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Plant oxidative status under ozone pollution as predictor for aphid population growth: The case of *Metopolophium dirhodum* (Hemiptera: Aphididae) in *Triticum aestivum* (Poales: Poaceae)

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ABSTRACT

Ozone is a secondary air pollutant that affects plants and animals through several physiological mechanisms that involve changes in redox status. However, the consequences of ozone pollution on aphids are not well understood. Therefore, we have experimentally tested: if oxidative stress on the host plant affects lipid peroxidation in aphids or aphid population growth. Wheat plants (*Triticum aestivum*) were exposed to 140 p.p.b. of ozone or filtered air in open top chambers for three consecutive days and *Metopolophium dirhodum* (Walker, 1849, Hemiptera: Aphididae) aphids were transferred to the plants immediately after ozone exposure or 72 h later. Ozone exposure reduced antioxidant potential within plant tissues and had no effect on plants' lipid peroxidation. Lipid peroxidation in aphids fed upon these plants was similar among treatments. Although aphids successfully colonised the plants in all the treatments, the populations established on plants immediately after ozone exposure grew at higher rates than those established 72 h after ozone exposure had ended, independently of ozone level. In conclusion, aphids were tolerant to plant mediated effects of ozone. Therefore, a greater attention should be put in the direct effects of ozone on *M. dirhodum* - *T. aestivum* interaction.

1. Introduction

Ozone has an important biological impact on plants and animals, besides its effect as a greenhouse gas (Myhre et al., 2013). Ozone is largely produced in the lower atmosphere from primary air pollutants, such as nitric oxides, sulphur oxides, carbon oxides and hydrocarbons in the presence of sunlight (Iriti and Faoro, 2009). As any photochemical pollutant, ozone formation depends on solar radiation. This leads to its episodic and cyclic nature (Booker et al., 2009; Schnell et al., 2009; Vingarzan, 2004). Besides the increase in the background concentrations of ozone during the past century (Vingarzan, 2004), acute ozone episodes that reach over 120 ppb during the day currently occur at diverse locations (Assareh et al., 2016; Domínguez-López et al., 2015; Schnell et al., 2009) and have a negative impact on vegetation and food production (Avnery et al., 2011).

This negative effect of ozone arises from the disturbance of the equilibrium between production and scavenging of reactive oxygen species (ROS), within animal and plant tissues (Iriti and Faoro, 2007). The outermost biological surfaces have an antioxidant system which provides a primary defence against atmospheric ROS (Cross et al., 2002). When this barrier is overcame, ROS enter the cells and produce an oxidative burst which is counteracted by a diverse set of soluble (ascorbate, glutathione, tocopherol, carotenoids and phenolic compounds) and enzymatic antioxidants (superoxide dismutase, catalase, glutathione peroxidase, guaiacol peroxidase, peroxiredoxins and enzymes of the ascorbate-glutathione cycle) (Caverzan et al., 2016; Fangmeier et al., 1994; Foyer and Noctor, 2005; Li et al., 2013; Valkama et al., 2007; Wang et al., 2014). As ozone enters plant cells, it produces ROS such as H_2O_2, superoxide (O_2^-) and hydroperoxyl (HOO^-) radicals (Ahsan et al., 2010). The following oxidative burst involves changes in the oxidative signalling pathways through the production of ROS (Baier et al., 2005; Foyer and Noctor, 2005; Kangasjärvi et al., 2005) and upregulates the expression of proteins associated with antioxidant defense mechanisms, carbon metabolism, secondary

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metabolism and nitrogen metabolism (Ahsan et al., 2010). Moreover, ozone downregulates the expression of proteins associated with photosynthesis pathways (Ahsan et al., 2010), ultimately reducing carbon uptake, and/or photosynthetic carbon fixation, with consequences on plant growth and on the translocation of fixed carbon to other plant tissues (Wilkinson et al., 2012).

Several parallelisms can be established between plants and animals in terms of their susceptibility to ozone injury, as antioxidant defences have been highly conserved along evolutionary history. For instance, plants' hypersensitive response (HR) is frequently compared to animal inflammatory responses (Cross et al., 2002). Insects are susceptible to oxidative stress (Cross et al., 2002; Holmstrup et al., 2011; Telesnicki et al., 2015) and to the accumulation of ROS (Smith and Boyko, 2007). In the case of aphids, antioxidants play an important role in terms of nutrition, defence against environmental stress and coping with ROS mediated plant defence (Goggin et al., 2010; Kerchev et al., 2012; Mai et al., 2013). Aphids have a complex feeding behaviour, which allows them to furtively feed on plant tissues without causing major injuries (Züst and Agrawal, 2016). Additionally, the salivary secretions of aphids modulate or suppress the phytohormonal and defensive response of susceptible plants and modify source-sink relationships in the translocation of nutrients (Giordanengo et al., 2010; Goggin, 2007; Powell et al., 2006; Züst and Agrawal, 2016).

