Environmental Pollution 226 (2017) 104–117

Contents lists available at ScienceDirect

Environmental Pollution

journal homepage: www.elsevier.com/locate/envpol

Arbuscular mycorrhiza formation and its function under elevated atmospheric O_3: A meta-analysis☆

Shuguang Wang [a,*], Robert M. Augé [b], Heather D. Toler [b]

[a] Department of Environmental Science and Engineering, Beijing University of Chemical Technology, Beijing, 100029, China
[b] Department of Plant Sciences, University of Tennessee, Knoxville, TN 37996, USA

ARTICLE INFO

Article history:
Received 6 September 2016
Received in revised form
22 March 2017
Accepted 28 March 2017
Available online 12 April 2017

Keywords:
Arbuscular mycorrhiza
Elevated O_3
Plant biomass
Yield
Mycorrhizal colonization rate (MCR)

ABSTRACT

We quantitatively evaluated the effects of elevated O_3 on arbuscular mycorrhiza (AM) formation and on AM role in promoting plant growth in regard to several moderating variables (O_3 levels, O_3 exposure duration, plant types, AM fungi family, and additional stress) by means of meta-analysis of published data. The analysis consisted of 117 trials representing 20 peer-reviewed articles and 16 unpublished trials. Relative to non-mycorrhizal controls, AM inoculation did not significantly alter plant growth (shoot biomass, root biomass, total biomass and plant height) when O_3 concentration was less than 80 ppb, but at concentrations above 80 ppb symbiosis was associated with increases of 68% in shoot biomass and 131% in root biomass. AM effects on plant growth were affected by the duration of O_3 exposure but did not differ much with AM fungi taxa or plant type. AM symbiosis has also led to higher yields under O_3 stress, relative to the non-mycorrhizal plants, and the AM effects have been more pronounced as O_3 concentration increases. As with biomass, AM effects on yield have been affected by the duration of O_3 exposure, with the greatest increase (100%) occurring at 61–90 d. AM-induced promotion of yield differed with fungal species but not with plant type or other abiotic stress. Colonization of roots by AM fungi has been negatively affected by elevated O_3 compared to ambient O_3; total mycorrhizal colonization rate (MCR), arbuscular MCR, vesicular MCR and hyphal coil MCR declined as O_3 levels rose. AM colonization rates were affected by duration of O_3 exposure, plant type, AM fungal taxa and other concurrent stresses in most cases. The analysis showed that AM inoculation has the potential to ameliorate detrimental effects of elevated O_3 on plant growth and productivity, despite colonization rates being negatively affected by elevated O_3.

1. Introduction

Elevated atmospheric O_3 has become one of the world's major environmental problems. Although the increasing trend in O_3 levels has leveled off or reversed in some regions (IPCC, 2013), surface O_3 concentrations continue to increase in most regions in recent years, especially in China, Pakistan and India (Wang et al., 2007). The Intergovernmental Panel on Climate Change (IPCC) (2013) predicted that ambient O_3 levels may rise up to 80 ppb with peaks occasionally exceeding 200 ppb. Therefore, O_3 remains the most important global phytotoxic air pollutant (Ashmore, 2005; Van Dingenen et al., 2009). As a strong oxidant, elevated O_3 can cause substantial negative impacts on plant growth and productivity, related to decreased photosynthetic rate and physiological activity, heavy leaf injury and senescence, which often lead to great economic loss (Ismail et al., 2014; Wang et al., 2015). It has been revealed that O_3 pollution led to decreased yields of maize and soybean of roughly 5% and 10%, respectively, from 1980 to 2011, costing approximately $9 billion annually in the USA (McGrath et al., 2015). Total global agricultural losses (wheat, maize and soybean) are projected to be $12–21 billion to $17–35 billion annually from 2000 to 2030 (Avnery et al., 2011). Nawahda and Yamashita (2013) estimated, based on AOT40 (Accumulated Exposure Over the Threshold of 40 ppb), that the relative yield loss induced by ozone in wheat and soybean crops in China will be ca. 30.5% and 19.0%, respectively, in the year 2020. Since increase in O_3 concentration appears unavoidable, it is desirable to explore how to reduce negative effects of elevated O_3 on crops.

