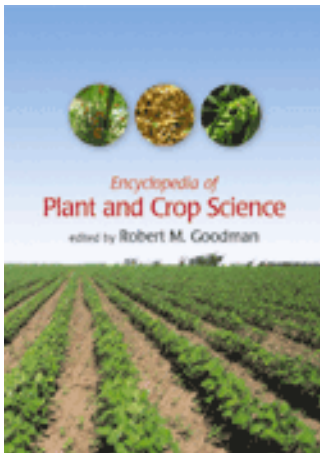


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Anoxia Effects on Plant Physiology

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Abstract

The response of plants to anaerobiosis is characterized by a dramatic change in gene expression. The availability of molecular tools for genome-wide analyses of *Arabidopsis thaliana* seedlings transcriptome opens new opportunities for the study of plant responses to anoxia. Anoxia exerts a dramatic effect on the transcriptome. In this article we analyse the results obtained by transcript profiling of *Arabidopsis* seedlings under anoxia and discuss the results in relation to the existing literature on the anaerobic response of higher plants.

INTRODUCTION

Plants are aerobic organisms requiring oxygen for their life. However, plants can experience a lower oxygen availability (hypoxia) or total absence of oxygen (anoxia) owing to flooding of the soil or as a consequence of the anatomical structure of some tissues. Plants cannot survive for long periods of time under hypoxia or anoxia, but some species can avoid or withstand anaerobiosis.

The physiological mechanism(s) allowing some plant species to survive in oxygen-deprived environments are still largely unknown. In this review, we describe some classical aspects of the physiology of plants under limited oxygen availability, highlighting new evidences of gene modulation by anoxia arising from recent microarray experiments using *Arabidopsis* seedlings.^[1]

ANOXIA REPRESSES LIPID METABOLISM, ENHANCES SUCROSE SYNTHASES-DRIVEN SUCROSE UTILIZATION, AND ACTIVATES ALCOHOLIC FERMENTATION

Genes coding for enzymes of the lipid degradation pathway are repressed by anoxia, mostly at the level of lipases, while the genes encoding β -oxidation and the glyoxylate cycle genes are unaffected or moderately induced by anoxia.^[1] Repression of lipases may avoid the buildup of fatty acids, which cannot be metabolized because of the inactivity of β -oxidation in the absence of molecular oxygen.

The microarray results^[1] highlight the strong induction of two sucrose synthase genes (*At3g43190*; *At5g20830*), which, together with the repression of a neutral invertase (*At1g35580*) and the activation of

an invertase inhibitor (*At1g47960*), suggest that a sucrose-synthase pathway predominates for sucrose utilization under anoxia, as previously proposed for rice seedlings.^[2] The effects of anoxia on starch synthesis genes are limited,^[1] and the pathway of starch degradation is not induced under anoxia in *Arabidopsis thaliana*.

Several glycolytic genes are strongly induced by anoxia. Among these genes we find those involved in alcoholic fermentation such as alcohol dehydrogenase (*At1g77120*), pyruvate decarboxylase1 (*At4g33070*), and pyruvate decarboxylase2 (*At5g54960*).

The concerted action of pyruvate decarboxylases and alcohol dehydrogenase may be unable to consume the pyruvate accumulating as a consequence of the inactivity of the Krebs cycle. The induction of an alanine aminotransferase (*At1g17290*) allows the conversion of the excess pyruvate to alanine. The production of alanine is indeed relevant in rice roots, reaching up to 1.2% of the dry weight after 24 hr under anoxia.^[3]

REDOX GENES: ANOXIA INDUCES STRONGLY A NON-SYMBIOTIC HEMOGLOBIN AND ACTIVATES THE ASCORBATE–GLUTATHIONE CYCLE

Although the activation of the alcoholic fermentation will likely mitigate the excessive buildup of Nicotinamide adenine dinucleotide reduced (NADH), activation of other genes able to compensate for the redox imbalance could be of importance. Non-symbiotic hemoglobin (*Ahb1*, *At2g16060*) is the most induced gene in the group of redox genes, while a class 2 non-symbiotic hemoglobin (*At3g10520*) is repressed.^[1] Although the role of *Ahb1* in the physiology of plants

is still largely unknown, it has been proposed that *Ahb1* may be functioning as a NADH-dependent nitric oxide (NO) oxidizing factor, producing nitrate that is in turn converted back to NO by nitrate reductase.^[4] Remarkably, nitrate reductase1 (*NRI*, *At1g77760*) is induced by anoxia.^[1] Beside the important role of the fermentative metabolism, the *Ahb*/*NRI*-dependent NADH utilization can be useful to regenerate nicotinamide adenine dinucleotide (NAD) under anoxia.

