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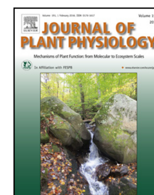

Short communication

Barley yellow dwarf virus infection and elevated CO_2 alter the antioxidants ascorbate and glutathione in wheat

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ABSTRACT

Plant antioxidants ascorbate and glutathione play an important role in regulating potentially harmful reactive oxygen species produced in response to virus infection. *Barley yellow dwarf virus* is a widespread viral pathogen that systemically infects cereal crops including wheat, barley and oats. In addition, rising atmospheric CO_2 will alter plant growth and metabolism, including many potential but not well understood effects on plant-virus interactions. In order to better understand the wheat-BYDV interaction and any potential changes under elevated CO_2, the total concentration and oxidised fraction of ascorbate and glutathione was measured in leaves of a susceptible wheat cultivar (*Triticum aestivum* L. 'Yitpi') infected with *Barley yellow dwarf virus*-PAV (Padi Avenae virus) and grown under elevated CO_2 in controlled environment chambers. Virus infection decreased total leaf ascorbate and glutathione concentrations and increased the fraction of oxidised ascorbate (dehydroascorbate). Elevated CO_2 decreased the fraction of oxidised ascorbate. In this work, we demonstrate that systemic infection by a phloem-restricted virus weakens the antioxidant pools of ascorbate and glutathione. In addition, elevated CO_2 may decrease oxidative stress, for example, from virus infection, but there was no direct evidence for an interactive effect between treatments.

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1. Introduction

One of the first responses of a plant exposed to a viral pathogen is the localised production of a large amount of reactive oxygen species (ROS), known as the 'oxidative burst', that can potentially damage cells by oxidation and disruption of cell metabolism (Torres, 2010). The ability of a plant to coordinate its defences against virus-induced ROS and prevent cell damage depends on antioxidants and associated enzymes that can metabolise ROS via redox reactions. The two principal plant antioxidants ascorbate and glutathione play an important role during plant-virus interactions by scavenging and reacting non-enzymatically with ROS (Foyer and Noctor, 2011). Ascorbate and glutathione are generally maintained in a highly reduced state (ASC or GSH, respectively), and are oxidised to dehydroascorbate (DHA) and glutathione disulfide (GSSG), respectively, during interactions with ROS. Oxidative stress may occur when antioxidant defence systems cannot effectively regulate excess ROS and maintain antioxidants in the reduced state. Therefore, ascorbate and glutathione concentration and redox state have been proposed as markers for oxidative stress and antioxidant defence capacity during both biotic and abiotic stress (Dempsey et al., 2012; Tausz et al., 2004).

During plant-virus interactions, ROS can play different roles in pathogenesis or inhibition of virus spread, likely depending on localised concentrations (Shetty et al., 2008), and the speed of host responses (Hernández et al., 2015). During incompatible plant-virus interactions, a down-regulation of antioxidant activity and buildup of ROS surrounding the infection site can promote the hypersensitive response (HR) that kills local plant cells and restricts virus movement (De Gara et al., 2003; Fodor et al., 1997). In contrast, compatible plant-virus interactions do not produce a HR, but instead can result in systemic virus infection and visual disease

Abbreviations: %DHA, oxidised fraction of ascorbate (dehydroascorbate); %GSSG, oxidised fraction of glutathione (glutathione disulfide); ASC+DHA, total ascorbate; BYDV, Barley yellow dwarf virus; dpi, days post-inoculation; eCO_2, elevated CO_2; GSH+GSSG, total glutathione; PAV, Padi Avenae virus; ROS, reactive oxygen species.

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symptoms associated with oxidative stress (Riedle-Bauer, 2000). The lack of HR during compatible interactions may either be a result of enhanced antioxidant scavenging ability that prevents local ROS buildup, or ROS production that is below the threshold to cause local cell death (Riedle-Bauer, 2000). For compatible plant-virus interactions, it has also been proposed that a decrease in antioxidant scavenging capacity may be necessary for successful virus replication and subsequent spread (Clarke et al., 2002; Hernández et al., 2006). For example, studies of compatible plant-virus interactions have been associated with decreases in total ascorbate and glutathione concentrations, and increases in their oxidised fractions, interpreted as weakened antioxidant defence capacity associated with oxidative stress (Hakmaoui et al., 2012; Jaiswal et al., 2013; Li and Burritt, 2003; Wang et al., 2011). In apparent contrast, some compatible interactions have also been found to involve increased concentrations of total ascorbate and glutathione that are also in a more reduced state (Rodríguez et al., 2012; Sgherri et al., 2013). Different responses may be due to the particular plant-virus interaction, method of inoculation, stress intensity, sampling time or environmental conditions (Hernández et al., 2015). The only one of these studies that included a phloem-restricted virus, found a decrease in total ascorbate concentration, but did not investigate glutathione or the oxidation states of either antioxidant (Jaiswal et al., 2013).

Barley yellow dwarf virus-PAV (BYDV-PAV, Padi Avenae virus) is a widespread viral pathogen of the *Luteovirus* genus that systemically infects cereal crops including wheat, barley, oats, maize and rice. In Australia, BYDV has been found to reduce wheat (*Triticum aestivum* L.) yields by up to 50–79% (Banks et al., 1995; Smith and Sward, 1982). BYDV-PAV is phloem-restricted and is transmitted between plant by aphids. BYDV-PAV infection in susceptible wheat cultivars is an example of a compatible plant-virus interaction, and the disease is characterised by yellow chlorotic streaking of leaves, stunted growth, reduced root biomass and grain quality (Jensen and D'Arcy, 1995).

