



Antioxidative responses of three oak species under ozone and water stress conditions



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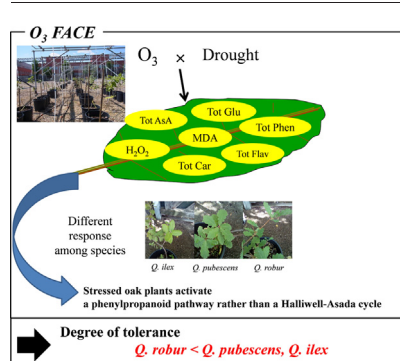
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HIGHLIGHTS

- Detoxification mechanisms at the basis of the high plasticity of oak species
- Ozone and drought had antagonistic effects on biochemical traits.
- Intrinsic physiological and biochemical mechanisms contribute to stress tolerance.

GRAPHICAL ABSTRACT



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ABSTRACT

Plants are frequently exposed to adverse environmental conditions such as drought and ozone (O₃). Under these conditions, plants can survive due to their ability to adjust their metabolism. The aim of the present study was to compare the detoxification mechanisms of three oak species showing different O₃ sensitivity and water use strategy. Two-year-old seedlings of *Quercus ilex*, *Q. pubescens* and *Q. robur* were grown under the combination of three levels of O₃ (1.0, 1.2 and 1.4 times the ambient O₃ concentration) and three levels of water availability (on average 100, 80 and 42% of field capacity i.e. well-watered, moderate drought and severe drought, respectively) in an O₃ Free Air Controlled Exposure facility. Ozone and drought induced the accumulation of reactive oxygen species (ROS) and this phenomenon was species-specific. Sometimes, ROS accumulation was not associated with membrane injury suggesting that several antioxidative defence mechanisms inhibited or alleviated the oxidative damage. Both O₃ and drought increased total carotenoids that were able to prevent the peroxidation action by free radicals in *Q. ilex*, as confirmed by unchanged malondialdehyde by-product values. The concomitant decrease of total flavonoids may be related to the consumption of these compounds by the cell to inhibit the accumulation of hydrogen peroxide. Unchanged total phenols confirmed that *Q. ilex* has a superior ability to counteract oxidative conditions. Similar responses were found in *Q. pubescens*, although the negative impact of both factors was less efficiently faced than in the sympatric *Q. ilex*. In *Q. robur*, high O₃ concentrations and severe drought induced a partial rearrangement of the phenylpropanoid pathways. These antioxidative mechanisms were not able to protect the cell structure (as confirmed by ROS accumulation) suggesting that *Q. robur* showed a lower degree of tolerance than the other two species.

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1. Introduction

Evidence for changing climate, associated with higher atmospheric concentrations of greenhouse gases, continues to increase. The years 2014 and 2015 are currently considered the warmest years in Europe since instrumental records began, *i.e.* >1.1 °C warmer than the pre-industrial level (EEA, 2017). For these years, the exceptional heat covered the whole summertime with mean precipitation (June to August) significantly decreased by up to 20 mm per decade. The series of summer heatwaves affecting Europe since 2003 has also contributed to several intense tropospheric ozone (O₃) episodes. In 2015, 18 of the 28 states of the European Union (EU) and four other European countries outside the EU registered concentrations above the EU O₃ target value for the protection of human health (EEA, 2017).

Due to favorable meteorological conditions, both drought and O₃ are very likely to occur simultaneously. As a general rule, seasonal drought is typically associated with high insolation, and such conditions are conducive to the photo-oxidative formation of high O₃ levels (Butkovic et al., 1990). In addition, a rise in temperature significantly increases the emission rates of most biogenic volatile organic compounds that can contribute to O₃ production (Avery, 2006). Under drought, plants usually suffer from the impairment of many physiological and biochemical processes, such as (i) alteration of photosynthetic performance, (ii) cell dehydration, (iii) high production of reaction oxygen species (ROS) and, finally, (iv) early senescence and/or leaf necrosis (Chaves et al., 2003). Similar effects have also been attributed to O₃ (Cotrozzi et al., 2017a; Jolivet et al., 2016). A combination of drought and O₃ can induce responses considerably different from those observed when each stressor is applied independently (Bohler et al., 2015). Interestingly, the effects of drought and O₃ can be antagonistic, so that a simultaneous occurrence may be partially beneficial to plants. The most common combined response, in fact, is that drought mitigates the negative effects of O₃, basically by closing stomata and thus reducing O₃ uptake into the plant (Pollastrini et al., 2013; Gao et al., 2017). However, other results suggest that drought can exacerbate O₃ damage: Alonso et al. (2014) reported that the combination of both stressors caused further decreases in accumulated aboveground biomass in two subspecies of *Quercus ilex*. It appears that the combination of drought and O₃ is highly dependent on (i) the severity and length of occurrence of both stress factors and (ii) the balance between stomatal O₃ uptake (*i.e.*, Phytotoxic O₃ Dose, POD) and detoxification capacity of foliar cells (Dizengremel et al., 2013; Bohler et al., 2015).

