



Unveiling the Redox Control of Plant Reproductive Development during Abiotic Stress

Gaurav Zinta^{1,2*†‡}, Asif Khan^{3*†}, Hamada AbdElgawad^{2,4}, Vipasha Verma^{5†} and Ashish Kumar Srivastava⁶

¹ Centre of Excellence Plant and Vegetation Ecology, Department of Biology, University of Antwerp, Antwerp, Belgium, ² Integrated Molecular Plant Physiology Research, Department of Biology, University of Antwerp, Antwerp, Belgium, ³ Research Group Germline Biology, Centre for Organismal Studies Heidelberg, University of Heidelberg, Heidelberg, Germany, ⁴ Department of Botany, Faculty of Science, University of Beni-Suef, Beni-Suef, Egypt, ⁵ Department of Biotechnology, Dr Y S Parmar University of Horticulture and Forestry, Solan, India, ⁶ Nuclear Agriculture and Biotechnology Division, Bhabha Atomic Research Centre, Mumbai, India

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*Correspondence:

Gaurav Zinta
gzinta@gmail.com;
Asif Khan
asif.khan@cos.uni-heidelberg.de

† Present Address:

Gaurav Zinta and Vipasha Verma,
Shanghai Center for Plant Stress
Biology, Shanghai Institutes of
Biological Sciences, Chinese
Academy of Science, Shanghai, China

‡ Equal first authors.

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Plants being sessile in nature are often challenged to various abiotic stresses including temperature fluctuations, water supply, salinity, and nutrient availability. Exposure of plants to such environmental perturbations result in the formation of reactive oxygen species (ROS) in cells. To scavenge ROS, enzymatic and molecular antioxidants are produced at a cellular level. ROS act as a signaling entity at lower concentrations maintaining normal growth and development, but if their levels increase beyond certain threshold, they produce toxic effects in plants. Some developmental stages, such as development of reproductive organs are more sensitive to abiotic stress than other stages of growth. As success of plant reproductive development is directly correlated with grain yield, stresses coinciding with reproductive phase results in the higher yield losses. In this article, we summarize the redox control of plant reproductive development, and elaborate how redox homeostasis is compromised during abiotic stress exposure. We highlight why more emphasis should be given to understand redox control of plant reproductive organ development during abiotic stress exposure—to engineer crops with better crop yield. We specifically discuss the role of ROS as a signaling molecule and its cross-talk with other signaling molecules such as hormones and sugars.

Keywords: oxidative stress, antioxidants, sexual reproduction, anther, gynoecium, pollen

INTRODUCTION

The entire life cycle of flowering plants is a succession of distinct growth phases, where plants depict various developmental stages. The growth phase between seed germination and vegetative maturity is termed as “vegetative-phase”; and the subsequent phase including formation of reproductive organs, sexual reproduction, and seed set is termed as “reproductive-phase.” Plant performance in these growth phases, and transition from vegetative to reproductive phase is under tight control of genetic network (Huijser and Schmid, 2011). Moreover, signaling mediators such as reactive oxygen species (ROS), reactive nitrogen species (RNS), calcium, and phytohormones play crucial roles in integrating information from various endogenous and environmental cues, thus regulating plant growth and developmental transitions (Kocsy et al., 2013; Considine and Foyer, 2014; Traverso et al., 2014). Of these, ROS or redox mediated signaling has recently emerged as a core signaling

pathway that shows crosstalk with calcium (Steinhorst and Kudla, 2013; Gilroy et al., 2014) and hormone-mediated signaling (Bartoli et al., 2013; Xia et al., 2015). The redox state is a broad term often described as an integrated ratio of different redox couples present inside the cell (König et al., 2012). Each developmental stage possess a specific redox pattern, determined by the concerted action of various ROS producing [NADPH oxidase (NOX), ascorbate oxidase (AO), and alternative oxidase (AOX)] and scavenging [superoxide dismutase (SOD), catalase (CAT), peroxidase(POD), ascorbate peroxidase (APX), glutathione peroxidase (GPX), and glutathione reductase (GR)] antioxidant enzymes and antioxidant molecules like ascorbate, glutathione, and tocopherols (Considine and Foyer, 2014). In addition, redox state is regulated by various sugars and amino acids, which apart from playing role in plant metabolism are now considered an integral part of ROS scavenging machinery (Bolouri-Moghaddam et al., 2010; Hayat et al., 2012; Matros et al., 2015).