Atmospheric CO_2 will continue to rise from the current level of 400 μmol mol^{-1} to 650 μmol mol^{-1} before the end of the century, and is expected to increase yields and reduce the quality of wheat crops (Ainsworth and Long, 2005; Fernando et al., 2012; IPCC, 2013). Elevated CO_2 (eCO_2) may also have complex interactions with biotic factors, including viral pathogens (Luck et al., 2011). For example, eCO_2 may have a greater proportional effect on the biomass of virus-infected plants compared to noninfected controls, promoting persistence of infected plants in future environments (Malmström and Field, 1997; Trębicki et al., 2015; Ye et al., 2010). In addition, eCO_2 may alleviate oxidative pressure (e.g. from virus infection), because oxidative pathways in chloroplasts, such as photorespiration or Mehler reactions, are downregulated in favour of carbon fixation (Foyer and Noctor, 2009). However, the response of key antioxidants to eCO_2 is unclear, with studies finding either decreases (McKee et al., 1997; Pérez-López et al., 2010) or increases (Sanità di Toppi et al., 2002; Sgherri et al., 2000) in ascorbate and glutathione, or no consistent changes (Tausz-Posch et al., 2013). The potential effect of eCO_2 on antioxidants during systemic plant-virus interactions has not previously been addressed.

In this study, we assessed the response of two key antioxidants, ascorbate and glutathione, after systemic BYDV infection of wheat, and assessed whether growth under eCO_2 changed this response. We hypothesised that (1) analogous to other compatible plant-virus interactions, infection with phloem-restricted BYDV would cause an imbalance in the total concentration and redox state of ascorbate and glutathione, and that (2) eCO_2 will ameliorate oxidation of ascorbate and glutathione, because oxidative pathways (e.g. photorespiration) are downregulated under eCO_2.

2. Materials and methods

2.1. Plant growth conditions

Twenty-four seeds of a BYDV-susceptible wheat cultivar (*T. aestivum* 'Yitpi') were individually sown in 0.68 L pots containing potting mix with added nutrients, divided equally into two groups and grown in controlled environment chambers maintained at 20 °C and a L14:D10 photoperiod (900 μmol m^{-2} s^{-1} in the PAR 400–700 nm range) (TPG-1260, Thermoline Scientific, Australia). Pots were placed evenly in trays and bottom watered equally between groups. After virus inoculation (see "*Virus inoculation and vector colony*"), CO_2 treatment was applied by maintaining chamber CO_2 concentrations at 400 μmol mol^{-1} (ambient) or 650 μmol mol^{-1} (elevated). Plants and CO_2 treatments were alternated between chambers weekly to avoid any chamber effect (as per Trębicki et al. (2015)).

2.2. Virus inoculation and vector colony

An isolate of BYDV-PAV was collected from an oat plant in Horsham, Australia and maintained in wheat in controlled environment chambers (see "*Plant growth conditions*"). A colony of *Rhopalosiphum padi* L. was established from a single parthenogenetic female collected from Horsham and maintained on BYDV-infected wheat plants. Ten days after planting, once the first leaf unfolded (DC 11 growth stage, according to Zadoks et al. (1974)), six plants within each chamber were inoculated with BYDV-PAV by aphid transmission by inserting the first leaf into a small clear plastic tube containing eight live viruliferous adult *R. padi* and sealing with cotton wool. Tubes and aphids were removed from plants after 72 h.

2.3. Sampling

At 32 days post-inoculation (dpi, inoculation = introduction of viruliferous aphids) (DC 29 growth stage), the youngest fully-expanded leaf from the primary tiller was collected during a 2 h time window at midday, snap frozen in liquid nitrogen and freeze-dried for three days prior to antioxidant analysis (Alpha 1-4 LDplus, Christ, Germany). Leaves were sampled from BYDV-infected plants prior to exhibiting any visual yellowing disease symptoms. In comparison, the second youngest leaves on all infected plants exhibited disease symptoms. The presence of BYDV-PAV was assessed for two tiller samples by tissue-blot immunoassay (TBIA) method (Makkouk and Comeau, 1994). Inoculated plants that tested negative for BYDV-PAV were excluded from analyses. Leaves, tillers and roots were separated, dried at 60 °C for 72 h and weighed. Biomass data were corrected for the leaf removed for antioxidant sampling. Root:shoot ratio was determined by dividing root dry weight by aboveground (leaves and tillers) dry weight.

2.4. Ascorbate and glutathione analysis

Total ascorbate (ASC + DHA), total glutathione (GSH + GSSG), reduced ascorbate (ASC) and oxidised glutathione (glutathione disulfide, GSSG) were determined on freeze-dried leaf samples with methods based on Knörzer et al. (1996) as modified by Dempsey et al. (2012). The concentration of oxidised ascorbate (dehydroascorbate, DHA) was determined by subtracting reduced ascorbate from the total concentration.

2.5. Statistical analysis

Two-way ANOVAs were performed in R (including the 'car' package) with CO_2 treatment and virus treatment as fixed factors (R Core

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