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Commentary

Ozone risk assessment for plants: Central role of metabolism-dependent changes in reducing power

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We propose reducing power, Rubisco/PEPc ratio and water use efficiency as additional indicators in ozone risk assessment for plants.

Abstract

The combination of stomatal-dependent ozone flux and total ascorbate level is currently presented as a correct indicator for determining the degree of sensitivity of plants to ozone. However, the large changes in carbon metabolism could play a central role in the strategy of the foliar cells in response to chronic ozone exposure, participating in the supply of reducing power and carbon skeletons for repair and detoxification, and modifying the stomatal mode of functioning. To reinforce the accuracy of the definition of the threshold for ozone risk assessment, it is proposed to also consider the redox pool (NAD(P)H), the ratio between carboxylases and the water use efficiency as indicators of the differential ozone tolerance of plants.

Keywords: Antioxidants; NAD(P)H; Ozone; Rubisco/PEPc ratio; Water use efficiency

1. Introduction

Levels of tropospheric ozone have increased considerably in the last century and are predicted to continue to rise in the near future (Marenco et al., 1994; Stockwell et al., 1997). Ozone is well known as a phytotoxic air pollutant causing a series of damage including visible injury (chlorotic and necrotic lesions), growth decrease, yield loss and leading ultimately to death. It is of particular importance to note that chronic long-term exposures to low ozone concentrations will affect physiological and biochemical processes (hidden injury, e.g. decreased photosynthesis) prior to any development of visible injury (Heath and Taylor, 1997). In Europe, in order to predict the effects of ozone on higher plants, a critical level of ozone was proposed, based upon a long term cumulative parameter: the AOT40 concept which is the sum of the hourly ozone concentrations above a threshold of 40 nl L^{-1} during daylight hours of the growing season (Fuhrer et al., 1997). For forest trees, exceedance of a value of 10 ppm.h would indicate a risk of biomass loss of about 10% (LRTAP, 2004). Taking into account the fact that phytotoxicity will depend on the actual ozone flux within the mesophyll through the stomata, more recent studies (Ashmore et al., 2004; Karlsson et al., 2004; Grünhage et al., 2004) developed a flux-based concept. This method, although biologically more relevant, in particular for early biochemical events, presents some limitation since it ignores the defence mechanisms linked to the detoxification system of leaf cells (Matyssek et al., 2004). For that reason, in order to refine the concept of ozone risk assessment, the concept of an ‘‘effective ozone flux’’, which is the balance between stomatal flux and

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intra-leaf detoxification, was recently introduced (Musselman et al., 2006; Tausz et al., 2007; Wieser and Matyssek, 2007). The question thus arises as to the ways to consider the nature and effectiveness of a putative detoxifying barrier which could contribute to the definition of different degrees (levels) of sensitivity of the plant to ozone attack. In this context, the degree of sensitivity of the foliar cells will depend on the actual amount of pollutant reaching the target sites as well as the capacity of the cells to restore homeostatic equilibrium by developing adapted changes in the metabolism. The aim of this paper is to develop the role the reducing power could play in this context.

