eXtra Botany

Viewpoint

Does the alternative respiratory pathway offer protection against the adverse effects resulting from climate change?

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Elevated greenhouse gases (GHGs) induce adverse conditions directly and indirectly, causing decreases in plant productivity. To deal with climate change effects, plants have developed various mechanisms including the fine-tuning of metabolism. Plant respiratory metabolism is highly flexible due to the presence of various alternative pathways. The mitochondrial alternative oxidase (AOX) respiratory pathway is responsive to these changes, and several lines of evidence suggest it plays a role in reducing excesses of reactive oxygen species (ROS) and reactive nitrogen species (RNS) while providing metabolic flexibility under stress. Here we discuss the importance of the AOX pathway in dealing with elevated carbon dioxide (CO_2), nitrogen oxides (NOx), ozone (O_3), and the main abiotic stresses induced by climate change. Recent advances in our understanding concerning the *in vivo* regulation of alternative oxidase (AOX) and its structural properties suggest that novel AOXs with altered regulatory properties could be used in future gene editing strategies. We suggest that fine-tuning modulation of the regulatory properties of AOX and targeting its expression in different plant tissues could improve plant growth and productivity under climate change conditions promoted by elevated greenhouse gasses (GHGs). Moreover, we also emphasize the need for extensive study on the interactive effects of major global change factors on AOX respiration and the importance of studies differentiating between the roles of AOX in sink versus source tissues under field conditions in order to improve plant productivity in response to elevated GHGs.

Climate change is associated with an elevation of the greenhouse gases such as (CO_2), nitrogen oxides (NOx), ozone (O_3), and methane (CH_4), and with increased events of adverse conditions for plants including drought and high temperature stress as well as flooding (Min *et al.*, 2011; Pall *et al.*, 2011). Such abiotic stress conditions in combination with increasing biotic stresses are challenging plant and agricultural research to adopt new strategies for developing more climate-resilient crops with high yield and productivity in order to meet the enhanced global population food demand (Dhankher and Foyer, 2018). Considering that respiration and photosynthesis are the main components of plant carbon balance, alterations in respiration can potentially affect plant growth and productivity (Zhang *et al.*, 2018; Amthor *et al.*, 2019). In particular, the AOX pathway has been demonstrated to improve plant performance under different physiological conditions—mainly due to its roles both in providing metabolic flexibility and in lowering the level of mitochondrial reactive oxygen species (ROS) (Vanlerberghe, 2013; Selinski *et al.*, 2018; Del–Saz *et al.*, 2018a). As such, it probably functions to protect plants against the adverse effects of climate change (Fig. 1).

