Water Air Soil Pollut (2016) 227: 33
DOI 10.1007/s11270-015-2715-9

A Review Study on Past 40 Years of Research on Effects of Tropospheric O_3 on Belowground Structure, Functioning, and Processes of Trees: a Linkage with Potential Ecological Implications

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Received: 30 June 2015 / Accepted: 27 November 2015 / Published online: 23 December 2015

Abstract Woody plants constitute a great sink of carbon storage, mitigating thus the greenhouse effect phenomenon. They are considered key players in ecosystems, and among others, they help in decreasing soil erosion and in maintaining soil moisture. Over the last decades, researches have shown negative effects of the ambient ozone (O_3) on many woody species, not only on canopy but also on belowground part of trees. Negative effects of elevated O_3 (eO_3), which usually refers to any O_3 dosages above the current ambient levels, on belowground structure, function, and processes may have consequences to ecosystem sustainability. We reviewed reports of research published over the past 40 years and dealing with woodies belowground response to eO_3. eO_3 induces changes in C dynamics into plants and alterations in their metabolism accordingly, as a result of different strategies followed by the trees in order to compensate with eO_3 stress effects. In these strategies, phenolics seem to have a detrimental role in shoot/root allometry. Root and soil chemical composition can be also influenced, threatening thus the soil biodiversity, soil fertility, and nutrient cycling. Elevated O_3 impact is discussed with linkage to other potential ecological consequences.

Key Message Ozone impacts the root dynamics of trees and forest soil. Ecological implications.

Note This review did not always follow the interpretation of the authors of the original publications, but it was written mostly based on the results of the statistical analysis of the data.

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Keywords Air pollution · Carbon cycle · Changing environment · Climate change · Ecosystems · Ozone

1 Introduction

Nowadays ground-level ozone (O_3) is a well-known threat to plants (e.g., Matyssek et al. 2012), and it has been characterized as a novel plant "pathogen" (Lorenzini and Saitanis 2003). Current evidence shows that O_3 threatens cultivated (Emberson et al. 2009; Tiwari and Agrawal 2010; Feng et al. 2008, 2015; Agathokleous et al. 2015a) and wild (Temple 1989; Bermejo et al. 2003; Manning et al. 2003; Agathokleous et al. 2015b) plants. Although O_3 levels are currently high enough to damage plants (e.g., Emberson et al. 2009) and some species at risk have been characterized as ozonophobic (Agathokleous et al. 2015b), the problem remains unsolved and seems to be worsening (Yamaji et al. 2008). Data analysis of 214 European monitoring sites for air pollutants during the previous decade shows that O_3 concentrations are still increasing in the cities (Sicard et al. 2013). In addition, O_3 is present at high concentrations in nonindustrial areas or remote agricultural regions due to in situ formation and its transportation (Kleanthous et al. 2014; Saitanis et al. 2015a) through the aerial mass exchanges between regions and countries (Ganev et al. 2014). In our previous review study, we found that 378 wild plant species were damaged and almost 100 response variables were affected by eO_3 (Agathokleous et al. 2015b).

Many reviews have documented that elevated O_3 dosages adversely affect woody species (e.g., Karnosky et al. 2005; Paoletti and Grulke 2005; Valkama et al. 2007; Wittig et al. 2009; Ainsworth et al. 2012; Agathokleous et al. 2015b; Vaultier and Jolivet 2015) by impacting plenty of phenological characteristics and physiological functions (Karnosky et al. 2005; Yamaguchi et al. 2011; Matyssek et al. 2012; Koike et al. 2013). This impact is often carried-over, worsening, thus, the plant vigor over time (e.g., Muller et al. 1996; Andersen and Scagel 1997; Oksanen and Saleem 1999; Le Thiec and Manninen 2003).

Roots are the "hidden" half of plants and play a crucial role in forest sustainability under the changing environment (e.g., Eshel and Beeckman 2013; Matyssek et al. 2012; 2013). It has been supported that O_3 does not affect only the aboveground part of the plant but also—indirectly—the belowground (Andersen 2003; Karnosky et al. 2005; Matyssek et al. 2012; 2013; Wang et al. 2015a). Such negative O_3 effects on rhizosphere may have implications in ecosystem sustainability in near future. Although numerous reviews have dealt with O_3 effects on trees, the majority of them focus on the aboveground part of the trees and only very few of them examine its effect on belowground (e.g., Wittig et al. 2009). The available review publications include only a limited number of studies on tree species or they include studies from one or very few geographical regions though (e.g., Chappelka and Samuelson 1998; Grantz et al. 2006; de Bauer and Hernandez-Tejeda 2007; Huttunen and Manninen 2013). It is notable that there is not an extensive review hitherto focusing on the O_3 effects on belowground of trees and also to other issues related with ecological processes.

By composing this review, we aim to give a holistic insight on the current knowledge on O_3 impact on belowground environment of trees with linkage to ecological implications.

2 Overview of the Literatures

2.1 Survey of Literatures

We surveyed literature dealing with O_3 effects on woody plants from the scientific databases of Web of Science (Thompson-ISI, Philadelphia, PA, USA) and SilverPlatter (Ovid Technologies, New York, NY, USA). Additional attempt was made to trace missing publications by searching in Google search engine (Google Inc., CA, USA). A total of 358 publications was collected and surveyed, covering the period from 1973 to 2013. The surveyed publications were checked if belowground-related variables were studied, and if so, they were selected for review. Thus, 143 publications including results of belowground-related variables were reviewed.

2.2 Profile of Literatures

The selected 143 publications covered the period from 1974 to 2013. Some of the publications included more than one taxon (families, species, varieties, ecotypes, hybrids, clones), and some taxa were studied in different publications. Each taxon studied in a publication constitutes a case; if the same taxon was tested in more than one experiment in the same study, then each experiment constitutes different cases for that taxon. Thus, a total of

261 studied cases were finally reviewed. One hundred one (39 %) of these cases concern conifers, 157 (61 %) deciduous and 3 (1 %) shrubs. The total number of studied taxa was 73 (70 trees and 3 shrubs) belonging to 29 genera and 19 families. Twenty-three of the taxa (32 %) were conifers, and 44 (60 %) were deciduous trees.

As elevated O_3 (eO_3) exposure is considered any exposure to O_3 concentrations above the current ambient levels, with some exceptions where comparison was made between charcoal-filtered air and ambient air. Usually, the exposure lasted from several consecutive weeks within a growing season to two or more growing seasons, and for more than 6 h day^{-1}. Data and results of statistical analyses of eO_3 effect on dry root mass (RbM) were provided for 239 cases. In 95 (40 %) of the cases, statistically significant decrease of RbM was found, in 6 (3 %) increase and in 138 (58 %) neutral eO_3 effect. Data and statistical analyses of eO_3 effect on shoot/root ratio (S/R) were provided for 104 cases, of which 28 (27 %) found statistically significant increase, 5 (5 %) decrease, and 71 (68 %) neutral (i.e. statistically insignificant) effect.

3 Discussion

3.1 Response Variables

3.1.1 Root Biomass (RbM)

As mentioned before, the research findings about the root biomass are quite contradictory, with 40 % cases having reported eO_3-induced reduction in RbM and ~60 % having reported no effects. Often, under eO_3, the standing RbM (fine, intermediate, coarse, or total) is significantly smaller (Table 1). Such a reduction, when observed, is usually attributed to the fact that the growth of the roots depends on the photosynthates, and as the leaves are damaged, it is physical to produce less photosynthates and to partition even lesser to roots (Wittig et al. 2009). It seems that root production may be suppressed even if the foliage growth is not impacted (e.g., Karnosky et al. 1996). As already mentioned, when the O_3-mediated visible injury is present, the photosynthates are going to decrease; thus, the roots are going to be negatively impacted. But, as it seems, this is not a rule of thumb: significant reductions of C allocation to roots may happen even in absence (e.g., Kress and Skelly 1982; Gorissen et al. 1994; Shan et al. 1996; Matsumura 2001; Zhang et al. 2012), or in presence of minimal (Kress and Skelly 1982; Davis and Skelly 1992), of O_3-mediated visible leaf injury.

