Plant Cell Monographs

Volume 21

Series Editor:
Peter Nick
Karlsruhe, Germany

For further volumes:
http://www.springer.com/series/7089

Joost T. van Dongen • Francesco Licausi
Editors

Low-Oxygen Stress in Plants

Oxygen Sensing and Adaptive Responses to Hypoxia

Springer

Editors
Joost T. van Dongen
RWTH Aachen University
Aachen, Germany

Francesco Licausi
Institute of Life Sciences
Scuola Superiore Sant´Anna
Pisa, Italy

Series Editor
Peter Nick
Botanisches Institut
Molekulare Zellbiologie
Kaiserstr. 2
76131 Karlsruhe
Germany

ISSN 1861-1370 ISSN 1861-1362 (electronic)
ISBN 978-3-7091-1253-3 ISBN 978-3-7091-1254-0 (eBook)
DOI 10.1007/978-3-7091-1254-0
Springer Wien Heidelberg New York Dordrecht London

Library of Congress Control Number: 2013958222

Cover picture: Image of an *Arabidopsis thaliana* leaf epidermis after modified pseudo-Schiff propidiumiodide (mPS-PI) staining showing basal cells of a removed trichome. Courtesy of Dr. Ruth Eichmann.

Printed on acid-free paper

Springer is part of Springer Science+Business Media (www.springer.com)

Preface

Throughout the history of Earth, a tight relationship was established between the high availability of oxygen in the atmosphere and the biological population. Oxygen enrichment of the Archean Earth's atmosphere was initiated by cyanobacteria and further boosted as a consequence of the colonization of the planet's surface by photosynthetic and multicellular eukaryotes which developed into land plants (Bendall et al. 2008). Nowadays, oxygen accounts for about one-fifth of our atmosphere and represents an essential element, which sustains the life of most multicellular organisms, including fungi, animals, and plants. Not only oxygen is required as terminal electron acceptor to ensure respiratory energy production via oxidative phosphorylation, but it also acts as primary substrate in a majority of metabolic reactions that produce structural and signaling components throughout all kingdoms of life. Consequently, when oxygen availability is reduced below the levels required to sustain these biological processes, a situation of crisis is generated. This is especially serious for sessile organisms, such as plants, which are limited in their possibility to move towards area where oxygen availability is sufficient.

For plants, the most common case of restriction in oxygen availability is caused by submergence, due to the slower diffusion of gases in water than in air and exacerbated by the competition for oxygen consumption by soil microorganisms, whose anaerobic metabolism in turn leads to the accumulation of phytotoxic metabolites (Bailey-Serres and Voesenek 2008). Plants do not need to be completely submerged to suffer from oxygen deficiency: reduced oxygen levels (hypoxia) or complete absence of oxygen (anoxia) in waterlogged soil is sufficient to put plant's survival at stakes and has dramatic effect on crop yield (Ahmed et al. 2013). The consequent reduction in size and functionality of the root apparatus of a flooded or waterlogged plant reduce water and nutrient transport towards the shoot. The high probability that every plant will experience restriction in oxygen availability at sometimes throughout its lifespan suggested the concept that these organisms must have evolved efficient strategies to cope with this situation orchestrated by perception and signaling mechanism that integrated them into developmental and growth programs (Bailey-Serres et al. 2012). Additionally, the notion that oxygen availability is not equal to all plant cell types and certain tissues or organs actually develop at oxygen levels lower than those available in the atmosphere put this element in the perspective of a developmental signal.

