the catabolism of ERFs, presumably determined by the availability of O_2 and/or NO.

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Besides participating in avoidance responses, ethylene is considered to be involved in acclimation strategies.[1,17] In examining the response of hypoxic maize roots [6] the execution of the avoidance or acclimation pathway was dependent on how cells managed ethylene synthesis and response, and was associated with the developmental stage of the cells along the root profile. Meristematic or early differentiating cells in proximity of the root apical meristem suppressed pathways associated with ethylene synthesis and response that resulted in acclimation, i.e. improved cell survival and root growth during hypoxia. This was in contrast to fully differentiated cells in more mature sections of the root where hypoxia induced ethylene synthesis and response genes, accompanied by increased levels of NO and reactive oxygen species (ROS) with evidence of PCD, processes normally associated with the formation of aerenchyma.

Do phytoblobins act as a molecular switch for acclimation or avoidance responses?

Phytoglobins (Pgbs) are highly expressed in the root tip[18,19] and are effective scavengers of NO,[20] a signal molecule integrated in ethylene signaling. It has been established that NO modulates ethylene production in the hypersensitive response [21] and that Pgbs mediate that response.[22] Many hypoxic responses are also regulated by Pgbs through NO;[6,23,24,25] some of these responses are linked to ethylene. For example, suppressing either *Pgb1* or *Pgb2* expression in Arabidopsis resulted in increased production of both ethylene and NO during hypoxia [25] It was also noted that root flooding resulted in increased shoot *Pgb1* expression that correlated with ethylene-induced hyponastic growth. The authors conclude that Pgbs may influence hyponasty through both ethylene-dependent and ethylene-independent pathways and hypothesize that this occurs through the Pgb-scavenging of NO. Suppression of *Pgb* in maize suspension cultures was found to increase ethylene levels in either normoxic or hypoxic conditions, while imposing hypoxic conditions actually reduced ethylene production compared with normoxia in the suspension cultures.[24] Suppressing *Pgb* enhanced ACC oxidase enzyme activity as opposed to affecting genes associated with ethylene synthesis.

The link among Pgb, NO and ethylene holds true also for acclimation and avoidance responses of hypoxic roots. Aerenchyma formation, a hypoxia-avoidance strategy, occurs in fully differentiated cortical cells as a consequence of reactive oxygen species (ROS) and ethylene-induced PCD.[1] In maize, ethylene-induced aerenchyma formation requires the up regulation of respiratory burst oxidase genes, producing ROS and culminating with PCD.[26] Execution of the death program was precluded by the use of an NADPH oxidase inhibitor. Reducing *Pgb* expression during hypoxia resulted in elevated NO levels that induced the expression of respiratory burst oxidase homologs (*RBOHs*), ethylene-associated genes, and PCD.[6] Phytoglobins, like other hemoglobins, are only known to sequester a few gaseous ligands, like oxygen and NO, and react in the oxygenated form in redox reactions, such as the conversion of NO to nitrate reviewed in.[20] The most immediate explanation for the above observations would, therefore, be related to oxygen binding and/or reaction with NO, upstream of ethylene synthesis and response.

If conditions of low *Pgb* expression increase NO, ethylene synthesis and responses, and PCD in aerenchyma-forming cortical cells, elevated P*gb* levels have opposite effects. This is the case of meristematic and differentiating cells of hypoxic RAMs where the high levels of *Pgbs* reduce NO, the expression of ethylene synthesis and responses, and ultimately protect cells from dying.[6] Therefore, presence or absence of Pgbs is a factor determining whether root cells undergo acclimation (in meristematic and differentiating cells) or avoidance (in fully differentiated cells) during hypoxia. Meristematic and differentiating cells experienced more general and larger increases in *Pgb* expression during hypoxia, whereas in mature cells *Pgb* expression was more localized to specific cell types.

One debatable question resulting from Mira *et al.*[6] is whether the effects of NO occur upstream of the ethylene synthesis and response pathways or downstream of them. The suggestion that Pgbs and NO act downstream of ERFs in the hypoxic stress response [2] is difficult to reconcile with the observation that, in the meristematic tissue of hypoxic roots, an elevation of NO by suppressing *Pgb* increases ethylene synthesis and response genes. This discrepancy might be the result of the different physiologic state of the cells where these processes occur.