REDOX REGULATION OF PLANT SEXUAL REPRODUCTION

In flowering plants, flower is a seat of plant sexual reproduction encapsulating both male and female reproductive organs. The sterile part of flower consists of calyx and corolla, and the fertile part consists of androecium (male) and gynoecium (female). The detailed structure of plant reproductive organs and the sequence of events leading to fertilization are described in the legend of **Figure 1**. Starting from male or female gametogenesis through meiosis, followed by pollen/embryo sac growth, pollen-pistil interaction, and double-fertilization—the entire process is redox regulated.

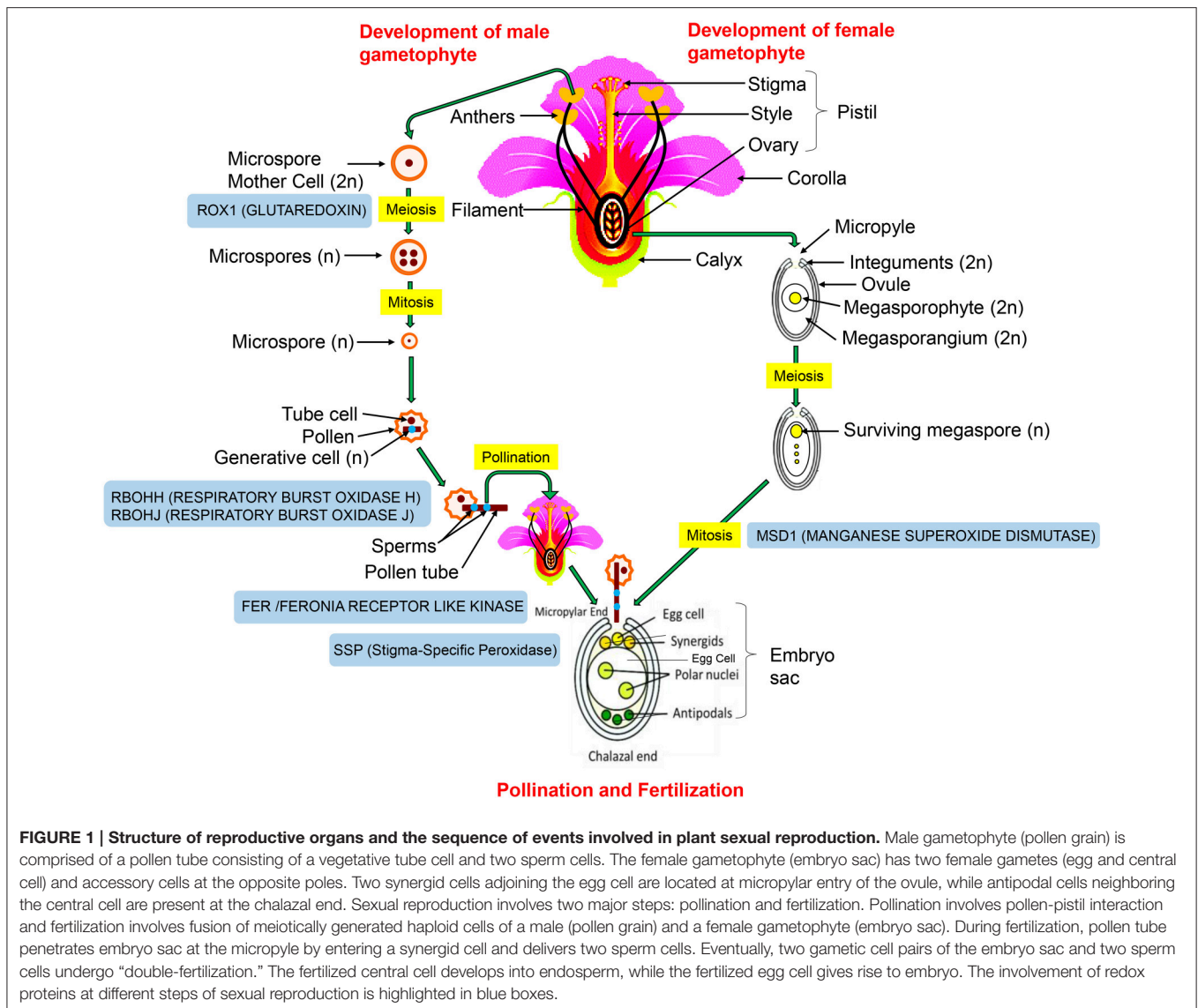
Specific ROS levels, antioxidant molecules, and enzyme activities control the individual steps of sexual reproduction (**Figure 1**). *Arabidopsis roxy1* mutant, deficient in CC-type GRXs (glutaredoxins: glutathione dependent oxidoreductases) displays reduced petal number and male-sterile phenotype. A deeper analysis revealed that this mutant lacks ability to enter meiotic phase (Xing and Zachgo, 2008). Furthermore, generation of reductive environment through exogenous supplementation of KI rescued the *mscal* (male sterile converted anther1: a CC-type GRX) mutant phenotype of maize, confirming that excess ROS formation was mainly responsible for male sterility (Kelliher and Walbot, 2012). *Arabidopsis* phytoalexin-deficient (*pad2-1*) mutant which is impaired in glutathione (GSH) synthesis shows poor pollen germination, indicating that GSH is essential for pollen development (Zechmann et al., 2011). Also, proper ROS gradient is required for pollen tube elongation. The *rbohH* and *rbohJ* (respiratory burst oxidase homolog H and J) double mutant of *Arabidopsis*, which lacks the ability of ROS burst shows severe reduction in pollen tube tip growth (Kaya et al., 2014). Similarly, ROS homeostasis is important for female gametophyte development, where mitochondrial SOD (MSD1) plays a crucial role in regulating ROS levels (Martin et al., 2013). The *mee33* (maternal effect embryo arrest 33) mutant lacking MSD1 activity shows defects in embryo sac development. The