Almost 40 % of the cases found lessened RbM, albeit there was no clear sensitivity of particular species (Table 1). Based on experiments with five poplar ecotypes, it has been reported that the faster growing clones (more productive) had greater growth reduction due to eO_3 than slower growing ones (Dickson et al. 1998). However, in two different studies, five (Kelly et al. 1993) or three (Horton et al. 1990) loblolly pine families exhibited a similar response to eO_3. Nevertheless, the direction (positive or negative) and the size of the O_3 impact to RbM, when observed, has been reported to differ among taxa and even within species (e.g., ecotypic variation) under the same environmental conditions (e.g., Kress and Skelly 1982; Paakkonen et al. 1993; Oksanen and Saleem 1999; Landolt et al. 2000; Saleem et al. 2001; Yamaji et al. 2003; Nikolova et al. 2010; Hoshika et al. 2013a) or under differed environmental conditions (Landolt et al. 2000; Oksanen et al. 2001).

The research materials seem to confound the plant responses to eO_3: Jensen and Dochinger (1974) found that while terminal cuttings of the parental trees showed reduced RbM after exposure to eO_3 (150 nmol mol^{-1} × 6 weeks (5 days $week^{-1}$) × 8 h day^{-1}), there was no significant response of basal cuttings under the same conditions. Furthermore, there could be some variation in responses to eO_3 between seedlings and mature individuals. Materials at a very young stage (e.g., seedlings) may prevent and/or overcome negative effects by eO_3, and, although at the beginning may show a tremendous belowground response, this response may be eliminated or minimized later - while mature trees may show high response (Samuelson and Edwards 1993; Edwards et al. 1994; Samuelson and Kelly 1996). For example, eO_3 affected the N content in fine and coarse roots in mature trees of red oak but not in seedlings (Kelly et al. 1995). As a result, O_3 effects on seedlings may underestimate the O_3 impact on adult trees with mature physiology.

3.1.2 Root Classes

Roots are the foundations of the aboveground part of the plants because they support them mechanically (i.e., coarse roots) and they provide them with water and nutrients (i.e., fine roots). Fine roots constitute an interface between plants and soils and their role in forest carbon (C), nutrient, and water cycles is important

Table 1 Effect of ozone on root biomass (or on roots classes) for the studied cases; each taxon or each experiment studied in each publication constitutes a separate case (see Sect. 2)

Taxa	Ozone effect		
	Positive (increased)	Negative (decreased)	Neutral
Altingiaceae			
Liquidambar styraciflua		Kress and Skelly (1982) [2; s]	
Anacardiaceae			
Rhus trilobata			Temple (1989) [1; s]
Aquifoliaceae			
Ilex integra			Zhang et al. (2012) [1; s]
Betulaceae			
Alnus incana			Mortensen and Skre (1990) [1; s]
Betula ermanii			Hoshika et al. (2013a) [1; s]
B. papyrifera		Keane and Manning (1988) [1; s]	Keane and Manning (1988) [1; s]
B. pendula	Yamaji et al. (2003) [1; S]	Paakkonen et al. (1993) [2; s]; Kytoviita et al. (1999) [1; s]; Oksanen and Saleem (1999) [2; S]; Saleem et al. (2001) [1; S]; Karlsson et al. (2003) [1; S]	Paakkonen et al. (1993) [5; s]; Paakkonen and Holopainen (1995) [1; s]; Paakkonen et al. (1996) [2; S]; Paakkonen et al. (1997) [1; S]; Paakkonen et al. (1998a) [4; S]; Oksanen and Saleem (1999) [1; S]; Saleem et al. (2001) [1; s]; Riikonen et al. (2004) [2; M]; Kasurinen et al. (2005) [2; M]
B. platyphylla var. japonica	Hoshika et al. (2013a) [1; s]	Matsumura (2001) [3; s]	
B. pubescens			Mortensen (1995) [1; s]
B. sp		Mortensen and Skre (1990) [1; s]	
Cupressaceae			
Chamaecyparis obtusa			Matsumura (2001) [2; s]
Cryptomeria japonica		Matsumura (2001) [4; s]	
Sequoiadendron giganteum			Temple (1988) [1; s]
Fabaceae			
Caesalpinia echinata			Moraes et al. (2006) [1; s]
Fagaceae			
Fagus crenata	Watanabe et al. (2010) (fine) [1; s]	Izuta et al. (1996) [1; s]; Matsumura (2001) [2; s]; Yonekura et al. (2001) [1; s]; Yamaguchi et al. (2007a [1; s], Yamaguchi et al. 2007b [1; s]); Watanabe et al. (2010) (coarse) [1; s]	

Table 1 (continued)

Taxa	Ozone effect		
	Positive (increased)	Negative (decreased)	Neutral
F. sylvatica		Winkler et al. (2009) [1; S]	Kozovits et al. (2005a) [2; s]; Thomas et al. (2006) [1; s]; Nikolova et al. (2010) [1; M];
Quercus glauca			Zhang et al. (2012) [1; s];
Q. mongolica			Matsumura (2001) [1; S]
Q. petraea		Broadmeadow and Jackson (2000) [1; s]	
Q. phellos			Kress and Skelly (1982) [2; s]
Q. rubra		Davis and Skelly (1992) [1; s]; Edwards et al. (1994) [1; s]	Samuelson and Edwards (1993) [1; s]; Samuelson (1994b) [1; s]; Kelly et al. (1995) [1; s]
Q. serrata		Watanabe et al. (2007) [1; s]	
Hamalidaceae			
Liquidambar formosana		Zhang et al. (2012) [1; s]	
Lauraceae			
Cinnamomum camphora			Zhang et al. (2012) [1; s]
Neolitsea sericea			Zhang et al. (2012) [1; s]
Magnoliaceae			
Liriodendron chinense		Zhang et al. (2012) [1; s]	
L. tulipifera	Loats and Rebbeck (1999) [1; s]		Kress and Skelly (1982) [1; s]; Chappelka et al. (1985) [1; s]; Chappelka et al. (1988) [1; s]; Tjoelker and Luxmoore (1991) fine or coarse [1; s]; Davis and Skelly (1992) [1; s]; Cannon et al. (1993) [1; s]
Myrtaceae			
Eucalyptus globulus		Pearson (1995) [1; s]	
Oleaceae			
Fraxinus americana		Kress and Skelly (1982) [2; s]	
F. excelsior			Broadmeadow and Jackson (2000) [1; s]
F. pensylvanica			Kress and Skelly (1982) [2; s]; Loats and Rebbeck (1999) [1; s]
Pinaceae			
Abies firma		Matsumura (2001) [1; S]	
A. fraseri			Tseng et al. (1988) [1; s]; Seiler et al. (1994) [1; s]

Table 1 (continued)

Taxa	Ozone effect		
	Positive (increased)	Negative (decreased)	Neutral
A. homolepis		Matsumura (2001) [2; S]	
A. veitchii		Matsumura (2001) [2; S]	
Larix kaempferi		Matsumura (2001) [2; s]	
Picea abies		Matsumura (2001) [1; S]	Van Den Driessche and Langebartels (1994) [1; s]; Karlsson et al. (1995) [1; s]; Lippert et al. (1996) [1; s]; Karlsson et al. (1997) [1; s]; Kainulainen et al. (2000) [1; s]; Utriainen and Holopainen (2001a) [1; s]; Utriainen and Holopainen (2002) [1; s]; Kozovits et al. (2005a) [2; s]; Thomas et al. (2005) [1; S]; Nikolova et al. (2010) [1; M];
Picea sitchensis			Bambridge et al. (1996) [2; s]
P. rubens	Taylor et al. (1986) [1; s]	Amundson et al. (1991) [1; s]	
Pinus armandii		Shan et al. (1995) [1; s]; Shan et al. (1996) [1; s]	
P. densiflora		Matsumura (2001) [4; S]; Nakaji and Izuta (2001) (fine) [1; s]	Nakaji and Izuta (2001) (coarse) [1; s]; Nakaji et al. (2004) (fine + coarse) [1; s]
P. halepensis		Kytoviita et al. (2001) [1; s]; Le Thiec and Manninen (2003) [1; s]	Kytoviita et al. (1999) [1; s]
P. jeffreyi		Temple (1988) [1; s]	
P. mugo		Diaz de Quijano et al. (2012) [1; S]	
P. ponderosa		Andersen et al. (1991) [1; s]; Andersen and Scagel (1997) [1; s]; Scagel and Andersen (1997) [1; s]; Andersen et al. (1997) [1; s]; Grulke et al. (1998) (peak root growth in the spring,) [1; M]	Grulke et al. (1998) (end of growing season) [1; M]
P. rigida		Kress and Skelly (1982) [1; s]	Kress and Skelly (1982) [1; s]
P. sylvestris	Dueck et al. (1998), saplings fine [1; s]		Anttonen and Karenlampi (1995) [1; s]; Dueck et al. (1998), coarse [1; S]; Broadmeadow and Jackson (2000) [1; s]; Kainulainen et al. (2000) [1; s]; Utriainen et al. (2000) [1; s]; Utriainen and Holopainen (2001b) [1; s]; Utriainen and Holopainen (2002) [1; s]
P. taeda		Kress and Skelly (1982) [1; s]; Edwards et al. (1990) [1; s]; Horton et al. (1990) [1; s]; Tjoelker and Luxmoore (1991) coarse [1; s]; Edwards et al. (1992a),	Kress and Skelly (1982) [3; s]; Adams et al. (1988) [5; s]; Adams et al. (1990) [5; s]; Edwards et al. (1991) [1; s]; Tjoelker and Luxmoore (1991)