Hypoxia, as well as reoxygenation, affects the production of reactive oxygen species (ROS), and the production of antioxidant molecules is likely of importance for survival.^[5] The ascorbate–glutathione cycle (Halliwell–Asada pathway) may operate to reduce hydrogen peroxide (H₂O₂).^[5] The genes involved in this pathway are modulated by anoxia, with induction of ascorbate peroxidase (*At4g35000*), monodehydroascorbate reductase (*At3g09940*), dehydroascorbate reductase (*At1g19570*), and glutathione reductase (*At3g24170*).^[1]

LACK OF OXYGEN AFFECTS HORMONE SYNTHESIS AND SIGNALING

A low-oxygen environment induces the production of ethylene in several plant species, where it plays a role in petiole/internodes elongation and/or in aerenchyma and adventitious root formation.^[6] Ethylene production under anoxia is prevented by the lack of oxygen, required for the conversion of 1-aminocyclopropane-1-carboxylic acid (ACC) to ethylene, while production of this hormone is observed under hypoxia. Loreti et al.^[1] show that none of the 11 genes coding for 1-aminocyclopropane-1-carboxylic acid synthase (ACS) or ACS-like proteins are induced by anoxia in *Arabidopsis*. On the contrary, a gene coding for an ACC oxidase (*Aco*, *At2g19590*) is induced by anoxia. Remarkably, a number of genes involved in ethylene sensing and signal transduction are induced by anoxia. Flooding induces an *AtEtr1* homologue in *Rumex*,^[7] and our results show that the *Etr2* (*At3g23150*) gene is induced by anoxia. Induction of *Etr2* by hypoxia in *Arabidopsis* root cultures has also been reported by Klok et al.^[8] Eight genes coding for putative ethylene responsive elements are also induced by anoxia.^[1] Induction of these genes by anoxia, when ethylene cannot be synthesized, rules out the possible induction by hypoxia-triggered ethylene synthesis. As outlined by Vriezen et al.^[7], induction of elements involved in the synthesis, perception, and/or signaling pathway may enhance the response to ethylene, produced during flooding or after flooding, when oxygen is available and may drive a burst of ethylene production during postanoxia.

Anoxia plays a negative role on the physiology of auxin.^[1] Among the repressed genes, there are four genes

coding for proteins involved in auxin transport (*At1g70940*, *At1g23080*, *At1g77690*, and *At2g01420*). Repression of auxin transport is indeed of importance for flooding-dependent adventitious root formation, as proposed by Visser et al.^[9] A large group of genes encoding auxin-regulated proteins is downregulated by anoxia.

Abscisic acid (ABA) signaling appears to be activated under anoxia.^[1] ABA level increases in flooded tomato plants, although no increase in ABA levels was detected in *Arabidopsis* under hypoxia (De Bruxelles et al.^[10]). It has been proposed that ABA may contribute to the induction of alcohol dehydrogenase (ADH) and, indeed, exogenous ABA does increase the *Adh* transcript level. However, ADH induction by hypoxia is retained in ABA-insensitive mutants, suggesting that distinct signaling pathways control the induction of ADH by ABA and hypoxia.^[10] ADH is also induced by cold stress, and the cold and ABA-inducible protein Kin1 (*At5g15960*) is induced under anoxia.^[1]

Gibberellins may play a role in petiole elongation under anoxia, as proposed by Rijnders et al.^[11] in *Rumex* species. The impact of anoxia on the physiology of gibberellins in *Arabidopsis* seedlings appears however to be limited.^[1] Cytokinins (CK) may play a role in flooding tolerance. Transgenic *Arabidopsis* plants expressing an *Agrobacterium* CK biosynthetic gene controlled by the senescence-specific SAG12 promoter tolerate flooding and submergence better than wild-type plants.^[12] The SAG12 promoter is activated in *Arabidopsis* leaves from flooded plants,^[12] but the 6 hr anoxia treatment we used did not affect its expression, indicating that SAG12 is activated as a consequence of the flooding-induced senescence rather than by oxygen absence. A limited number of genes involved in CK physiology are modulated under anoxia.^[1]

A small number of genes involved in brassinosteroids, jasmonate, and salicylate physiology are induced by anoxia. Involvement of these signaling molecules under anoxia has not been reported before, with the exception of the microarray study by Klok et al.,^[8] showing the induction of jasmonate and brassinosteroid-related genes.