Susceptibility of plants to various abiotic and biotic stresses can be aggravated by climate change-induced ROS including the superoxide anion (O_2^-), hydrogen peroxide (H_2O_2), and the hydroxyl radical ($\cdot OH^-$) (Cassia *et al.*, 2018). These ROS originate from various sources such as the mitochondria, chloroplast, peroxisome, and the plasma membrane NADPH oxidase (Mittler, 2017). Various stresses additionally induce nitric oxide (NO), which in turn reacts with ROS, leading to the production of reactive nitrogen species (RNS) such as peroxynitrite ($ONOO^-$), nitric dioxide (NO_2), nitrosyl anion (NO^-), dinitrogen trioxide (N_2O_3), dinitrogen tetroxide (N_2O_4), and nitrous acid (HNO_2). Low levels of these free radicals trigger important signals; however, if they are produced in higher levels, they can cause adverse effects such as damage to lipids, proteins, and DNA, and consequently impact on plant growth and development. Plants have accordingly evolved various machineries that can deal with elevated ROS, including ascorbate peroxidase (APX), catalase (CAT), superoxide dismutase (SOD), and other enzymes involved in the ascorbate–glutathione cycle (Choudhury *et al.*, 2017). Among mitochondrial proteins, the AOX controls mitochondrial ROS production and plays a role in adaptive plasticity. Briefly, AOX
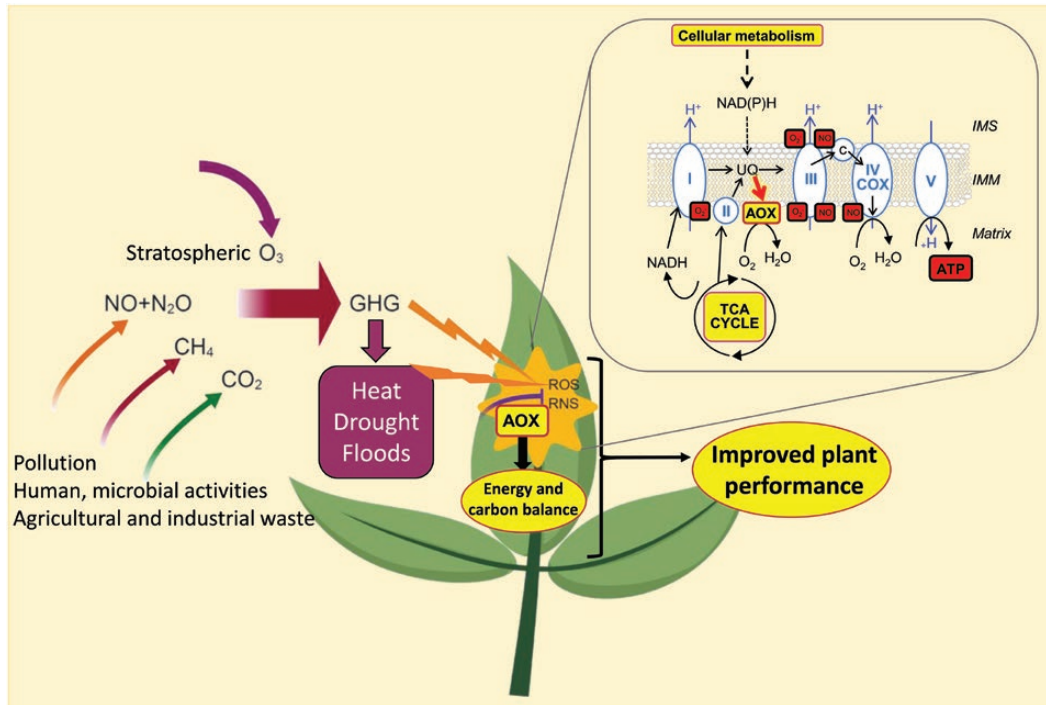
Fig. 1. The role of the alternative oxidase (AOX) pathway in mitigating the effects of climate change and improving plant growth. Environmental, human, and microbial activities lead to increased greenhouse gases (GHGs). These GHGs can elevate ROS and RNS directly or directly via inducing various stresses. AOX can reduce excess ROS and RNS while maintaining energy and carbon balance to improve plant growth. In the inset, a schematic representation of the plant mitochondrial electron transport chain (mETC) is shown. The mETC contains the classical components involved in oxidative phosphorylation [I, II, III, IV (or cytochrome oxidase, COX), and V], which yields ATP. Complexes I, III, III, and IV are also sources of superoxide (O_2^-) and nitric oxide (NO), which can be transformed into other ROS and RNS. The AOX is inserted at the inner mitochondrial membrane (IMM) and diverts electrons from the ubiquinone (UQ) pool by reducing O_2 to H_2O without proton (H^+) translocation into the intermembrane space (IMS). In this way, the AOX can stabilize the reduction level of the UQ pool and other mETC components, thus preventing the formation of O_2^- and NO. At the same time, the AOX activity renders respiration independent of adenylate control, thus allowing the reoxidation of matrix and extramitochondrial NAD(P)H under high-energy charge or COX restriction. Several physiological situations can require the action of AOX to maintain or enhance the activities of the TCA cycle and other cellular metabolic processes under energy and carbon imbalance. Yellow and red boxes indicate induced and reduced molecule levels or processes by the action of AOX, respectively.

protein is inserted in the inner membrane of plant mitochondria and branches the cytochrome *c* oxidase (COX) pathway at the level of the ubiquinone (UQ) pool bypassing two sites of proton translocation associated with ATP production (Fig. 1). In this manner, the AOX pathway can stabilize the UQ reduction level and prevent the production of excessive ROS. Furthermore, the activity of the AOX pathway renders respiration independent of adenylate control, thus allowing the continuation of respiratory metabolism, which is crucial for plants to cope with different stress conditions (Del-Saz *et al.*, 2018*a*) such as those promoted by climate change.

The AOX pathway in modulating ROS and RNS induced by greenhouse gases

Different studies have reported that AOX expression is responsive to a variety of greenhouse gases such as O_3, NO, and CO_2. O_3 is an important component of the stratosphere. It aids in filtering dangerous UV. In contrast, in the troposphere, O_3 is deleterious to plant performance. O_3 in the stratosphere is made by reaction between NOx, CO_2, CH_4, and volatile organic compounds (VOCs) in the presence of sunlight (Hickman, 2010). Increased O_3 can cause adverse effects on plants. For instance,

exposure of plants to O_3 causes massive changes in transcription, translation, and metabolism, resulting in decreases in plant productivity of up to 15% (Wilkinson *et al.*, 2012). In addition, increased formation of numerous free radicals has been reported in plants after O_3 exposure (Fiscus *et al.*, 2005). These radicals can disrupt various organelles, causing programmed cell death and reducing yield in various crops (Mills *et al.*, 2011). AOX can protect plants against damage imposed by ozone.