Table 1 (continued)

Taxa	Ozone effect		
	Positive (increased)	Negative (decreased)	Neutral
		fine [1; s]; Kelly et al. (1993), fine [1; s]; Estes et al. (2004) [2; s]	fine [1; s]; Edwards et al. (1992a) coarse [1; s]; Kelly et al. (1993) fine [5; s] and coarse [6; s]
P. thunbergii			Matsumura (2001) [2; s]
P. uncinata		Diaz de Quijano et al. (2012) [1; S]	
P. virginiana			Kress and Skelly (1982) [2; s]
Platanaceae			
Platanus occidentalis		Kress and Skelly (1982) [1; s]	
Rosaceae			
Photinia × *fraseri*			Zhang et al. (2012) [1; s]
Prunus serotina		Davis and Skelly (1992) [1; s]; Neufeld et al. (1995) [1; s]; Kouterick et al. (2000) [1; s]	Samuelson (1994a) [1; s]; Loats and Rebbeck (1999) [1; s]
Salicaceae			
Populus deltoides × *nigra*		Dickson et al. (1998) [3; C]	Dickson et al. (1998) [3; C]
P. deltoides × *trichocarpa*		Jensen and Dochinger (1974) [1; terminal C]	Jensen and Dochinger (1974) [1; basal C]
P. maximoviczii		Matsumura (2001) [1; S]	
P. maximoviczii × *berolinensis*		Hoshika et al. (2013b) (fine and coarse) [1; C];	
P. maximowiczii × *P. nigra*		Bucker and Ballach (1992) [1; C]	
P. nigra		Bucker and Ballach (1992) [1; C]	
P. nigra × *maximowiczii*		Dickson et al. (1998) [1; C]	
P. tremuloides		Dickson et al. (2001) [1; C]; Karnosky et al. (1996) [2; C] and [1; s]; Volin and Reich (1996) low nitrogen availability [1; s]	Karnosky et al. (1992) [2; C]; Dickson et al. (2001) [1; C]; Karnosky et al. (1996) [2; C]; Volin and Reich (1996) high nitrogen availability [1; s]
P. tremuloides × *P. tremula*		Oksanen et al. (2001) [3; S]	Oksanen et al. (2001) [6; S]
P. tristis × *P. balsamifera cv. Tristis*		Tjoelker et al. (1993), unshaded [1; C]	Tjoelker et al. (1993), shaded [1; C]
Sapindaceae			
Acer rubrum			Davis and Skelly (1992) [1; s]; Samuelson (1994a) [1; s]
A. saccharum		Tjoelker et al. (1993) shaded [1; s]; Topa et al. (2001) [1; s]; Topa et al. (2004) [1; s]	Kress and Skelly (1982) [1; s]; Noble et al. (1992) [1; s]; Tjoelker et al. (1993) unshaded [1; s]; Gaucher et al. (2003) [1; s]

Table 1 (continued)

Taxa	Ozone effect		
	Positive (increased)	Negative (decreased)	Neutral
Theaceae			
Schima superba			Zhang et al. (2012) [1; s]
Ulmaceae			
Zelkova serrata		Matsumura (2001) [1; s]	Matsumura (2001) [1; s]

In brackets, the number of cases and the stage of plant material (*s* seedlings, *C* cuttings, *S* saplings, *M* mature trees) are shown, e.g., [2; s] indicates that, in the relevant publication, two cases with plants at the stage of seedlings were studied. The results are based on the single effects of O_3 in the final harvest of the experiments with the criterion of statistical significance set at significance level $\alpha = 0.05$. Where the data analyses results of total root biomass are not presented, the class of the presented impacted root is indicated next to the reference

(Lukac 2012). However, the impact of O_3 seems to be unequal among root classes.

In loblolly pine seedlings (Edwards et al. 1992a; Kelly et al. 1993), at the end of the third growing season, the fine root production was inhibited by twice ambient O_3 dosage; however, coarse root production was not inhibited. Similarly, in the same species, the reduction was almost double in fine roots than coarse roots at the end of the second growing season, not at the end of the third growing season (Edwards et al. 1991). In Japanese red pine (Nakaji and Izuta 2001) seedlings, exposed to ≈60 nmol mol^{-1} O_3 for 173 days (8 h day^{-1}), fine roots were decreased but not coarse roots. Such a phenomenon appeared in the same species, after being exposed to O_3 for two growing seasons, but only with simultaneous elevated soil N loading (Nakaji et al. 2004).

Unlike, there are other findings supporting a different response. In loblolly pine seedlings (Edwards et al. 1990) and northern red oak seedlings (Edwards et al. 1994), the coarse roots were impacted by twice ambient O_3 levels (one growing season) while fine roots were not. In aspen-birch mix, aspen-maple mix and pure aspen communities O_3 decreased coarse roots by 9–29 %, with the latter experiencing the largest decrease (King et al. 2005), while fine roots were not significantly affected. In Siebold's beech seedlings, after being exposed for some weeks to eO_3, fine roots were increased but coarse roots were decreased (Watanabe et al. 2010). In a study with European beech saplings, it was revealed that O_3 increased the proportion of fine roots up to a depth of 2 m, suggesting a stronger impairment of coarse compared to fine roots (Winkler et al. 2009).

3.1.3 Root Depth

In a study (Grulke et al. 1998) with mature trees of Ponderosa pine (*Pinus ponderosa* Douglas ex C. Lawson) in natural forest stands at three sites differing in anthropogenic O_3 exposure, it was found that, during the period of peak root growth in the spring, root biomass at the least polluted site was 6–14 times greater than that observed at the most polluted site. The roots were differently affected at different soil depths. There were no significant differences between the upper (0–20 cm) and middle (20–40 cm) soil horizon for either the fine or medium root biomass in the July sampling, but medium roots in the 0–20-cm soil horizon were significantly reduced relative to those in the 20–40-cm soil horizon (although only at the mostly polluted site) in September.

When the "vertical distribution" of fine and coarse roots of beech seedlings exposed to doubled O_3 concentrations (four growing seasons) was assessed down to 2 m in depth, O_3 affected neither the maximum rooting depth nor the standing biomass of coarse roots in the soil depth of 0–20 cm, but it strongly reduced it in the soil depths from 20 to 200 cm (Winkler et al. 2009).

3.1.4 Shoot/Root Allometry (S/R)

Root growth has been suggested as one of the most sensitive indicators of chronic exposure to O_3 (Heck et al. 1986; Cooley and Manning 1987; Karnosky et al. 1996). However, evidence indicates that the total RbM or the aboveground biomass, when used as a measure for quantifying O_3 effects may underestimate the impact of O_3 to the biomass of various tree species because, in fact, the impact on mass partitioning is imbalanced (e.g., Kress and Skelly 1982; Kouterick et al. 2000; Matsumura 2001; Karlsson et al. 2003; Thomas et al. 2005; Hoshika et al. 2013a). Newer reports have suggested that root or shoot biomass alone might be an inadequate variable to assess the O_3 effects (Novak et al. 2008; Zhang et al. 2012), and it should be fairly reasonable to measure the S/R rather than measure the shoot biomass or RbM alone. Specifically, the RbM may not differ between treatments, but the S/R may differ (e.g., Samuelson 1994a; Oksanen et al. 2001; Thomas et al. 2005; Hoshika et al. 2013a). The S/R can be altered by eO_3, even if O_3-induced visible injury in canopy is absent (Shan et al. 1996). Kelly et al. (1993) found greater foliage C storage and Karlsson et al. (2003) reported strongly reduced C allocation to roots by eO_3. The latter is in agreement with the finding of Coleman et al. (1995a, b) who reported significant reduction of ^{14}C allocated from mature source leaves to roots of plants of aspen clone treated with eO_3. Mature leaves of O_3-tolerant species, under eO_3, can maintain C allocation almost equal to, or greater than, counterpart leaves under O_3-free air (Coleman et al. 1995a, b). The sensitivity of C allocation to O_3 differs among species (Braun et al. 2004; Hoshika et al. 2013a) or ecotypes (Saleem et al. 2001; Yamaji et al. 2003) and may also depend on the growth stage of trees (Braun et al. 2004). The increase in S/R suggests that roots were stressed proportionately more than shoots (Matyssek et al. 1995; Chappelka and Samuelson 1998; Edwards et al. 1994).