If NO is acting in signal transduction pathways[27] and Pgbs are involved in regulating signal transduction they must be present in the cell nucleus. This has been shown to be the case in rice [28] and alfalfa.[29] Furthermore, the concentration of Pgb in the alfalfa cell nucleus was found to be higher than that in the cytoplasm. The concept of Pgb regulating signal transduction is supported by recent work from our laboratory showing that Pgb is effective in enhancing Arabidopsis somatic embryogenesis only when it is targeted to the nucleus.[30]

Phytoglobins at the crossroads of hormonal responses

In attempting to determine how the expression of *Pgbs*, by regulating cellular NO levels, could affect ethylene-induced events during hypoxic stress, it may be instructive to look at research examining the effects of *Pgb* expression on hormonal pathways regulating somatic embryogenesis. Suppression of Arabidopsis *Pgb2* enhanced auxin-induced somatic embryo formation by increasing the expression of genes related to auxin synthesis.[31] This enhancement was attributed to increase cellular NO levels, as a result of reduced Pgbs, that inhibited the transcription factor *MYC2*, a repressor of the auxin biosynthetic pathways.[32] Further studies indicated that the more immediate effect of NO was on genes related to jasmonic acid synthesis, yielding elevated jasmonic acid levels that in turn suppressed *MYC2* and increased *JAZ1*, resulting in stimulated auxin synthesis.[33,34] ERFs integrate signals from ethylene and jasmonate in plant defense [35] and there is some evidence that MYC2 may interfere upstream of ERF1 to regulate these responses.[36] In addition, MYC2 antagonizes ethylene-promoted apical hook formation in Arabidopsis by repressing EIN3.[37]

A model accounting for the cell-specific regulation of acclimation and avoidance in hypoxic roots

Cell-specific management of ethylene synthesis and response appears to be a determinant factor in acclimation and avoidance strategies of hypoxic roots (Fig. 1). Our results suggest

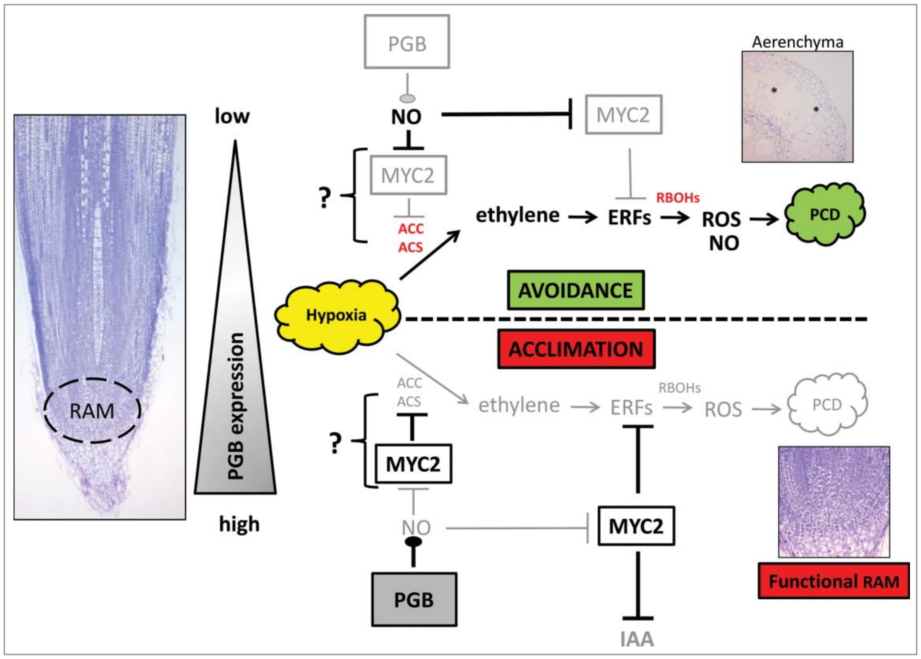

Figure 1. Schematic representation of Pgb-regulation of avoidance (aerenchyma formation) and acclimation (maintenance of a functional root meristem) responses in hypoxic maize roots. The gradient of Pgb along the root profile determines the type of response. High levels of Pgbs at the root tip lower the hypoxia-induced accumulation of ethylene by scavenging NO, and attenuate ethylene responses possibly through regulation of MYC2. These effects reduce ROS-induced PCD and auxin over-production in the meristematic cells that remain functional. In mature tissue, characterized by low expression of Pgb, the accumulation of ethylene triggers PCD contributing to the formation of aerenchyma (*). In this response NO production is also induced by ethylene. Repressed responses are faded. ACS, 1-aminocyclopropane-1-carboxylic acid synthase; ACO, 1-aminocyclopropane-1-carboxylic acid oxidase; ERFs, ethylene response factors; RBHOs, respiratory burst oxidase homologs.

