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Redox regulation and antioxidative defence in *Arabidopsis* leaves viewed from a systems biology perspective

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Abstract

Redox regulation is a central control element in cell metabolism. It is employed to adjust photosynthesis and the antioxidant defence system of leaves to the prevailing environment. During recent years progress has been made in describing the redox-dependent alterations in metabolism, the thiol/disulfide proteome, the redox-dependent and cross-talking signalling pathways and the target genes of redox regulation. Some transcription factors have been identified as proteins that perform thiol/disulfide transitions linked to the redox-regulation of specific plant promoters. In addition first mathematical models have been designed to simulate antioxidant defence and predict its response. Taken together, a profound experimental data set has been generated which allows to approach a systems biology type of understanding of antioxidant defence in photosynthesising cells in the near future. Since oxidative stress is likely to limit plant growth under stress, such a systematic understanding of antioxidant defence will help to define novel targets for breeding stress-tolerant plants.

Keywords: Antioxidant defence; Gene regulation; plant; Redox regulation; Signalling; Systems biology

1. A systems biology approach in plants

Systems biology has moved into the focus of the post-genomic era and aims at constructing mechanistic models to describe whole plant functions. To reach this aim quantitative and qualitative data are used for constructing networks of dependencies and to establish predictive models (Mustacchi et al., 2006). So far no such comprehensive or tentatively global models exist. Owing to a combination of lack of data, capacity for integrative interpretation and theoretical tools (Oliver,

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Abbreviations: 2CPA, 2 cysteine peroxiredoxin A (At3g11630); ABA, abscisic acid; APx, ascorbate peroxidase; Asc, ascorbate; AtFer1, ferritin precursor (At5g01160); ATP, adenosine triphosphate; BAP1, BON1-associated protein (At3g61190); Grx, glutaredoxin; GSH, reduced glutathione; GSSG, oxidized glutathione; MDH, malate dehydrogenase; NAD(P)H, nicotinamide adenine nucleotide (phosphate); PQ, plastoquinone; Prx, peroxiredoxin; PS, photosystem; RNS, reactive nitrogen species; ROS, reactive oxygen species; SOD, superoxide dismutase; Trx, thioredoxin

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2006), smaller sub-systems have been and will have to be constructed first. The practical alternative to the broad and multiparallel approach ('horizontal analysis') at the whole genome, cell or tissue level may be the investigation of a subset of cell function ('vertical analysis'). That is where biochemistry and molecular biology meet genome research, bioinformatics and biomathematics to generate a systems biology type of understanding of selected processes such as cell cycle progression in budding yeast (Alberghino et al., 2003) and flagellar movement in bacteria (Chiu et al., 2006). Thus, it is the challenge to ensure that emerging modules can be joined up in a seamless manner to finally arrange a working model of a living cell that makes experimentally testable predictions and can be used to explain empirical data.

Single cell prokaryotes represent the most promising models to address questions of systems biology such as function and coordination of metabolic pathways and gene regulatory networks. Small genome sizes, limited metabolic capacities, often simple operon structures and hierarchical regulatory networks foster data acquisition by '-omics'-technology and data interpretation (Francke et al., 2005). In higher eukaryotic organisms such as plants with large genomes, cells differentiate into more than 70 different cell types, which respond differentially to environmental stimuli, and give rise to a set of experimental draw backs, e.g. cell type mixtures in tissue extracts, complexity of transcript and protein patterns, compartmentalisation and site-specific regulation of metabolism.

This review presents a view how a selected topic of plant biology can be approached from a systems biology perspective. Case studies will be presented that exemplarily illustrate the central role of redox regulation in plant networks. Antioxidant defence in context of photosynthesis is a *conditio sine qua non* for plant survival and has been explored in many studies, recently also by exploiting 'omics-technology and mutants and designing first models. Especially in the field, oxidative damage is a major factor in limiting plant productivity. The detailed comparison of sensitive and tolerant genotypes and species, and a systematic understanding of antioxidant defence promise new ways for efficient breeding and targeted genetic engineering of plants with improved performance.

2. Inventory of players in redox regulation and antioxidant defence

The first step for a systematic understanding is establishing the inventory of components involved in biological processes. Plants evolved a large set of metabolic and regulatory mechanisms to cope with environmental changes of both biotic and abiotic origin. (i) Redox imbalances are often linked to stressful conditions, e.g. drought, heat, heavy metal exposure and excess light. (ii) In addition, developmental processes, such as seed germination and seedling growth, lead to generation of reactive oxygen (ROS) and reactive nitrogen species (RNS) with significant rates (Schopfer et al., 2001; Pena-Ahumanda et al., 2006). (iii) In mature tissues, the electron transport chains in mitochondria and plastids as well as oxidative metabolism of peroxisomes provide sources for ROS and RNS (Foyer and Noctor, 2005). Generated in specific compartments in response to intrinsic and environmental stimuli, ROS and RNS trigger signalling cascades and can have a positive impact on plant development and metabolism. However, uncontrolled generation and accumulation is cytotoxic. To counteract ROS and RNS, plant cells activate metabolic and genetic programmes antagonizing ROS and RNS formation and accumulation, and repairing damage at cell structures.

2.1. Hierarchical structure of redox signalling

Hierarchical redox signals are exploited in order to activate defence responses in proximity to the first indications of imbalances. In this context three classes of redox signals have tentatively been defined: class 1 signals originate from specific redox pairs such as the plastoquinone pool (PQ/PQH_2) in the photosynthetic electron transport, class 2 signals have integrating function, for example thioredoxins (Trx_{red}/Trx_{ox}) and glutathione (2GSH/GSSG) in chloroplasts, while ROS and RNS have been defined as class 3 signals (Pfannschmidt, 2003; Dietz, 2003a). Each of the signals has the potential to function as developmental and environmental stimulus and to change the metabolic state of a given plant cell by short-term metabolic control within seconds to minutes or long term genetic mechanisms on the time scale of hours. Redox metabolites such as low molecular weight