Despite that in the literature the increased S/R has been prevailed as a general rule, this is not always confirmed. Our review shows that in 5 % of the cases, S/R was significantly reduced; in 27 % of the cases, it was significantly increased; and in 68 % of the cases, the S/R was not altered (Table 2). However, in about the half of the cases reporting no effect, the S/R ratio was increased although not statistically significantly.

The increase of S/R may result from (i) limited photosynthate production in the canopy with less C flux in the whole plant (Matyssek et al. 1995; Oksanen et al. 2001); (ii) more photosynthates remained in the leaves rather than partitioned to roots (Coleman et al. 1995a, b; Shan et al. 1995; Samuelson and Kelly 1996; Landolt et al. 1997); (iii) impaired phloem structure and function; and (iv) from plant strategies to maintain foliage rather than favor the replacement of the O_3-injured (Chappelka and Samuelson 1998; Davis and Skelly 1992; Landolt et al. 1997; Maurer and Matyssek 1997; Dickson et al. 2001). Enhanced S/R may also be associated with boosted foliar effective antioxidants, among which chlorogenic acid derivatives, defensive phenolics, etc. (Saleem et al. 2001; Yamaji et al. 2003). On the other hand, decrease in S/R is rarely observed and it can be confounded by water deficit stress (e.g., Tseng et al. 1988) or N availability (increased or decreased levels) in soil (e.g., Utriainen and Holopainen 2001b), as both had often been reported to decrease the S/R.

Yamaji et al. (2003) studied the physiological and chemical responses of 17 birch clones to eO_3 in open-field experiment (1.5–1.7 × ambient O_3 for two growing seasons) and found that in ten clones the S/R was decreased, in five clones it was increased, and in two clones it was unaffected. The variant S/R response was accordingly associated with three different strategies (previously suggested also by Saleem et al. 2001) of plants as well: (i) C allocation toward roots, by stomatal closure, and investment in low-cost foliar antioxidants to avoid and tolerate O_3 stress; (ii) inducible efficient high-cost antioxidants and boosted leaf production to maintain net photosynthesis; and (iii) high content of total phenolics, investment in low-cost antioxidants and distribution of N to leaves, and lower g_s, accordingly. Phenolics are important defense substances against stresses allowing plants to compensate for adverse terrestrial biotic and abiotic stress conditions (Karabourniotis et al. 2014). We underline the importance of phenolic compounds not only to understand the S/R but also to get a better understanding on the physiology of trees under O_3 stress.

Table 2 Effect of ozone on shoot:root allometry for the studied cases; each taxon or each experiment studied in each publication constitutes a separate case (see Sect. 2)

Taxa	Ozone effect		
	Positive (higher)	Negative (lower)	Neutral
Anacardiaceae			
Rhus trilobata			Temple (1989) [1; s]
Betulaceae			
Alnus incana			Mortensen and Skre (1990) [1; s]
Betula ermanii	Hoshika et al. 2013a [1; s]		
B. pendula	Matyssek et al. (1992) [1; C]; Matyssek et al. (1995) [1; C]; Landolt et al. (1997) [1; C]; Maurer and Matyssek (1997) [1; C]; Oksanen and Saleem (1999) [1; S]; Saleem et al. (2001) [1; S]; Matyssek et al. (2002) [1; s]; Karlsson et al. (2003) [1; S]	Paakkonen et al. (1998b) [1; S]; Yamaji et al. (2003) [1; S]	Paakkonen et al. (1993) [2; s]; Paakkonen and Holopainen (1995) [3; s]; Paakkonen et al. (1998a) [2; S]; Saleem et al. (2001) [1; S]; Riikonen et al. (2004) [2; s]
B. platyphylla var. japonica			Hoshika et al. (2013a) [1; s]
B. pubescens			Mortensen (1995) [1; s]
B. sp			Mortensen and Skre (1990) [1; s]
Fabaceae			
Caesalpinia echinata			Moraes et al. (2006) [1; s]
Fagaceae			
Fagus crenata	Yamaguchi et al. (2007a) [1; s]		Watanabe et al. (2010) [1; s]
F. sylvatica	Landolt et al. (2000) [1; s]		Kozovits et al. (2005b) [1; S]; Thomas et al. (2006) [1; s]; Winkler et al. (2009) [1; S]
Q. rubra	Edwards et al. (1994) [1; s]		Davis and Skelly (1992) [1; s]; Kelly et al. (1995) [1; s]
Magnoliaceae			
Liriodendron tulipifera			Chappelka et al. (1985) [1; s]; Chappelka et al. (1988) [1; s]; Tjoelker and Luxmoore (1991) [1; s]; Davis and Skelly (1992) [1; s]; Cannon et al. (1993) [1; s]; Loats and Rebbeck (1999) [1; s]
Oleaceae			
Fraxinus excelsior	Landolt et al. (2000) [1; s]		
F. pensylvanica			Loats and Rebbeck (1999) [1; s]
Pinaceae			
Abies fraseri			Tseng et al. (1988) [1; s]; Seiler et al. (1994) [1; s]
Picea abies	Kainulainen et al. (2000) [1; s]	Thomas et al. (2005) [1; S]	Lippert et al. (1996) [1; s]; Landolt et al. (2000) [1; s]; Utriainen and Holopainen (2001a) [1; s];

Table 2 (continued)

Taxa	Ozone effect		
	Positive (higher)	Negative (lower)	Neutral
			Utriainen and Holopainen (2002) [1; s]; Kozovits et al. (2005b) [1; S]
P. rubens			Taylor et al. (1986) [1; s]
Pinus armandii	Shan et al. (1995) [1; s]; Shan et al. (1996) [1; s]		
P. densiflora	Nakaji and Izuta (2001) [1; s]		
P. halepensis			Le Thiec and Manninen (2003) [1; s]
P. ponderosa	Andersen et al. (1997) [1; s]	Andersen et al. (2001) [1; s]	Andersen and Scagel (1997) [1; s]; Scagel and Andersen (1997) [1; s];
P. sylvestris			Anttonen and Karenlampi (1995) [1; s]; Kainulainen et al. (2000) [1; s]; Landolt et al. (2000) [1; s]; Utriainen and Holopainen (2000) [1; s]; Utriainen et al. (2000) [1; s]; Utriainen and Holopainen (2001b) [1; s]; Utriainen and Holopainen (2002) [1; s]
P. taeda		Tjoelker and Luxmoore (1991) [1; s]	Adams et al. (1988) [5; s]; Edwards et al. (1990) [1; s]; Horton et al. (1990) [1; s]; Edwards et al. (1991) [1; s]
P. uncinata	Diaz de Quijano et al. (2012) [1; S]		
Rosaceae			
Prunus serotina	Samuelson (1994a) [1; s]; Kouterick et al. (2000) [1; s]		Davis and Skelly (1992) [1; s]; Neufeld et al. (1995 [1; s]); Loats and Rebbeck (1999) [1; s]
Populus deltoides × nigra	Dickson et al. (1998) [1; C]		Dickson et al. (1998) [3; C]
P. nigra × maximowiczii	Dickson et al. (1998) [1; C]		
P. tremuloides			Dickson et al. (2001) [2; C]
Salicaceae			
Populus × euramericana	Matyssek et al. (1993b) [1; C]		
P. tremuloides × P. tremula	Oksanen et al. (2001) [4; S]		Oksanen et al. (2001) [5; S]
Sapindaceae			
Acer rubrum			Davis and Skelly (1992) [1; s]; Samuelson (1994a) [1; s]
A. saccharum			Topa et al. (2001) [1; s]

In brackets, the number of cases and the stage of plant material (*s* seedlings, *C* cuttings, *S* saplings, *M* mature trees) are shown, e.g., [2; s] indicates that, in the relevant publication, two cases with plants at the stage of seedlings were studied. The results are based on the single effects of O_3 in the final harvest of the experiments with the criterion of statistical significance set at significance level $\alpha = 0.05$. Where the data analyses results of total root biomass are not presented, the class of the presented impacted root is indicated next to the reference

The size of S/R alteration due to O_3 can differ among species growing under the same conditions (Samuelson 1994a; Landolt et al. 2000; Kozovits et al. 2005b; Zhang et al. 2012). When some taxa are grown in shading may exhibit a higher eO_3-induced increase in S/R (Landolt et al. 2000), compared with full-sun exposed, or others may have not light-dependent allometry (Topa et al. 2001). These findings suggest a species-specific response of S/R to eO_3.