Initially, research on plant anaerobiosis developed in the fields of biochemistry, due to its direct effect on primary metabolism, and ecology, as broad differences in tolerance to flooding were traditionally known in wild and cultivated species. Biochemical studies first focused on the metabolic switch from the aerobic respiration to fermentative pathways (reviewed in Davies 1980), but later explored the global adjustment and re-routing of primary metabolic reactions opening the debate over an adaptation of respiratory rates to hypoxia. On the other hand, ecophysiological approaches aimed at the identification and characterization of the strategies adopted by different plant species to restricted oxygen availability throughout evolution (Jackson and Colmer 2005). The characterization of the molecular elements, involved in low oxygen sensing and signaling, initiated at the end of the 1990s and beginning of the current century (Hoeren et al. 1998; Klok et al. 2002) but, in comparison with other abiotic stresses such as heat, cold, and high salinity, knowledge in this field lagged behind. Nevertheless at the descriptive level, very detailed overviews of the transcriptomic adjustment to oxygen deprivation were produced, including time-, oxygen-concentration-, and cell type-specific-resolved analyses (Mustroph et al. 2009; Mustroph et al. 2010). This generated a deep knowledge related to the dynamics of the anaerobic response and greatly contributed to the identification of general and tissue-specific responses. In the last 10 years, two main breakthrough set milestones in the applied and theoretic knowledge with respect to the plant adaptation to low oxygen availability, respectively. First, a joint team of agronomists, physiologists, and molecular biologists revealed the genetic basis for submergence tolerance in wild rice varieties and described for the first time a quiescent metabolic adaptation aimed at saving energy and resources for short-lasting floods (Xu et al. 2006). An opposite strategy was shown a couple of years later to occur in deep-water rice varieties (Hattori et al. 2009). More recently, studies conducted in Arabidopsis converged to the identification of an oxygen-dependent pathway for the degradation of transcription factors that orchestrate the core of the anaerobic response in plants (Gibbs et al. 2011; Licausi et al. 2011). Not surprisingly, these three studies hit on the same class of transcription factors, suggesting that species-specific modes of action to respond to low-oxygen stress evolved from the same basic genetic elements. Concomitantly, the gaseous phytohormone ethylene emerged as a key-regulator of the response to flooding and its interaction with other growth regulators such as gibberellins, auxin, and abscisic acid was shown to shape plant growth (Bailey-Serres and Voesenek 2008).

With this book, we bring together the different fields of research which deal with low oxygen conditions in plants and algae to provide an overview of the deep interconnection between their achievements. The monograph consists of seven sections, starting from the mechanisms adopted by plant cells to *perceive oxygen availability and initiate the signaling cascade* that leads to the activation of conserved and species-specific adaptive responses. In this section, both direct oxygen sensing (Kosmacz and Weits, Chap. 1) and biochemical parameters that are affected as consequence of decreased oxygen availability are discussed, including the level of reactive oxygen species (Blokhina et al., Chap. 2), nitric oxide (Igamberdiev et al., Chap. 3), and pH (Ishizawa, Chap. 4). The *molecular response of plants to hypoxia* is presented in the following section, with a focus at the transcriptional (Giuntoli and Perata, Chap. 5) and the posttranscriptional (Sorenson and Bailey-Serres, Chap. 6) level with an additional chapter dedicated to the hormonal interplay that integrate the adaption to oxygen deficiency into growth and developmental programs (Steffens and Sauter, Chap. 7). The third section of this book is dedicated to the *metabolic adaptations* that take place as consequence of a decrease in the oxygen—and thus energy—availability. This section is not limited to higher plants but takes into consideration also green algae whose anaerobic metabolism is of potential economic interest, such as *Chlamydomonas reinhardtii* (Yang et al., Chap. 8). The role of alternative energy storage units, such as PPi, is discussed by Mustroph et al. (Chap. 9) while the effect of changing oxygen availability on respiratory energy production is described by Paepke et al. (Chap. 10). Oxygen-dependent effect on nitrogen and amino acid metabolism is reviewed by Limami (Chap. 11) and Geigenberger (Chap. 12) describes storage metabolism under oxygen limitations. Most of the molecular and metabolic changes described in the previous sections are ultimately aimed at sustaining prolonged conditions of hypoxia, which is also achieved via *morphological adaptations* that ameliorate oxygen supply and transport within the plant tissues (Armstrong and Armstrong, Chap. 14), namely the formation of aerenchyma (Takahashi et al., Chap. 13) and the production of adventitious roots (Sauter and Steffens, Chap. 15). Species-specific strategies which have been developed by plants to maintain photosynthetic activity under water (Pedersen and Colmer, Chap. 16) and cope with flooding conditions (van Veen et al., Chap. 17) are discussed in a specific section dedicated to the *ecophysiological aspects* of the response to low oxygen. Furthermore, the occurrence and impact of low oxygen responses in agricultural practice are discussed taking into consideration the difficulty of oxygen diffusion into bulky fruits (Nicolai et al., Chap. 18), the oxygen supply in artificial substrates used in horticulture (Wessel et al., Chap. 19), and presenting the effect of herbicides that mimic the hypoxic response in plants (Zabalza and Royuela, Chap. 20). Our book concludes with a review about the state-of-the-art techniques used in the past *to measure oxygen concentrations in vivo* and the novel molecular strategies that are being developed to do so in the least intrusive way (Ast and Draaijer, Chap. 21).