Aphid-plant interactions under ozone pollution are not clearly understood. Under ozone stress, individual and population growth rates, developmental time and fecundity of aphids either increase, decrease or remain untouched (Awmack et al., 2004; Brown et al., 1992; Holopainen, 2002; Holopainen and Kossi, 1998; Jackson, 1995; Menéndez et al., 2010; Mondor et al., 2010; Warrington, 1989). Ozone may affect aphids directly (Telesnicki et al., 2015), indirectly or by the interaction of direct and indirect effects, when plants and aphids are simultaneously exposed to ozone (Awmack et al., 2004; Brown et al., 1992; Holopainen and Kossi, 1998; Menéndez et al., 2010; Mondor et al., 2010; Warrington, 1989). Simultaneous exposure of plant and aphids to ozone offers a realistic approach to study ozone's effect on aphid-plant interaction. However, the isolated exploration of the direct and indirect effects of ozone on aphids allows a clearer distinction of ozone's effect on aphids from the sum of effects of ozone on each member of this interaction. In the case of the direct exposure of aphids to ozone, ozone has been shown to lead to oxidative stress accumulation, increased mortality and reduced aphids' dispersion ability (Telesnicki et al., 2015).

Regarding the indirect effects of ozone on aphids, two main mechanisms have been considered to explain ozone-driven changes in aphid populations: (1) changes in plant nutritional quality (reviewed in Valkama et al., 2007; Dermody et al., 2008) and (2) the activation of plants crossed-response to biotic and abiotic stress factors (crosstalk) through modification of the oxidative status of the plant (Menéndez et al., 2009). On one hand, no correlation was found between nutrient content and aphid performance in increased ozone environments (Dermody et al., 2008; Valkama et al., 2007). Actually, in these studies, ozone had no consistent effect on either carbon (C) concentration, nitrogen (N) concentration, C:N ratio, or on the relative growth rate of individual aphids (RGR) or population size (Dermody et al., 2008; Valkama et al., 2007). On the other hand, several secondary metabolites with antioxidant capacity, such as phenolic acids, flavonoids, glutathione and ascorbate have been shown to increase significantly after plant exposure to ozone (Fangmeier et al., 1994; Foyer and Noctor, 2005; Valkama et al., 2007; Wang et al., 2014). Moreover, aphids can benefit from feeding on plants with enhanced antioxidant content (Kerchev et al., 2012). As abiotic stress also leads to antioxidant accumulation (Kangasjärvi et al., 2005; Sharma and Davis, 1997), it has been hypothesized that it could reduce the effectiveness of plant defence against insects (Łukasik and Goławska, 2013).

Therefore, the aim of this study is to evaluate the indirect effect of ozone on aphids at biochemical scale and its impacts at aphid population scale. We conducted two independent experiments to test the following hypothesis: 1) oxidative stress accumulation in aphids depends on plants oxidative stress status and 2) ozone-induced increase in plant antioxidant potential has a positive effect on aphid population growth.

2. Materials and methods

Two independent experiments were conducted at IFEVA (Faculty of Agronomy, University of Buenos Aires, 34° 35′S, 58° 29′W) to test the abovementioned hypotheses. Treatments were designed to mimic the occurrence of acute ozone episodes and patchy aphid infestations occurring before or after the plant exposure to the contaminant. The aphid oxidative stress experiment was aimed at testing the first hypothesis and the aphid population growth experiment was aimed at testing the second hypothesis. In both experiments, the plants were exposed to ozone or charcoal filtered air for three consecutive days before receiving the aphids. Aphids were not exposed to ozone at any moment, as the experiments were designed to exclusively evaluate the indirect effect of ozone on aphids. Since ozone-induced changes in plant antioxidant potential vary over time (Kangasjärvi et al., 2005), the indirect effect of ozone was evaluated at two different moments: 0 h after ozone exposure and 72 h after exposure had ended.

2.1. Plants

A total of 140 spring wheat plants (*Triticum aestivum* L. cv. 'Cronox', Don Mario, Chacabuco, Argentina) were individually grown in 2 L plastic pots containing a 50% soil, 25% peat moss and 25% perlite potting mixture and were used for both experiments. The pots were placed inside plastic containers with a water reservoir to keep the soil under constant moisture. Plants were kept in a glasshouse (mean temperature 18.5 °C) until tillers were completely formed. Then, they were transferred to the open top chambers to allow for plant acclimation one week prior to ozone exposure.

2.2. Ozone exposure

Plant exposure to ozone was performed in 8 m^3 "open-top" chambers (OTC) with crystal PVC (polyvinyl chloride) walls mounted on a metal structure which allowed ozone level regulation (Hogsett and Tingey, 1985; Lefohn et al., 1986). Ozone was generated from charcoal-filtered air by a spark discharge-type ozone generator (Dobzono, Buenos Aires, Argentina). Ozone concentration inside the OTC was continuously monitored using a Model 450 Ozone Monitor API-Teledyne Instrument (Teledyne Advanced Pollution Instrumentation, San Diego, CA). The eight chambers were laid in a radial array and ozone level was randomly assigned to each chamber. Each OTC was provided with an air conditioning system. Mean (±SEM) temperature within the OTC during ozone exposure was 24.6 °C ± 1.1 °C. Near surface ozone currently reaches maximum concentrations over 100 p.p.b. (Andersson et al., 2017; Wang et al., 2017) and projections also show increases in background ozone levels (Lin et al., 2017; Sicard et al., 2017). Therefore, ozone and filtered air were mixed in different proportions to obtain two contrasting ozone exposure conditions: 0.0 ± 0.7 p.p.b. or 140 ± 14 p.p.b. The plants received an acute, 5-h ozone exposure treatment during three consecutive days, which is sufficient to induce changes in antioxidant related gene expression and antioxidant enzymatic