Besides, no interactive effects of O_3 and the following factors on S/R have been reported: atmospheric CO_2 (Mortensen 1995; Lippert et al. 1996; Dickson et al. 1998, 2001; Utriainen et al. 2000; Riikonen et al. 2004; Kozovits et al. 2005b; Watanabe et al. 2010), simulated acid rain (SAR) (Chappelka et al. 1988; Edwards et al. 1990, 1991; Davis and Skelly 1992; Shan et al. 1995), mist (Taylor et al. 1986), watering treatment (Tseng et al. 1988; Beyers et al. 1992; Cannon et al. 1993; Lippert et al. 1996; Paakkonen et al. 1998a; Paakkonen et al. 1998b; Le Thiec and Manninen 2003), competition of trees with grasses (Andersen et al. 2001) and community composition (Kozovits et al. 2005b).

As a conclusion, it seems that alteration in S/R, under O_3 stress, may result from very complex processes and it is hitherto unknown and unpredictable if and at what direction and magnitude will occur.

3.1.5 Shoot-Root Feedback

The bulk of contents of dried roots are C compounds derived from photosynthesis and only a tiny amount is consisted of non-C compounds (Uren 2007). It seems that carbohydrates which are produced in leaves (through photosynthesis) are primarily partitioned to the nearby canopy tissues—to heal the O_3 induced damage to leaf tissues—and a smaller part of them is sent to the roots which are located quite away of the production point of carbohydrates. If the allocation of C to roots is diminished, then the root growth can be rapidly suppressed (Landolt et al. 1997; Diaz de Quijano et al. 2012).

In conditions of limited carbohydrate supply to roots, reduced uptake of ions can also be found (White 2012) because the root surface area becomes smaller and thus the absorption decreases (Horton et al. 1990). This may lead to less water and nutrient supply to shoot, resulting to reduced formation of new leaves (Hoshika et al. 2013b). At the same time, as the foliage area (or mass) is becoming proportionally higher than that of roots (Matyssek et al. 1992; Dueck et al. 1998), the foliage water potential (Ψ_p) seems to be limited by increasing shoot transpiration (*E*) (Dueck et al. 1998).

Another indirect shoot-root feedback response results from the correlation of photosynthetic C assimilation activity in canopy with the amount of extra-matrical hyphae (Kytoviita et al. 2001). Thus, any eO_3-induced suppression of mycorrhizae is expected to affect photosynthesis in canopy.

3.1.6 Ecophysiology at Canopy

In this review, we have focused on the effects of eO_3 on roots. However, it is the canopy that is exposed to O_3; roots of trees are never directly exposed to O_3, with a few exceptions where roots can be partly developed above the soil surface. Hence, whatever happens to roots is expected to be directly or indirectly related to the plant physiology processes in canopy.

Under eO_3, the demand for energy and C in leaves increases (Temple 1988; Kelly et al. 1993; Samuelson and Kelly 1996; Dickson et al. 2001), with amplified 2-(phosphonooxy)acrylic acid carboxylase (*PEPc*) activity, malate levels (Landolt et al. 1997) and antioxidants (Yamaji et al. 2003), due to a need for injury compensation, repair process and detoxification (Schier 1990; Friend et al. 1992; Kelly et al. 1993; Landolt et al. 1997; Maurer and Matyssek 1997; Topa et al. 2001; Yamaji et al. 2003). These reactions will eventually lead to less available C for the roots. Some of these reactions concern morphological characteristics such as number of leaves (Mortensen and Skre 1990), leaf size (Matyssek et al. 1993a; Oksanen and Saleem 1999), leaf mass (Tjoelker et al. 1993; Neufeld et al. 1995; Scagel and Andersen 1997; Oksanen et al. 2001) and foliage area (Mortensen and Skre 1990; Paakkonen et al. 1993; Tjoelker et al. 1993; Neufeld et al. 1995; Volin and Reich 1996; Oksanen and Saleem 1999; Saleem et al. 2001; Topa et al. 2001; Thomas et al. 2006). It is obvious that less photosynthetic area leads to less production of carbohydrates not only for the aboveground but also for the belowground (i.e., roots). In addition, there could be an indirect effect on belowground: less leaves will lead to less litter on the forest floor and therefore the input of minerals into soil will be diminished. As such, there could be an impact on C and N flow.

Although not many aboveground anatomical variables have been studied simultaneously with belowground, some have been found to be altered while the roots were impacted. These include the size of xylem ray and tracheid cells (Matyssek et al. 2002), lignified tracheids and total number of cells (Matyssek et al. 2002), number of plastoglobuli/chloroplast (Oksanen and Saleem 1999) and peroxisomes and mitochondria (Oksanen et al. 2005), cell wall–lower epidermis (Oksanen and Saleem 1999) and palisade (Paakkonen and Holopainen 1995) thickness, and cortex parenchyma (Matyssek et al. 2002). It is however not understood yet if it is all about an anatomical plasticity to adapt to O_3 stress or a direct impact of O_3.

Other reactions concern biochemical properties such as chlorophyll content (Izuta et al. 1996; Oksanen and Saleem 1999), RuBisCO (Izuta et al. 1996; Oksanen and Saleem 1999; Nakaji and Izuta 2001; Yonekura et al. 2001; Yamaguchi et al. 2007a, 2007b), foliar nutrient status, such as potassium (K) that is involved in protein synthesis and stomata regulation (Kelly et al. 1993; Matyssek et al. 1993b; Oksanen and Saleem 1999; Topa et al. 2001; Oksanen et al. 2005), acidic and non-polar amino acids (Yamaguchi et al. 2007b), total soluble protein (Yamaguchi et al. 2007b), and phenolic compounds (Saleem et al. 2001; Yamaji et al. 2003). It was mentioned above that less leaf litter may lead to diminished mineral input into soil. Increased foliar N, P, and K may point out nonlimiting supplies under reduced C fixation or nutrient retranslocation from prematurely senescenced leaves (Matyssek et al. 1993b). Alterations in nutrient content of foliage, and therefore the litter, may have severe consequences in the decomposition process, one of the most important ecological belowground processes. It is however an open question whether the nutrient retranslocation will be sustained under eO_3.

They also include physiological variables such as net photosynthesis (e.g., Tjoelker et al. 1993; Pearson 1995; Izuta et al. 1996; Shan et al. 1996; Yonekura et al. 2001; Oksanen et al. 2001; Topa et al. 2004; Yamaguchi et al. 2007a, b), stomatal conductance (g_s) (Pearson 1995; Oksanen and Saleem 1999; Oksanen et al. 2001; Yamaguchi et al. 2007a; Diaz de Quijano et al. 2012), photosynthetic nitrogen use efficiency (PNUE) (Yamaguchi et al. 2007a) and internal CO_2 concentration (${}_iCO_2$) (Pearson 1995), carboxylation efficiency (Loats and Rebbeck 1999; Nakaji and Izuta 2001; Yonekura et al. 2001; Yamaguchi et al. 2007b), leaf dark (Tjoelker et al. 1993; Volin and Reich 1996) and light (Edwards et al. 1994) respiration, transpiration (Shan et al. 1996), water use efficiency (*WUE*) (Shan et al. 1996), accelerated senescence (Saleem et al. 2001; Topa et al. 2001), and phloem loading and phloem fibers (Matyssek et al. 1992; Landolt et al. 1997; Matyssek et al. 2002). Photosynthesis is the core function of plants and essential for sustaining life on Earth. If photosynthesis is suppressed not only the carbon for root per se will be diminished but the mutualism of root hosts could be altered in turn as well. Impacted phloem loading may directly limit root growth and may affect leaf differentiation (Matyssek et al. 1992). Recently assimilated $^{14}CO_2$ to roots might also be maintained at the expense of respiration (Topa et al. 2004).