Intriguingly, Ederli *et al.* (2006) reported that exposure of tobacco plants to 300 ppb O_3 strongly induced AOX expression. Moreover, Tosti *et al.* (2006) reported that O_3 exposure resulted in the induction of AOX protein promoted by a crosstalk between ethylene and NO signalling. Furthermore, induction of AOX occurs via the inhibition of the cytochrome *c* pathway by O_3, and at the same time the inhibition of the cytochrome pathway by O_3 leads to production of H_2O_2. Consequently, the H_2O_2 produced causes further induction of *AOX1a* via retrograde signalling (Tosti *et al.*, 2006). While the extent of the effect of O_3 on *in vivo* AOX activity has not yet been determined, it follows that the overexpression of AOX in crop plants may offer plant resistance to O_3 injury by reducing the levels of ROS.

Excess NOx (such as NO and NO_2), which occur within the natural atmosphere, can be problematic since they are both components of GHGs as well as being inducers of other GHGs

such as O_3 (Hickman *et al.*, 2010). NO, a free radical signal molecule, is a component of NOx. Excess NO can cause tyrosine nitration of proteins, thus inhibiting their activities. Several free radicals and metabolites such as pyruvate and citrate are inducers of AOX (Vanlerberghe, 2013). Among them, NO is an inducer of the AOX at the transcript and protein level (Huang *et al.*, 2002; Kumari *et al.*, 2019). Treatment of cell suspensions with NO leads to an increased capacity of the AOX pathway, and inhibition of AOX leads to increased NO sensitivity to cell death, suggesting that NO is induced to protect cells from cell death (Kumari *et al.*, 2019). Fu *et al.* (2010) has shown that AOX is important in the prevention of cell death induced by *Tobacco mosaic virus*. Since O_3 also causes cell death, the induced AOX can help in the protection from cell death (Overmeyer *et al.*, 2005). The AOX pathway prevents excess ROS and NO production (Maxwell *et al.*, 1999; Cvetkovska and Vanlerberghe, 2012; Alber *et al.*, 2017; Vishwakarma *et al.*, 2018). NO reacts with superoxide, leading to production of $ONOO^-$ which can cause tyrosine nitration and reduces function of various enzymes. In this context, the capacity of AOX to control both NO and ROS production makes it a very powerful machinery for the protection of plants against these molecules. Recently, it was demonstrated that AOX not only scavenges NO under normoxia induced by flg22 (flagellin) but also generates NO under hypoxia (Vishwakarma *et al.*, 2018). In contrast to normoxia, hypoxia–induced NO does not react with superoxide, but rather is scavenged by phytoglobin1 via metaphytoglobin reductase activity. The scavenged NO has a role in recycling nitrate, maintenance of the redox status, and operation of the phytoglobin–NO cycle to generate ATP (Vishwakarma *et al.*, 2018). NOx emissions also contribute to increased temperature, which indirectly can increase flash floods with the consequent hypoxic atmosphere in soil. Hence AOX can play a role under flooding conditions to improve energy efficiency and survival.

Although CO_2 is important for photosynthesis, elevated CO_2 can have some negative impacts on plants. The study of Loladze (2014) based on >130 species and crop species found that elevated CO_2 can reduce mineral content on average by 8% and increases the ratio of soluble carbohydrates to proteins. Several important elements such as zinc and iron diminished in several food crops such as rice, wheat, and soybean in the presence of high CO_2 (Myers *et al.*, 2014). Elevated CO_2 also induces ROS (Cheeseman, 2006) and, in order to detoxify ROS, plants also induce various antioxidants (AbdElgawad *et al.*, 2016). Several reports suggest that AOX protein is highly responsive to elevated CO_2 (Yoshida and Noguchi, 2009; Dahal and Vanlerberghe, 2018a). The relationships between yield, ROS production, and mineral nutrition in AOX-modified plants under elevated CO_2 (eCO_2) remain to be investigated and could provide more insights into the protective role of AOX.