2. Detoxification and reducing power

Although the stomatal resistance could be considered as the main obstacle to the ozone flux (Kollist et al., 2000), the direct reaction of the pollutant with cell wall ascorbate is frequently involved (Plöchl et al., 2000). Ozone dissolves in the intercellular spaces giving a series of potentially damaging reactive oxygen species (ROS) triggering an antioxidant response (Baier et al., 2005). Detoxification processes actively participate in constitutive and inductive aspects (Fig. 1) according to Musselman et al. (2006). The first detoxifying barrier, which can be considered as constitutive since it represents the antioxidant system found in the cell (apoplasm + symplasm) at the time of ozone attack, will scavenge ozone and its derivatives. This system is tightly linked to the level of ascorbate and especially apoplastic ascorbate, which was primarily proposed as a good indicator for ozone tolerance (Turcsányi et al., 2000; Tausz et al., 2007). It is thus tempting to establish a simple link between the amount of ascorbate (or total antioxidative capacity) present in the cell wall and the degree of sensitivity of the plant. However, elevated apoplastic ascorbate levels did not seem to be sufficient to explain tolerance (D'Haese et al., 2005; Eller and Sparks, 2006). In fact the antioxidative capacity of the apoplastic space is considered much weaker than inside the cell (Foyer and Noctor, 2005b) and it can be overwhelmed by a too important ozone flux. An *inductive* response, triggered by the ROS, takes place allowing exchanges of antioxidants between the symplastic detoxification system and the apoplasm. Although the resulting increased level of symplastic ascorbate could serve as a predictor of the resistance to ozone attack (Eltayeb et al., 2006), other molecules and the cellular ability to regenerate antioxidants could be more relevant (Eller and Sparks, 2006; Noctor, 2006). Unlike the apoplasm, the symplasm contains glutathione and NAD(P)H implicated into the Halliwell–Asada cycle. The reduction of GSSG into GSH occurs through the functioning of glutathione reductase (GR). The GSH/GSSG couple plays a redox sensor role (Foyer and Noctor, 2005a), allowing the further reduction of ascorbate to occur. GSH is not only the reducing co-factor for several enzymes involved in ROS detoxification but could also conjugate to proteins to avoid their oxidation and this process is catalyzed by enzymes such as glutaredoxins (Rouhier et al., 2004). Other enzymes like thioredoxins and peroxiredoxins could also play an important role in thiol-based regulation (Schürmann and Jacquot, 2000; Dietz et al., 2006). Finally, NAD(P)H clearly appears as a key compound for supplying the needed reducing power to drive most of these processes.

3. Metabolic changes

3.1. Carbon metabolism and NAD(P)H production

The capacity for the regeneration of antioxidants within the cell (2nd detoxifying barrier), driven by an "oxidative signalling" process and linked to appropriate changes in reducing power (NAD(P)H), depends on carbon metabolism changes concomitant with alteration in gene expression (Dizengremel, 2001; Foyer and Noctor, 2005a).

As demonstrated in several higher plants, chronic ozone fumigation provokes a progressive diminution in photosynthetic

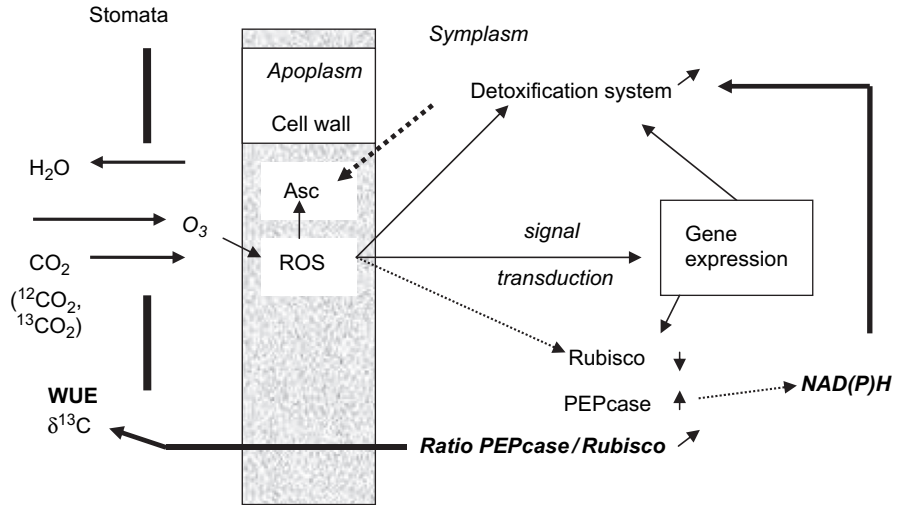

Fig. 1. Summary of the relationships between stomatal uptake, metabolic changes and detoxification system under chronic ozone attack in plant cells. Asc, ascorbate; PEPcase, phosphoenolpyruvate carboxylase; ROS, reactive oxygen species; Rubisco, ribulose-1,5-bisphosphate carboxylase oxygenase; WUE, water use efficiency; $\delta^{13}C$, fractionation between ^{12}C and ^{13}C.