In some publications, the O_3 impact to photosynthesis was associated with reductions in growth. However, we recommend such attributions to be avoided, especially in studies including only a few variables, because (a) O_3 impact to growth is not a result only from leaf-level photosynthesis, (b) other variables such as leaf area and partitioning of recently assimilated C into starch (Topa et al. 2001, 2004) may be impacted long before photosynthesis is impacted, (c) the impact to such variables can be even stronger than on photosynthesis (Topa et al. 2001), (d) photosynthesis and photosynthesis-related variables are not always changed due to O_3 (e.g., Taylor et al. 1986; Noble et al. 1992; Karlsson et al. 1997; Nakaji and Izuta 2001; Diaz de Quijano et al. 2012) or change only later in growing season while root is suppressed (e.g., Edwards et al. 1994; Yamaguchi et al. 2007a; Diaz de Quijano et al. 2012), and (e) photosynthesis may significantly be impacted by eO_3 without evident RbM reductions (Tseng et al. 1988; Samuelson 1994a; Paakkonen et al. 1996; Moraes et al. 2006). Physiological functions, such as photosynthetic response to eO_3, of seedlings differ from mature trees resulting to underestimation of the O_3 impact when using juveniles (Samuelson and Edwards 1993; Edwards et al. 1994; Kelly et al. 1995), and particular attention should be paid in relating root suppression of seedlings with photosynthesis.

3.1.7 Chemical Composition of Roots

Carbohydrates Chemical composition of roots is another critical aspect that must be taken into account. Monosaccharide concentration in fine roots of beech seedlings was decreasing with increasing O_3 dosage (7.6 to 28 μmol mol^{-1} h and 10 to 46.9 μmol mol^{-1} h, in the first and second growing seasons, respectively) when grown in pots for 2 years (Braun et al. 2004). However, it was higher when the plants grown in ambient O_3

condition, compared to charcoal-filtered air, and out of pots for 3 years (Thomas et al. 2006). Monosaccharide levels were increased in the fine roots of spruce saplings, leading to boosted total soluble carbohydrates (TSCs) in fine roots (Thomas et al. 2005). O_3-induced increase in total soluble sugar content was found in roots of red spruce seedlings as well, while at the same time, the sugar content of foliage was decreased (Amundson et al. 1991). This suggests a strategy or a need of some plant species to accumulate sugar in roots as a response to eO_3, something that is worth to be further investigated.

In other studies, however, the total sugar content of root tissue of loblolly pine (*Pinus taeda* L.) (Meier et al. 1990), of ponderosa pine (Andersen et al. 1991, 2001), and of a sensitive aspen clone (Coleman et al. 1995a, b) seedlings decreased by eO_3. In fine and coarse roots of ponderosa pine, glucose, fructose, sucrose, and monosaccharide were also separately reduced by eO_3 (Andersen et al. 1997), but in another experiment (Andersen et al. 2001), glucose and fructose of fine roots decreased while sucrose was unaffected. Sugar content in fine roots of a hybrid poplar cuttings and sugar maple seedlings was unaffected as well (Tjoelker et al. 1993). Increasing soil Mg availability increased reducing sugars (Friend et al. 1992).

Concerning the main nonstructural carbohydrate content (NsC) in roots, it has been reported (Bucker and Ballach 1992) to be decreased in a hybrid poplar cuttings. However, no change in roots NsC was observed in black poplar cuttings (Bucker and Ballach 1992), loblolly pine (Friend et al. 1992), a hybrid poplar (Tjoelker et al. 1993), sugar maple (Tjoelker et al. 1993), red oak (*Quercus rubra* L.) (Samuelson and Kelly 1996) seedlings, and red oak mature trees (Samuelson and Kelly 1996). Light condition was reported to have no interactive effect with O_3 on total NsC (Tjoelker et al. 1993).

Besides, the contents of the following variables were not affected by O_3: soluble carbohydrate (SC) content (hexose or sucrose) in roots of loblolly pine seedlings (Meier et al. 1990) and SC (glucose, sucrose, fructose) in roots of red oak seedlings and mature trees (Samuelson and Kelly 1996), total SC in roots of loblolly pine seedlings (Friend et al. 1992), and Sitka spruce cuttings (Bambridge et al. 1996). Also, in individuals of two clones of silver birch (*Betula pendula* Roth.) no effect of eO_3 ($2\times$ambient O_3 levels for 3 growing seasons, 12 or 14 h day^{-1}) was found on root carbon/nitrogen (C/N) ratio (Kasurinen et al. 2005). These findings may suggest that carbohydrate content in root does not vary between seedlings, saplings, and mature trees. Disturbances in C or carbohydrate content may negatively influence the root turnover (i.e., C flux). Light has to be yet shed on qualitative properties of carbohydrates.

Fatty Acids Eight fatty acids (namely 14:0, 16:0, 18:2, $18{:}3\Delta^5$, 18:3, 18:4, 20:3, 20:u-1-peak) (of the 16 measured) and the total fatty acids contents were drastically boosted by eO_3 in roots of Scots pine while the foliar fatty acids were unchanged (Anttonen and Karenlampi 1995).

Amino Acids Amino acids, water-methanol soluble, and residue content in coarse roots of an O_3-sensitive aspen clone boosted by eO_3, but nonreducing sugars and lipid concentrations diminished (Coleman et al. 1995a, b). 1-Aminocyclopropane-1-carboxylic acid (ACC, a disubstituted cyclic alpha-amino acid important in biosynthesis of ethylene hormone) content can become twice higher in roots than foliage after eO_3 exposure (Van Den Driessche and Langebartels 1994). The ability of regulation of ethylene production in spruce seedlings via a translocation of malonyl-ACC (MACC) to roots may associate the ethylene biosynthesis with the eO_3-resistance of Norway spruce (Van Den Driessche and Langebartels 1994).

Starch Starch concentration was reduced under eO_3 in roots of spruce seedlings (Braun et al. 2004) and saplings (Thomas et al. 2005), red spruce (Amundson et al. 1991), Scots pine (Anttonen and Karenlampi 1995), loblolly pine (Meier et al. 1990), ponderosa pine (Andersen et al. 1991, 1997), and an aspen clone (Coleman et al. 1995a, b) seedlings. When the starch was decreased in roots, it was diminished in stem too (Amundson et al. 1991; Andersen et al. 1997).

In another experiment with ponderosa pine grown in competition with *Elymus glaucus* (Andersen et al. 2001), starch content was unaffected by eO_3 in fine roots, stems, and needles. Similarly, it was unaffected in roots of Sitka spruce (Bambridge et al. 1996) and a hybrid poplar (Tjoelker et al. 1993) cuttings and loblolly pine (Friend et al. 1992) and sugar maple (*Acer saccharum* Marshall) (Tjoelker et al. 1993) seedlings, as well as in roots of red oak seedlings and mature trees (Samuelson and Kelly 1996). Light condition had no interactive effect with O_3 on starch content in fine roots of a hybrid poplar cuttings and sugar maple seedlings (Tjoelker et al. 1993).

Nutrient Content N, S, P, and Mg content of loblolly pine roots were not affected by eO_3, and there were no interactive effects with rainfall pH (Edwards et al. 1991). In red spruce fine and coarse roots, N content was not affected by eO_3 in seedlings, but it was affected in mature trees (Kelly et al. 1995). In an experiment with Aleppo pine (*Pinus halepensis* Miller) seedlings subjected to eO_3 and drought, the P, Ca, and Mg contents were unaffected by all treatments and K was enhanced only in eO_3 × drought seedlings (Inclan et al. 2005).

3.1.8 Chromosomal Response

Molecular studies are required to give a clear image of what is actually happening to the roots of the woody plants under O_3. Muller et al. (1996) assessed the O_3 stress in spruce plants exposed to O_3 by recording chromosomal aberrations in root tips. When the fumigation had ceased, after 6 weeks of exposure, the fumigated plants showed a significantly increased number of chromosomal aberrations as compared with the control ones, even if visible injury was not present. They also found a long-term carry-over effect of O_3 on the genetic material of spruce trees for 2 years: aberrations and stickiness were highly altered in six different time points within about 2 years after the end of fumigation. The aberrations were well described by chromosomal stickiness and breakage, and fragmentation, while the dominant abnormality of chromosomes was stickiness leading to cellular death.

3.1.9 CO_2 Efflux

Another important issue relating eO_3 with climate change is root respiration. The CO_2 output from soils is the result of root respiration (autotrophic) and physiological processes of the microorganisms (heterotrophic) involved in the decomposition of organic material (Cao and Woodward 1998; Munoz et al. 2010). Elevated O_3 may have both short- and long-term cumulative effects on belowground respiration (e.g., Kasurinen et al. 2004) and can be considered an appreciable factor affecting the C cycling in forest ecosystems. One mechanism by which eO_3 can affect CO_2 efflux is the reduction of the amount of the respirating RbM. The O_3-induced reduction of RbM leads to lower belowground CO_2 efflux (Edwards et al. 1994).