The AOX pathway in providing metabolic adaptations of plants to stresses aggravated by climate change

The AOX pathway provides flexibility in cellular energy and carbon metabolism under drought, elevated temperature, and CO_2 (Del-Saz *et al.*, 2018a; Dahal and Vanlerberghe, 2018a, b), which represent the major abiotic stresses challenging current agricultural productivity with regard to climate change. The beneficial role of such metabolic flexibility probably compensates the theoretical negative effects of AOX in reducing ATP and reductant availability required for growth (Vanlerberghe, 2013). In this context, Dahal and Vanlerberghe (2018b) importantly reported that plant growth was higher in tobacco plants overexpressing AOX as compared with wild-type plants after prolonged water deficit. The beneficial effect on growth has been linked to the ability of AOX to maintain a higher respiration in light, which improves chloroplast energy balance and photosynthesis (Dahal and Vanlerberghe, 2018b). The role of the AOX in improving photosynthesis has also been reported in other species under different conditions (reviewed by Del-Saz *et al.*, 2018a) and is probably among the main reasons explaining the beneficial role of AOX in plant growth and productivity. Nevertheless, there is also evidence suggesting that the *in vivo* AOX activity favours the synthesis of tricarboxylic acid (TCA)-derived metabolites with specific roles in protecting against high light (Florez-Sarasa *et al.*, 2016) and salinity stress (Del-Saz *et al.*, 2016).

Adjustments to the partitioning of electrons between AOX and COX pathways were associated with changes in tissue energy demands of plants exposed to long-term elevated CO_2 conditions (Gomez-Casanovas *et al.*, 2007). In addition, changes in mitochondrial electron partitioning to AOX were related to the improvement of leaf carbon balance and respiratory efficiency under different CO_2 growth conditions (Gonzàlez-Meler *et al.*, 2009). Recently, AOX overexpression has been shown to prevent both carbohydrate and energy imbalances in leaves of tobacco plants grown at elevated CO_2 (Dahal and Vanlerberghe, 2018a). All these studies suggest that increased AOX activity can be beneficial for plant growth under elevated CO_2 conditions.

Future perspectives

As discussed above, the use of AOX–transgenic plants has provided important insights into the role of AOX in photosynthetic tissues and growth. However, the effects of AOX genetic modification on root growth and metabolism under stress have received much less attention (Smith *et al.*, 2009, Keunen *et al.*, 2016). Importantly, AOX has a role in the synthesis of carboxylates in white lupin (Florez-Sarasa *et al.*, 2014), tobacco (Del-Saz *et al.*, 2017), and tomato (Del-Saz *et al.*, 2018b). The root exudation of carboxylates improves phosphate acquisition, which benefits photosynthesis and plant growth (Pang *et al.*, 2018). On the other hand, information about the impact of the AOX pathway on the growth of other sink and reproductive tissues, such as tubers and fruits, is limited (Xu *et al.*, 2012; Zidenga *et al.*, 2012) and represents an important area for future research. Given the evidence for tissue-specific roles for AOX, the use of more sophisticated genetic approaches specifically targeting sink and/or source tissues (Sonnewald and Fernie, 2018) will be required for disentangling the roles of AOX and its impact on plant growth and productivity. Genetic engineering of respiration involving

spatio–temporal changes of the target genes has been proposed as a crucial strategy to improve crop productivity (Amthor *et al.*, 2019). Particularly, fine-tuning alterations of AOX have been predicted to be among the most efficient strategies to achieve high biomass gains (Amthor *et al.*, 2019). In this respect, recent *in vitro* (Selinski *et al.*, 2018) and *in vivo* (Florez-Sarasa *et al.*, 2019) evidence on the predominant role of the TCA cycle intermediates on AOX regulation, together with new structural insights on its active site (May *et al.*, 2017), is paving the way to design new AOXs with altered and desirable regulatory properties. Finally, the interactive effects of major global change factors on AOX respiration remain to be determined. Some studies have highlighted the importance of (photo) respiratory metabolism under stress combination (Obata *et al.*, 2015; El Aou–Ouad *et al.*, 2018), although AOX was not investigated in these studies. Thus, the specific role of AOX under stress combination remains to be explored by means of genetic approaches and *in vivo* activity measurements. Given the evidence reported about the AOX involvement in plant tolerance to several individual biotic and abiotic stresses (reviewed in Vanlerberghe, 2013; Saha *et al.*, 2016; Del-Saz *et al.*, 2018*a*), we envisage that AOX will provide a beneficial role for plants under combined stress conditions induced by climate change.

Acknowledgements

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