Signaling

Calcium signals play a central role in the molecular responses of plants to anaerobiosis.^[13] The most induced genes in this cluster^[1] include two putative calmodulin coding genes (*At1g76640* and *At1g76650*), and the Ca²⁺-binding protein RD20 (*At2g33380*), both induced by anoxia. Interestingly, the RD20 transcript accumulates rapidly in response to dry, NaCl and ABA,^[14] suggesting that RD20 plays a role in an ABA-related signaling pathway. In this respect, the activation

of the ABA signaling by anoxia (see above), together with the activation of ABA-modulated proteins (RD20 and KIN1), indicates that ABA plays a role in response to anoxia, although the pathway appears to share common elements with other stress-signaling processes. Changes in cytosolic calcium levels originate from influx through the plasma membrane as well as from intracellular stores. The *Cax1* transcript (*At2g38170*), coding for a vacuolar calcium exchanger is repressed by anaerobic conditions.^[1]

CONCLUSIONS

We reported an overview of the effects of anoxia on the Arabidopsis transcriptome. Some results, as expected, confirm the available knowledge about the anaerobic response of plants, with a clear induction of previously identified anaerobic proteins such as sucrose synthases and genes involved in alcoholic fermentation. Besides the classical view of anoxic metabolism through fermentation, it has to be emphasized that a large number of genes not related to this pathway are remarkably affected by anoxia. However, most of these genes encode proteins of unknown function, and an effort to identify the function of these genes will hopefully lead to a more complete understanding of plant responses to anaerobiosis.

REFERENCES

- Loreti, E.; Poggi, A.; Novi, G.; Alpi, A.; Perata, P. Genome-wide analysis of gene expression in Arabidopsis seedlings under anoxia. *Plant Physiol.* **2005**, *137* (3), 1130–1138.
- Guglielminetti, L.; Yamaguchi, J.; Perata, P.; Alpi, A. Amylolytic activities in cereal seeds under aerobic and anaerobic conditions. *Plant Physiol.* **1995**, *109* (3), 1069–1076.
- Reggiani, R.; Bertani, A. Anaerobic amino acid metabolism. *Russ. J. Plant Physiol.* **2003**, *50* (6), 733–736.
- Dordas, C.; Hasinoff, B.B.; Rivoal, J.; Hill, R.D. Class-1 hemoglobins, nitrate and NO levels in anoxic maize cell-suspension cultures. *Planta* **2004**, *219* (1), 66–72.
- Blokhina, O.; Virolainen, E.; Fagerstedt, K.V. Antioxidants, oxidative damage and oxygen deprivation stress: a review. *Ann. Bot.* **2003**, *91* (Special Issue), 179–194.
- Dat, J.F.; Capelli, N.; Folzer, H.; Bourgeade, P.; Badot, P.M. Sensing and signalling during plant flooding. *Plant Physiol. Bioch.* **2004**, *42* (4), 273–282.
- Vriezen, W.H.; vanRijn, C.P.E.; Voeselek, L.A.C.J.; Mariani, C. A homolog of the Arabidopsis thaliana ERS gene is actively regulated in Rumex palustris upon flooding. *Plant J.* **1997**, *11* (6), 1265–1271.
- Klok, E.J.; Wilson, I.W.; Wilson, D.; Chapman, S.C.; Ewing, R.M.; Somerville, S.C.; Peacock, W.J.; Dolferus, R.; Dennis, E.S. Expression profile analysis of low-oxygen response in Arabidopsis root cultures. *Plant Cell* **2002**, *14* (10), 2481–2494.
- Visser, E.J.W.; Heijink, C.J.; Vanhout, K.J.G.M.; Voeselek, L.A.C.J.; Barendse, G.W.M.; Blom, C.W.P.M. Regulatory role of auxin in adventitious root-formation in 2 species of rumex, differing in their sensitivity to waterlogging. *Physiol. Plant* **1995**, *93* (1), 116–122.
- De Bruxelles, G.L.; Peacock, W.J.; Dennis, E.S.; Dolferus, R. Abscisic acid induces the alcohol dehydrogenase gene in Arabidopsis. *Plant Physiol.* **1996**, *111* (2), 381–391.
- Rijnders, J.G.H.M.; Yang, Y.Y.; Kamiya, Y.; Takahashi, N.; Barendse, G.W.M.; Blom, C.W.P.M.; Voeselek, L.A.C.J. Ethylene enhances gibberellin levels and petiole sensitivity in flooding-tolerant Rumex palustris but not in flooding-intolerant R-acetosa. *Planta* **1997**, *203* (1), 20–25.
- Zhang, J.; Van Toai, T.; Huynh, L.; Preiszner, J. Development of flooding-tolerant Arabidopsis thaliana by autoregulated cytokinin production. *Mol. Breed.* **2000**, *6* (2), 135–144.
- Subbaiah, C.C.; Sachs, M.M. Molecular and cellular adaptations of maize to flooding stress. *Ann. Bot.* **2003**, *91* (Special issue), 119–127.
- Takahashi, S.; Katagiri, T.; Yamaguchi-Shinozaki, K.; Shinozaki, K. An Arabidopsis gene encoding a Ca²⁺-binding protein is induced by abscisic acid during dehydration. *Plant Cell Physiol.* **2000**, *41* (7), 898–903.