sperm cell release from pollen tube is a redox (ROS) dependent process. It is regulated through FERONIA (FER) receptor kinase which induces the production of high ROS levels, especially hydroxyl radicals, at the entrance of female gametophyte to facilitate the rupture of pollen tube in a calcium dependent manner (Duan et al., 2014). Interaction between pollen and pistil during pollination is one of a key step that determines the fate of fertilization, and decides whether seed set will happen or not. ROS (H_2O_2) and NO (nitric oxide) mediated redox signaling is involved in pollen-pistil interactions (Sharma and Bhatla, 2013). Before pollen-pistil interaction, higher H_2O_2 production and enhanced activity of a Stigma-Specific Peroxidase (SSP) was observed at the receptive papillae, while pollen still retain high NO levels (McInnis et al., 2006; Bright et al., 2009; Zafra et al., 2010). After pollen landing on stigma, during the period of pollen-pistil interaction, the levels of H_2O_2 and activity of SSP declines dramatically in the stigmatic papillae. Following successful fertilization, formation of an embryo, and the development of mature seed requires extensive cell division and cell expansion, and both these processes are again redox regulated, and require low molecular weight antioxidants such as ascorbate and glutathione (Cairns et al., 2006; Livanos et al., 2012; Gallie, 2013). Thus, well-coordinated changes in the redox metabolism is essential for successful plant sexual reproduction. Such concept has also been proposed for other organisms such as *Caenorhabditis elegans* (De Henau et al., 2015) and mammals (Ufer et al., 2010).