Another mechanism is by influencing the respiration process in roots. Kelly et al. (1993) and Shan et al. (1996) found that eO_3 caused a significant decrease of root respiration. In experiments with Ponderosa pine, it was found that O_3 enhanced the rate of belowground O_2 uptake but, at the same time, the rate of belowground CO_2 release was highly enhanced, increasing overall the respiratory quotient (RQ, CO_2/O_2) (Andersen and Scagel 1997; Scagel and Andersen 1997). In addition, it has been reported that eO_3 reduced the maximum rate of the respiratory release of $^{14}CO_2$ by roots (Andersen and Rygiewicz 1995). An acute exposure to eO_3 decreased the root/soil respiration (Gorissen et al. 1994), suggesting that root respiration was significantly affected while the respiration of soil microfauna was less affected or unaffected.

Contrary to these findings, however, there are reports supporting that the effects of eO_3 on CO_2 efflux is quite complex and seem to depend on the genetic profile of plants (Kasurinen *et al.* 2004), the soil fertility (Andersen and Scagel 1997; Scagel and Andersen 1997), drought (Nikolova et al. 2010), etc. Some studies have shown that CO_2 efflux exhibits temporal variability (e.g., Kelly et al. 1993; Andersen and Scagel 1997; Scagel and Andersen 1997; Kasurinen et al. 2004). For instance, in silver birch, soil efflux of CO_2 was usually increased by eO_3 but its magnitude varied throughout the growing seasons with a trend to become more apparent by time (Kasurinen et al. 2004). Nikolova et al. (2010), who investigated the drought role in beech and spruce treated with O_3 for four growing seasons, found that drought can increase the belowground CO_2 efflux, overriding thus the net O_3 effects.

Enhanced belowground CO_2 efflux may reflect stimulation of root growth and/or respiration rate, increased root turnover, alteration of ectomycorrhizal network dynamics (e.g., enhanced fungal colonization on roots), stimulation of microbes and/or enzymes in rhizosphere, and boosted nutrient acquisition by fine roots (Hanson et al. 2000; Kasurinen et al. 2004; Nikolova et al. 2010).

3.1.10 Alcohols and Mycorrhizae

It has been reported that alcohols and disaccharide and trisaccharide concentrations in fine roots of spruce saplings (Thomas et al. 2005) and beech seedlings (Thomas et al. 2006) were not significantly affected by O_3. However, mannitol and trehalose, which are fungus-specific sugar alcohols, may be affected. If they are altered, they may have implications in altering mycorrhization, especially under increased N fertilization and O_3 (Thomas et al. 2005). Reduction of these fungus-specific sugar alcohols may lead to suppressed mycorrhization due to poor nutrient pool. On the other hand, increase of the fungus-specific sugar alcohols does not necessarily mean increase of mycorrhization. In contrast, this may lead to increase in mycorrhizae competition to colonize the roots, and, thus, to decreased mycorrhization at the end. Nevertheless, increase or decrease of mannitol and trehalose may have unknown implications in the mycorrhizal species richness.

3.1.11 Soil Mycorrhizae and Prokaryotic Organisms

Fungi play an important role in ecosystem processes (Huhta 2007; Tedersoo et al. 2014). Almost all the plants establish symbioses with microbes (Petrini 1986), and after the symbioses both partners have profit (Fuzy et al. 2014), while the microbe receives some benefit from the interaction at the expense of the host (Newton et al. 2010). The plants can access nutrients that previously could not, like P and Mg, and the symbionts large amounts of carbohydrates from the plant photosynthates (Izuta and Nakaji 2003; Finlay 2004; Smith and Read 2008; Chorianopoulou et al. 2015). Mycorrhization is not a direct function of the plants, but it is one of the most critical factors for woody plants' health (Wang et al. 2015b).

Ozone Effects on Mycorrhizae O_3 has the potential to strongly affect the mycorrhization of woody plant species (Blaschke 1990; Meier et al. 1990; Andersen and Rygiewicz 1995; Kasurinen et al. 2005). For instance, there is an evidence showing that, under eO_3, in the presence of mycorrhization, higher amount of photosynthates is accumulated to the roots while in the absence of mycorrhization photosynthates are accumulated to other assimilative parts (Andersen and Rygiewicz 1995). In Aleppo pine plants, under ambient air or eCO_2, mycorrhizae strongly accumulated ^{15}N. However, surprisingly, under eO_3, this pattern was reversed (Kytoviita et al. 2001).

Elevated O_3 increased the biomass of mycorrhizae colonizing the roots of Ponderosa pine seedlings (Kytoviita et al. 1999). The mass of active and total fungi on roots was tended to increase by eO_3 as well (Scagel and Andersen 1997; Kasurinen et al. 2004). Besides, an eO_3-induced increase in mycorrhizal infection levels observed in silver birch seedlings (Kasurinen et al. 2005). Two studies however reported that mycorrhizal infection was unaffected by eO_3 in loblolly pine seedlings (Adams et al. 1988; Kainulainen et al. 2000). In the study of Adams et al. (1988), since the fumigation lasted for only few months and taken into account that O_3 stress is cumulative (Amundson et al. 1991), it can be supported that such a short time (for long living tree species) exposure was not enough so as the O_3 damage to reach and affect mycorrhizae. However, in another study by Kainulainen et al. (2000), the mycorrhizae on short roots of Scots pine seedlings were unaffected even after three growing seasons of O_3 exposure (1.2, 1.5, and 1.7 × ambient O_3 levels for the first, second, and third growing seasons, respectively).

In the study of Kytoviita et al. (1999), exposure to eO_3 increased the amount of mycorrhizae (mg fresh weight) in Silver birch seedlings and the number of mycorrhizal Aleppo pine seedlings despite a reduction in the fungus (*Paxillus involutus* (Batsch) Fr.) extramatrical mycelium growth rate. The ectomycorrhizal frequency decreased on short and long root segments of Norway spruce saplings within Ah-horizon, while the nonmycorrhizal and necrotic short root frequencies increased (Blaschke 1990). The increase of mycorrhizal infection levels in O_3-exposed trees is correlated with greater amount of photosynthetic area (Kytoviita et al. 1999) and could be attributed to higher availability of soluble sugar or carbohydrate leakage to soil due to loss of root membrane integrity (Kasurinen et al. 2005).

However, increase in the root colonization by mycorrhizae in trees exposed to eO_3 is not always apparent. For example, in their study with loblolly pine seedlings, Meier et al. (1990) found that the total number of ectomycorrhizal tips (of any morphotypes) and the total number of tips per centimeter of long root were decreased, whereas the number of nonectomycorrhizal tips was increased by eO_3. In addition, in Aleppo pine seedlings, although there was no effect of eO_3 on the number of mycorrhizal tips, there was a smaller total area explored by the fungus (Kytoviita et al. 2001).

Interactions Effects of O_3 with Other Environmental Factors on Mycorrhizae Finally, O_3 can reduce the ^{14}C allocation in fungi of mycorrhizal plants and consequently the fungi respiration of $^{14}CO_2$, and their intact, extramatrical hyphal respiration (Andersen and

Rygiewicz 1995). This stresses a substantial impact of O_3 on C balance of the mycorrhizae.

No interactive effect of eO_3 with eCO_2 on mycorrhizal infection was observed in Silver birch seedlings (Kasurinen et al. 2005). In pine seedlings, it was found that eO_3 had a positive synergistic effect (to the direction of eO_3 effect) with eCO_2 on the number of mycorrhizal seedlings (Kytoviita et al. 1999), but no interaction with substrate type on active or total fungal mass (Scagel and Andersen 1997). Furthermore, no effects of eO_3 or its combination with eCO_2 were found on soil or root ergosterol concentrations (soil fungi mass), phospholipid-derived fatty acids (viable microbial community), 2-OH-FA (mycobacteria, fungi, yeast, and plant detritus), and 3-OH-FA (gram-negative bacterial community) (Kasurinen et al. 2005). The latter findings are very important in terms of the unique properties of these response variables, e.g., ergosterol can be found only in cell membranes of fungi and protozoa. Therefore, they are not confounded by plant components.

Keane and Manning (1988) found that O_3 had a significant interaction with acidic rain: paper birch (*Betula papyrifera* Marshall) seedlings with pH 3.5 SAR had decreased mycorrhizal infection only when exposed to charcoal-filtered air -there was no such a decrease when exposed to eO_3.

Mycorrhizae Ecology Under Elevated O_3 O_3-induced alterations in mycorrhizal community and reductions of sporocarp production in earlier harvest (but not at the final one) of *Betula pendula* Roth individuals were reported by Kasurinen et al. (2005) too. Kytoviita et al. (1999) reported that eO_3 has the potential to stimulate the spread of mycorrhizal infection from individuals of one species to individuals of a different species. The competition among mycorrhizal fungi can be altered resulting in shifts in species composition (Kelly et al. 1993). Such alterations were recently evidenced molecularly by Wang et al. (2015b).