Some studies have investigated the effects of combined drought and O₃ exposure on plant metabolism, especially in trees (see also Pollastrini et al., 2013; Cotrozzi et al., 2016; Yuan et al., 2016; Gao et al., 2017; Cotrozzi et al., 2017b). However, none of them investigated antioxidant molecules and/or physiological mechanisms. Whereas O₃ itself induces production of ROS and leads to a strong ROS accumulation, physiological responses to drought mostly use ROS as internally produced signalling molecules (Reddy et al., 2004), and severe drought may lead to photo-oxidative stress (Czarnocka and Karpiński, 2018). Consequently, accumulation of ROS is likely to be considerably higher during O₃ stress, and more closely located to chloroplasts under drought stress. Recently, Cotrozzi et al. (2017b) documented that hydrogen peroxide (H₂O₂) and superoxide anion (O₂⁻) were directly involved in the O₃-oxidative burst induced by an intense episode of O₃ exposure (200 ppb for 5 h) in three-year-old *Q. ilex* saplings. By contrast, H₂O₂ content did not change in plants subjected to drought (20% of the effective daily evapotranspiration, for 15 days). Such differences in ROS extent dynamics in relation to the stress factor suggested a complex network of events in signal transduction, involving other molecules (*e.g.*, salicylic and jasmonic acid) and processes (*e.g.*, proline biosynthesis).

Oaks (belonging to the genus *Quercus*) are widely distributed trees within the Mediterranean area and are able to cope with several environmental stressors due to the high plasticity of their phenotypic and physiological traits (Cotrozzi et al., 2016). Holm oak (*Q. ilex*) is likely

the most widely studied Mediterranean evergreen tree species and has been defined as “drought avoidant” (Bussotti et al., 2002) and “O₃-tolerant” (Cotrozzi et al., 2018a; Hoshika et al., 2018). Downy oak (*Q. pubescens*) is a typical Mediterranean deciduous tree distributed in Southern Europe and has been defined as “drought-” (Curtu et al., 2011) and “O₃-tolerant” (Cotrozzi et al., 2018a; Hoshika et al., 2018). Pedunculate oak (*Q. robur*) is one of the basic species in deciduous broadleaved forests of Europe and has been defined as “moderately drought-tolerant” (Vranckx et al., 2014) and “O₃-sensitive” (Hoshika et al., 2018).

The aim of the present study was to assess the combined effects of drought and O₃ exposure on the antioxidant metabolism of three oak species showing different water use strategies and O₃ sensitivities, exposed for one growing season to three levels of water availability and three levels of O₃ in an O₃ Free Air Controlled Exposure (FACE) facility. Specifically, we asked the following questions: (i) How much ROS are induced by realistic O₃ and water stress levels? (ii) Which antioxidant mechanisms are activated in response to individual stresses and to the combination of the stressors at different intensities? (iii) Are metabolic responses markedly species-specific? (iv) Are antioxidative metabolism and stomatal uptake of O₃ correlated? We postulated a protective effect of drought against O₃ and that the interactive effects of both factors may depend on plant species. In particular, we hypothesized that the evergreen tree species (which usually inhabits limiting environments) will have a greater tolerance to drought and O₃ exposure than the deciduous ones (characterized by shorter leaf lifespan), due to its stronger need to protect its long-lived leaves from different environmental cues. In a previous work, Cotrozzi et al. (2016) demonstrated that *Q. ilex* was able to successfully cope with several stressors due to the high plasticity of morpho-anatomical, physiological and biochemical traits.

2. Materials and methods

2.1. Plant material and experimental design

At the beginning of autumn 2014, two-year-old saplings of *Q. ilex*, *Q. pubescens* and *Q. robur* were transferred from nearby nurseries to the O₃-FACE facility of Sesto Fiorentino, Florence, Italy (43°48′59″N, 11°12′01″E, 55 m a.s.l.), where the experimental activities were conducted. The plants were established into 10-L pots containing peat:sand:nursery soil (1:1:1 in volume) and maintained under field conditions until the beginning of the treatment. Uniform-sized plants were selected and grown under the combination of three levels of O₃ (1.0, 1.2 and 1.4 times the ambient air concentration, denoted as AA, 1.2 × AA and 1.4 × AA, respectively) and three levels of water irrigation [100, 80 and 42% of field capacity on average, denoted as WW (well watered), MD (moderate drought) and SD (severe drought), respectively] from 1st June to 15th October 2015 (4.5 months). A detailed description of the O₃ exposure methodology is available in Paoletti et al. (2017). The maximum hourly ozone concentrations were 93 ppb in AA, 111 ppb in 1.2 × AA and 123 ppb in 1.4 × AA, respectively, throughout the experimental period. AOT40 (Accumulated exposure Over Threshold of 40 ppb) values during the experimental period were 17.8 ppm h, 29.7 ppm h and 40.3 ppm h in AA, 1.2 × AA and 1.4 × AA, respectively. Biomass results from this experiment were used for assessing O₃ risk in a previous paper (Hoshika et al., 2018), where further details on O₃ metrics are also available. The amount of irrigation was related to the soil field capacity, *i.e.* the maximum volume of water that was retained into the soil of the pots [volumetric soil water content was measured in the root layer by EC-5 soil moisture sensors equipped with an EM5b data logger, (Decagon Devices, Pullman, WA, USA), Hoshika et al. (2018)]. Three replicated plots (5 × 5 × 2 m) were assigned to each O₃ treatment, with three plants per each combination of species, O₃ level and water irrigation. At the end of the experiment, the first mature (fully expanded) top leaves of all three plants per plot (one leaf with 5th to 8th order per plant) in each O₃ × irrigation

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