Arbuscular mycorrhizal (AM) fungi belong to the phylum

☆ This paper has been recommended for acceptance by Dr. Hageman Kimberly Jill.

* Corresponding author.
E-mail address: shgwang2013@126.com (S. Wang).

http://dx.doi.org/10.1016/j.envpol.2017.03.074
0269-7491/© 2017 Published by Elsevier Ltd.

Glomeromycota and colonize the roots of many terrestrial plants (Smith and Read, 2008). AM symbioses have attracted much attention due to their many positive impacts on plants and soils (Koltai and Kapulnik, 2010). The fungi often increase plant growth and nutrient uptake, as well as enhance host plants' resistance to biotic stress (pathogens) and abiotic stress (drought, salinity, heavy metals, organic pollutants) (Fulton, 2011). In field trials, mycorrhizal colonization rate has been positively correlated with crop yield and P uptake, with yield increases exceeding 30% (Lekberg and Koide, 2005; Pellegrino et al., 2015). The role of AM symbiosis in mediating plant response to atmospheric change may be an important consideration in predicting effects of atmospheric pollutants on plants in agricultural lands and managed ecosystems (Shafer and Schoeneberger, 1991).

AM fungi are obligate biotrophs and, in the absence of the host plant, they are able to produce limited mycelial growth that aborts after a few days (Parniske, 2008). Proliferation of AM fungi completely depends on food supply from host plants. Because O_3 stress reduces plant photosynthesis and allocation of photosynthate to roots (Morgan et al., 2003; Feng et al., 2008), less carbon may be available for AM fungi, which may likely affect the interaction between symbionts. Colonization rates have been observed to decrease (McCool and Menge, 1984; Wang et al., 2015) or remain mostly unchanged (Duckmanton and Widden, 1994; Wang et al., 2011) under elevated O_3. AM stimulation of plant growth has decreased (McCool and Menge, 1984; Wang et al., 2011) or increased (Brewer and Heagle, 1983) with ozone exposure. It is necessary to more clearly understand the effects of AM inoculation on plant growth and productivity to maximize its use in agriculture under elevated O_3.

AM improvement of plant growth and productivity relies on adequate root colonization. The benefits of the association have been related to the extent of colonization (Abbott and Gazey, 1994), and reduced mycorrhizal functioning has been generally attributed to low root infection rates. Zangaro et al. (2007) found that there was positive correlation between the degree of plant responses to AM inoculation and the percentage of root colonized by AM fungi. AM formation is a complex process, involving spore germination under favorable conditions, hyphal growth into roots approach and penetration into the cortex where fungal organs form. This process can be affected by environmental conditions (e.g. soil pH, moisture, temperature, nutrients) and anthropogenic factors (e.g. environmental pollution, cultivation practices) (Entry et al., 2002). Elevated O_3 can affect AM fungi colonization of roots but results are not consistent. For example, in sugar maple (*Acer saccharum*), elevated O_3 had a subtle effect on overall levels of AM colonization but caused an increase in the frequency of vesicles, hyphal coils, and internal mycelia and a decrease in arbuscular frequency (Duckmanton and Widden, 1994). In snap bean (*Phaseolus vulgaris*), however, elevated O_3 slightly decreased overall and arbuscular colonization rates and more substantially increased vesicular colonization as well as decreased hyphal colonization (Wang et al., 2011).