ABIOTIC STRESS INDUCES REDOX IMBALANCE DURING REPRODUCTIVE GROWTH

Exposure of plants to abiotic stresses such as temperature fluctuations, water supply, and salinity, result in the formation of ROS (Gill and Tuteja, 2010; Suzuki et al., 2012; Zinta et al., 2014). Although, ROS acts as a signaling molecule at lower concentrations, its accumulation beyond threshold leads to oxidative damage of macromolecules, resulting in growth retardation (Mittler, 2002). Because the success of plant reproductive development determines grain yield, it is obvious that stress exposure during reproductive phase will reduce the crop yield (Dolferus et al., 2011; Sage et al., 2015). Therefore, it is essential to understand how stress affects redox homeostasis in the context of plant sexual reproduction.

Stress negatively affects male reproductive development in plants (De Storme and Geelen, 2014). Drought imposed to rice during anthesis resulted in generation of sterile pollen, due to higher ROS accumulation and lower expression of transcripts related to antioxidant enzymes (Selote and Khanna-Chopra, 2004; Nguyen et al., 2009). Similarly, a study performing the comparative analysis of anthers of a drought sensitive and tolerant rice lines (under drought stress) revealed sensitive line exhibiting higher malondialdehyde (MDA) content and lower activity of antioxidant enzymes (SOD, POD, and CAT) as compared to tolerant line (Fu et al., 2011). These studies indicate that stress-induced over accumulation of ROS leads to pollen



abortion and programmed cell death (PCD) of microspores in developing anthers, consequently resulting in male sterility.

Similarly, the female reproductive development is impaired by abiotic stress exposure (Moss and Downey, 1971; Sun et al., 2004; Loka and Oosterhuis, 2014). Heat stress caused activation of GR activity in the heat-stressed cotton pistils (Snider et al., 2009). Thermotolerant cotton variety showed higher pre-stress activity of SOD and GR in the pistil, suggesting it as a thermotolerance mechanism specific to female reproductive organs (Snider et al., 2011). Moreover, in salt stressed *Arabidopsis* plants, genes encoding ROS detoxifying enzymes, APX, and POD, were downregulated after ovules committed to abort. These changes in gene expression coincided with the accumulation of ROS in female gametophytes (Sun et al., 2005). This may have resulted from increased ROS biosynthesis, reduced ROS scavenging capacity or both, indicating that like

male gametophyte, female gametophyte is also susceptible to stress-induced ROS accumulation.

Sugars or sugar-mediated transcriptional control play an important role in ROS homeostasis in the reproductive organs during stress episode (Couée et al., 2006; Keunen et al., 2013). Reduction in starch content prior to anthesis and decline in total soluble sugar content in mature pollen grains resulted in decreased pollen viability in tomato plants exposed to high temperature (Pressman et al., 2002). Recent metabolomic and transcriptomic profiling of floral organs (anthers and pistil) of heat-tolerant (N22) and heat-sensitive (Moroberekan) rice cultivars identified modulation in sugar metabolism as a regulatory mechanism imparting heat and drought tolerance to floral organs (Li et al., 2015). Therefore, stress-induced redox imbalance due to inefficient antioxidant system or alterations in the sugar metabolism could lead to higher ROS accumulation,

which results in PCD of developing microspores/megaspores, finally leading to male sterility or ovule abortion.

ENGINEERING REDOX COMPONENTS FOR IMPROVED REPRODUCTIVE SUCCESS

A dynamic network of redox homeostasis related genes function to repair or abrogate stress-induced oxidative damage in the plant reproductive tissues (Meyer et al., 2012). Therefore, engineering redox components could be a way forward to impart stress tolerance in plants during reproductive phase.