that this management occurs through Pgbs controlling NO levels in specific cell types. In fully differentiated cortical cells of hypoxic root tissue, the low expression of *Pgbs* allows accumulation of NO, a suppressor of MYC2.[31,33,34] As MYC2 represses ethylene responses,[38] its suppression promotes ethylene responses and the up regulation of NADPH oxidase resulting in the death of cortical cells by PCD. These processes, possibly mediated by metacaspases which are executors of the death program and inhibited by Pgbs (Fig. 2A), lead to the formation of aerenchyma, an avoidance strategy. In meristematic or early differentiating cells the ethylene-induction of PCD is repressed due to the scavenging of NO by Pgbs that are preferentially

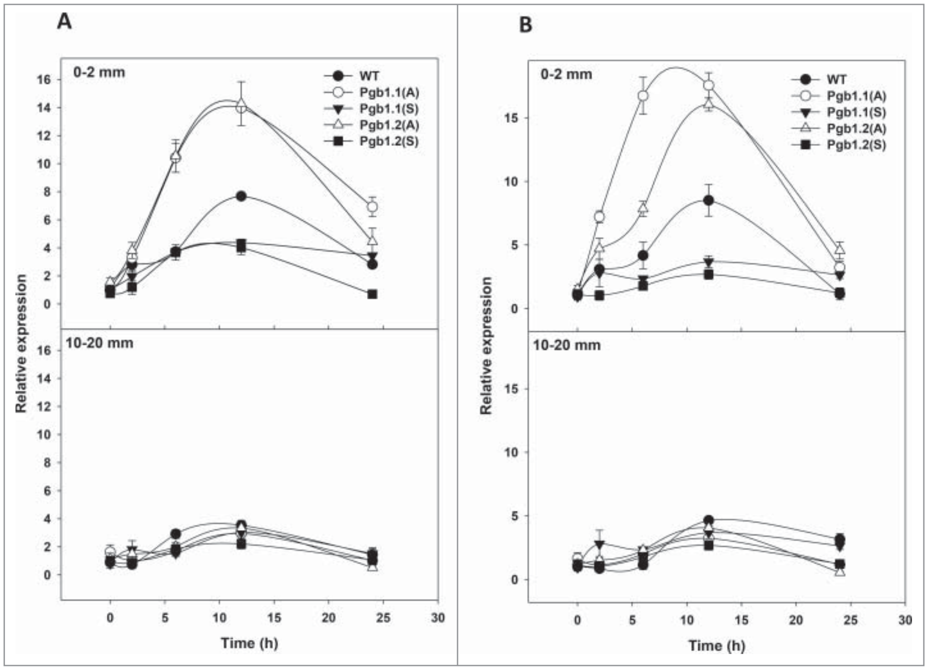

Figure 2. Relative expression of *metacaspase 9* (A) and *indole-3-acetamide hydroxylase* (*AMI*) (B) in root tips (0–2mm) and mature root segments (10–20 mm) of maize seedlings subjected to 4% oxygen treatments. Values ± SE are means of 3 biologic replicates and are normalized to the WT value of 0 hours (set at 1). Root segments were harvested from WT seedlings and seedlings over-expressing (S) or down-regulating (A) *Pgb1.1* and *Pgb1.2*.

expressed at the root tip. Presence of Pgbs in the meristematic cells of hypoxic roots might also be required to prevent the accumulation of indole-acetic acid (IAA), possibly by suppressing the expression of the last IAA biosynthetic enzyme indole-3-acetamide hydroxylase (AMI) (Fig. 2B). Over-production of IAA in the RAM induces the differentiation and consumption of the stem cells leading to an arrest in root growth.[39] These acclimation strategies ensure the survival of the stem cells, which upon the re-establishment of non-stress conditions can resume their activity and contribute to the growth of a functional root. If it holds true, this model argues that execution of acclimation and avoidance strategies is cell specific and dependent on the "physiologic" state and age of the cells. While the presence of Pgbs in young cells triggers acclimation responses, their absence in more mature cells triggers avoidance responses.

Disclosure of potential conflicts of interest

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