Meta-analysis provides a quantitative method for integrating the results of many experiments to answer broad questions, taking into account variation in replication and precision among studies and providing estimates for experimental effects and relationships among variables (Gurevitch and Hedges, 1999; Borenstein et al., 2009). Meta-analysis has been used to test responses of AM symbiosis to NaCl stress (Augé et al., 2014) and N, P and CO_2 fertilization (Treseder, 2004), to examine AM influence on zinc nutrition in crop plants (Lehmann et al., 2014) and stomatal conductance under varying water regimes (Augé et al., 2015), and to test dynamics of AM symbiosis in heavy metal phytoremediation (Audet and Charest, 2007). In this study, we used meta-analysis to synthesis available data and discuss effects of elevated O_3 on AM formation and its influence on plant growth, aiming to answer to the following questions:

(1) Does AM inoculation increase plant growth under elevated O_3?
(2) Does AM inoculation increase crop yield under elevated O_3?
(3) Is AM formation negatively affected by elevated O_3?
(4) Are above effects related to O_3 levels, O_3 exposure duration, plant types and AM fungal taxa?

2. Materials and methods

2.1. Data collection

Literature searches were conducted through September 20, 2015 in ISI Web of Science (http://apps.webofknowledge.com) and Google Scholar (http://scholar.google.com) using the following key terms: [“arbuscular mycorrhiza*” OR “endomycorrhiza*” OR “vesicular-arbuscular*” OR “AM symbiosis” OR “AM fungi” OR “VAM symbiosis” OR “VAM fungi” OR “VA mycorrhiza*”] AND [O_3 OR ozone]. Papers published in Chinese were searched in China Knowledge Resource Integrated (CNKI) Database (http://www.cnki.net). 37 unique articles were located. Our own unpublished data were also included. After examination of these articles, 17 were excluded because they did not meet our inclusion criteria: measurements were not provided variables about plant growth (shoot biomass, root biomass, total biomass and plant height), plant productivity (yield and pod number) or AM formation (total mycorrhizal colonization rate (MCR), vesicular MCR, arbuscular MCR, hyphal coil MCR); AM or non-AM treatments were not included; O_3 treatments were lacking.

We identified 20 articles that met our screening criteria (citation list and details of primary studies provided in Supplementary Material 1). Papers spanned 30 years and were in English and Chinese.

Treatment means, standard deviations (SD) (where available) and sample sizes (n) were collected for each trial in each article, for plant growth parameters (shoot biomass, root biomass, total biomass, plant height), plant productivity (yield and pod number) and AM formation (total MCR, arbuscular MCR, vesicular MCR, hyphal coil MCR). Data presented in graphs were digitized using WebPlotDigitizer (Rogatgi, 2011). When multiple observations at different times were reported for growth or MCR measures for one trial, the final measurement was used in the analysis. Multiple treatments or host/symbiont combinations from one article were treated as independent studies and represented an individual unit (termed “trial” subsequently) in the meta-analysis. For example, Miller et al. (1997) examined the effects of four O_3 concentrations on two AM treatments (AM fungi and AM fungi + *Rhizobium leguminosarum*), which resulted in eight trials for the meta-analysis from that article. Yoshida et al. (2001) investigated the impact of two O_3 concentrations on a host plant species *Elymus glaucus* from two locations having contrasting ozone histories, resulting in four trials from that article. Although designating multiple trials from one article has the disadvantage of increasing the dependence among trials that for the purposes of meta-analysis are assumed to be independent (Gurevitch and Hedges, 1999), the greater number of trials increases statistical power (Lajeunesse and Forbes, 2003). It also enables the analysis of moderator variables; the ability to examine influence of AM inoculation or elevated O_3 under different experimental conditions is lost when trials representing moderators are combined. This approach has been used commonly in mycorrhizal and plant biology meta-analyses (e.g. Morgan et al., 2003; Wittig et al., 2007; Hoeksema et al., 2010; Chandrasekaran et al., 2014). We derived 117 trials from the 20 articles and 16 unpublished trials. AM fungi were represented by 11 species and 2 genera and indigenous AM fungi, and host plants by 10 species and 10 genera.