The role of plant GRXs as master regulators of redox homeostasis during anther and gamete formation has been well-demonstrated (Kelliher and Walbot, 2012). A conserved plant specific CBSX (single cystathionine β -synthase domain) CC-type GRXs (ROXY1 and ROXY 2) genes and SQUAMOSA PROMOTER BINDING PROTEIN (SBP-box) transcription factors (target of miR156 and miR157) have been implicated in redox clean up during male reproductive development (Yoo et al., 2011). The role of these intriguing proteins was revealed in the studies using maize *mscal* mutant (Chaubal et al., 2003; Timofejeva et al., 2013). The CC-type GRXs, ROXY 1 and 2 act via interaction with basic leucine-zipper transcription factors, TGACG (TGA) motif-binding proteins TGA9 and TGA10 (Murmu et al., 2010). This association was demonstrated later in rice, where authors showed that rice MICROSPORELESS1 (MIL1) gene, coding for a similar CC-type GRX, functions in the formation of surrounding somatic layer of anthers and in the transition of microsporocytes from mitosis to meiosis (Hong et al., 2012).

The role of cytosolic ascorbate peroxidase 2 (APX2) in enhanced seed production subjected to chronic heat stress was illustrated in *Arabidopsis thaliana* (Suzuki et al., 2013). Similarly, heat-stressed microspores in tomato showed upregulation of ROS-scavenging SLAPX3, safeguarding spores against toxic ROS accumulation (Frank et al., 2009). These two are relevant findings in the context of global warming, and demonstrate the protective role of APX against heat-induced oxidative damage in reproductive tissues.

One of plant's remarkable strategy to deal with stress is to escape the stressful environment via reproduction. Hence, proper timing of transition from vegetative to reproductive phase determines the success of reproduction. The OXS2 (OXIDATIVE STRESS 2) is a member of zinc-finger transcription factor family, which is involved in maintaining vegetative growth, stress tolerance, and stress-induced reproduction (Blanvillain et al., 2011). OXS2 is a stress responsive nucleo-cytoplasmic protein, shuttling between cytoplasm (no stress) to nucleus under stress conditions promoting stress resilience. OXS2 autoactivates itself, while coherently activating other floral integrator genes via direct binding to floral integrator promoter SUPPRESSOR

OF CONSTANS (SOC1). This auto-regulatory loop of OXS2 may constitute an altruistic response choosing between stress tolerance to stress escape via reproduction (Blanvillain et al., 2011).

Two contrasting hypothesis have been proposed to explain the effects of redox status on meiosis and germline formation. The "reductive hypothesis" proposes that reduced ROS levels are required for successful meiosis (Kelliher and Walbot, 2014). This is supported by the evidences where chemical (Kelliher and Walbot, 2012) or genetic (Zechmann et al., 2011) approaches were used to reduce ROS levels, resulting in improved reproductive success as well as crop yield. In contrast, the "oxidative hypothesis" advocates increased ROS levels as a prerequisite for initiation of meiosis and sexual reproduction (Hörandl and Hadacek, 2013). In this view, the role of a meiotic protein SPO11 has been proposed. This protein initiates generation of DSBs (double-strand DNA breaks) during meiotic recombination and have antioxidant like properties to repair oxidatively damaged DNA (Hörandl and Hadacek, 2013). Moreover, oxidative stress can deregulate the epigenetic machinery comprising of DNA methylation and small RNA-based transcriptional regulation (Schmidt et al., 2015; Zhang et al., 2015). Thus, plant sexual reproduction is a highly complicated process which requires a fine-tuning of oxidative-reductive (redox) pathways as well as epigenetic mechanisms, hence complicating the engineering of modules for enhancing stress tolerance in plants.

CONCLUSIONS

The redox control of plant reproductive development has been the long standing dilemma of plant scientists. Understanding the reproductive cost of oxidative stress requires a targeted molecular approach for engineering transgenes responsible for stress resilience in plant's reproductive system. But our knowledge is demarcated by methods to intertwine regulatory networks underlying reproductive development. Although much of the studies now focus on *Arabidopsis* as a model organism, future research should input judicious use of major crop species ensuring yield robustness in meeting continual demands of an ever increasing human population.

AUTHOR CONTRIBUTIONS

GZ and AK conceived the idea and outline for the prescribed article and thereafter compiled and incorporated the different sections contributed by co-authors. All the authors read and approved the final version before submission.

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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