We expect that the detailed survey about the various aspects of low-oxygen stress in plants as it is discussed in this monograph will not just contribute to our understanding of the adaptation of plant to low oxygen stress but also extend its potential to the improvement of crops against the damage caused by flooding. Even more so, we hope it will pave the way towards new discoveries that are expected to further boost our knowledge in this field in the next years.

We would like to express our gratitude to all authors and reviewers that contributed to this book. Furthermore, we acknowledge Christiane Welsch for her excellent help in preparing the final manuscript.

Aachen and Pisa Joost van Dongen
June 2013 Francesco Licausi

References

Ahmed F, Rafii MY, Ismail MR, Juraimi AS, Rahim HA, Asfaliza R, Latif MA (2013) Waterlogging tolerance of crops: breeding, mechanism of tolerance, molecular approaches, and future prospects. BioMed Res Int 2013:10

Bailey-Serres J, Fukao T, Gibbs DJ, Holdsworth MJ, Lee SC, Licausi F, Perata P, Voesenek LACJ, van Dongen JT (2012) Making sense of low oxygen sensing. Trends Plant Sci 17:129–138

Bailey-Serres J, Voesenek LACJ (2008) Flooding stress: acclimations and genetic diversity. Annu Rev Plant Biol 59:313–339

Bendall DS, Howe CJ, Nisbet EG, Nisbet RER (2008) Introduction. Photosynthetic and atmospheric evolution. Phil Trans Roy Soc Lond B Biol Sci 363(1504):2625–2628

Davies DD (1980) Anaerobic metabolism and the production of organic acids. In: Davies DD (ed) The biochemistry of plants, Vol 2. Academic, New York, p 581–611

Gibbs DJ, Lee SC, Md Isa N, Gramuglia S, Fukao T, Bassel GW, Correia CS, Corbineau F, Theodoulou FL, Bailey-Serres J, Holdsworth MJ (2011) Homeostatic response to hypoxia is regulated by the N-end rule pathway in plants. Nature 479:415–418

Hattori Y, Nagai K, Furukawa S, Song X-J, Kawano R, Sakakibara H, Wu J, Matsumoto T, Yoshimura A, Kitano H, Matsuoka M, Mori H, Ashikari M (2009) The ethylene response factors SNORKEL1 and SNORKEL2 allow rice to adapt to deep water. Nature 460:1026–1030

Hoeren FU, Dolferus R, Wu Y, Peacock WJ, Dennis ES (1998) Evidence for a role for AtMYB2 in the induction of the Arabidopsis alcohol dehydrogenase gene (ADH1) by low oxygen. Genetics 149:479–490

Jackson MB, Colmer TD (2005) Response and adaptation by plants to flooding stress. Ann Bot 96:501–505

Klok EJ, Wilson IW, Wilson D, Chapman SC, Ewing RM, Somerville SC, Peacock WJ, Dolferus R, Dennis ES (2002) Expression profile analysis of the low-oxygen response in Arabidopsis root cultures. Plant Cell 14:2481–2494

Licausi F, Kosmacz M, Weits DA, Giuntoli B, Giorgi FM, Voesenek LACJ, Perata P, Van Dongen JT (2011) Oxygen sensing in plants is mediated by an N-end rule pathway for protein destabilization. Nature 479:419–422

Mustroph A, Lee SC, Oosumi T, Zanetti ME, Yang H, Ma K, Yaghoubi-Masihi A, Fukao T, Bailey-Serres J (2010) Cross-kingdom comparison of transcriptomic adjustments to low-oxygen stress highlights conserved and plant-specific responses. Plant Physiol 152:1484–1500

Mustroph A, Zanetti ME, Jang CJH, Holtan HE, Repetti PP, Galbraith DW, Girke T, Bailey-Serres J (2009) Profiling translatomes of discrete cell populations resolves altered cellular priorities during hypoxia in Arabidopsis. Proc Natl Acad Sci 106:18843–18848

Xu K, Xu X, Fukao T, Canlas P, Maghirang-Rodriguez R, Heuer S, Ismail AM, Bailey-Serres J, Ronald PC, Mackill DJ (2006) Sub1A is an ethylene-response-factor-like gene that confers submergence tolerance to rice. Nature 442:705–708

Contents

Part VI Agronomical and Horticultural Aspects of Low-Oxygen Stress

Part VII Technical Advances