Prokaryotic Organisms Regarding prokaryotic organisms in rhizosphere, there is a lack of evidence about eO_3 effects on them. Scagel and Andersen (1997) found that eO_3 led to increased bacterial mass in Ponderosa pine roots, but with an even higher O_3 dosage, the bacterial mass was decreased. The effects of eO_3 on the bacteria were independent of the type of the substrate. Later, it was found that plant growth-promoting rhizobacteria protected roots of loblolly pine seedlings against eO_3 (Estes et al. 2004), which could be a kind of mutualism. There could be an imbalance between eukaryotic and prokaryotic populations, as prokaryotic may be directly or indirectly negatively affected at a higher degree by eO_3 (Scagel and Andersen 1997).

3.1.12 Carry-Over Effect

Limited root growth due to limited carbohydrate availability (Oksanen and Saleem 1999; Saleem et al. 2001) may be reflected as a strong suppression of trees growth in the next growing seasons (Horton et al. 1990; Oksanen and Saleem 1999) due to so called carry-over (Oksanen and Saleem 1999) or cumulative (Topa et al. 2001) effects. For instance, a negative impact of eO_3 on RbM of tree species in the second (but not in the third) growing season was observed by Edwards et al. (1992a) and Broadmeadow and Jackson (2000). This would be attributed to the inability of O_3-suppressed trees to develop new roots. For example, Blaschke (1990) in a five-growing-season O_3 fumigation study with Norway spruce saplings found that O_3 caused high reduction of roots regeneration. Weinstein et al. (1998) using a model (TREGRO) estimated that root senescence and fine root growth were diminished in mature red oaks exposed to ambient O_3, suggesting that such diminishes may lead to inability of plants to replace the lost roots with new ones.

On the other hand, significant differences in RbM may be overestimated in some species in the first years (Broadmeadow and Jackson 2000), or acclimation of plants to eO_3 may occur (Matyssek et al. 1995). The carry-over effects may sometimes vary upon soil fertility (Andersen and Scagel 1997), and they could be critical to plant susceptibility to other stressors (Andersen et al. 1991, 1997).

All these strongly show that the potential of eO_3 to impact the root development is quite complex and highlight the necessity for long-term studies to clarify the alteration in roots response over the years (Temple 1988; Scagel and Andersen 1997; Nikolova et al. 2010).

3.2 Interacting Environmental Factors

3.2.1 Substrate Type

The substrate seems to play important role in the eO_3-induced suppression of RbM. For example, it has been reported a higher O_3 impact on RbM of loblolly pine seedlings grown in vermiculite-peat substrate in comparison to those grown in mineral-soil-peat (Horton et al. 1990). In another case, the RbM of paper birch seedlings grown in nonsteam-sterilized soil was not decreased by eO_3, while in those grown in steam-sterilized soil, it was significantly reduced (Keane and Manning 1988). However, such an interaction was not observed in red spruce (Taylor et al. 1986) and ponderosa pine (Scagel and Andersen 1997) seedlings grown in different types of soil.

3.2.2 Soil Nutrients and Properties

Soil nitrogen content is an important factor in O_3 studies, and aboveground responses of trees to eO_3 may depend on it (Bielenberg et al. 2001). Although it is known that, in general, nutritional status of plants may affect plant response to O_3, the relevant studies on the interaction between eO_3 and soil nutrients on root biomass are not so many. Many of the studies included in this review have reported that nitrogen (e.g., Tjoelker and Luxmoore 1991; Karnosky et al. 1992; Lippert et al. 1996; Nakaji and Izuta 2001; Utriainen and Holopainen 2001a, 2001b; Izuta and Nakaji 2003; Watanabe et al. 2007; Yamaguchi et al. 2007a, 2007b), phosphorus (P) (Utriainen and Holopainen 2001a, 2002), or magnesium (Mg) (Edwards et al. 1990, 1991, 1992a; Kelly et al. 1993) fertilization have no interaction with eO_3 on RbM production.

However, other studies have reported that some direct or indirect effects may occur. For instance, Nakaji et al. (2004) found that, with increased N loading, root growth, and mycorrhizal development in fine roots was negatively affected, resulting in reduced soil P and Mg uptake; O_3 did not affect the mycorrhizal development in fine roots in this study. Thus, the soil N should be taken into account in studies where the O_3 effects on belowground are investigated.

In other studies, the effects may be not observed directly as reduction of the RbM but as disturbance of the S/R ratio. For instance, Landolt et al. (1997) found that both high fertilization and eO_3 amplified the S/R in silver birch cloned cuttings and they had a positive synergistic effect. Such alterations have been reported also by Maurer and Matyssek (1997). A similar amplification in S/R as a result of interaction between O_3 and nutrient fertilization in a birch clone has been attributed to enhanced leaf formation by high fertilization (Maurer and Matyssek 1997), which may be associated with the size of phloem ray cells and the ratio of (periderm + phloem)/xylem (Matyssek et al. 2002). The early presence of visible O_3 foliar injury in plants grown either in low- or in high-fertilized soils show that good nutrition does not prevent O_3 injury but helps plants to recover (Landolt et al. 1997; Maurer and Matyssek 1997).

In addition, other studies suggest more complex interactive effects reflected in alterations in root physiological, response variables: soil N may behave as an antagonistic factor (Thomas et al. 2005) against O_3 or having no interactive effects with O_3 (Thomas et al. 2006) on starch concentration regulation, and does not interact with O_3 in TSCs in fine roots (Thomas et al. 2005; Thomas et al. 2006).

Elevated O_3 may alter soil chemistry which in turn may affect response to O_3. For example, a 3-year eO_3 fumigation did not change the soil pH, K, Ca, Mg, P, Mn, Na, NH_4-N, NO_3-N, NH_4-NO_3, and CEC of ponderosa pine seedlings; however, a 28-month O_3 fumigation tented to increase the NO_3 and decrease the SO_4 concentrations in soil of shortleaf pine (Shelburne et al. 1993). Soil properties are vital determinants of foliar photosynthetic traits and rates (Maire et al. 2015) and alterations of them would have effects on trees photosynthesis in turn. Meier et al. (1990), in experiments with loblolly pine seedlings under four O_3 dosages, found that soil base saturation, pH, K, Ca, Mg, P, and Mn were decreased, while exchangeable acidity, CEC, Zn, and Cu were increased after 12 weeks of exposure. Soil in which clones of European white birch were grown had not affected pH and concentrations of N, Ca, K, and P by chronic O_3 exposure (Oksanen et al. 2001).

There are several probable explanations for the contradictory findings: (a) different O_3 dosages or uptake, (b) different nutrient dosages or uptake, (c) species-specific response to O_3, (d) the ignored side effects of some agrochemicals applied during experimentation in order to protect plants (some agrochemicals are known to modify the plant response to eO_3) (Saitanis et al. 2015b), and (e) uncontrolled error.

Future research is needed for investigation of nutrient retranslocation under eO_3 and its influence on soil chemical status. More evidence is needed on the ratios between soil elements.

3.2.3 Water Availability

Watering treatment in combination with eO_3 has not been extensively studied. Some cases showed no interaction (e.g., Tseng et al. 1988; Beyers et al. 1992; Karlsson et al. 1995, 1997; Broadmeadow and Jackson

2000; Yonekura et al. 2001). In the case of Norway spruce (e.g., Karlsson et al. 1995, 1997; Lippert et al. 1996), no significant interaction with watering treatment was observed in total plant biomass (Karlsson et al. 2002) or total root biomass (Van Den Driessche and Langebartels 1994; Lippert et al. 1996). Others have found an eO_3-induced reduction of the positive effects of irrigation (Broadmeadow and Jackson 2000) or an eO_3-induced reduction of the negative effects of drought (Karlsson et al. 1997; Le Thiec and Manninen 2003) through a delayed growth of shoot, a delayed increase in total transpiring leaf area, and a less close of stomata during the drought period (Karlsson et al. 1997). Yet, eO_3 combined with drought leads to a decreased C translocation to roots and thus imbalanced C/N ratio (Gorissen et al. 1994; Gerant et al. 1996; Inclan et al. 2005). The interaction of water and eO_3 treatments may induce the activation of similar processes related to C and N metabolism (Inclan et al. 2005) and may be influenced by temporal factors and the ecotypic base of trees (Karlsson et al. 1997). Finally, drought combined with eO_3 may increase the N content of roots (Inclan et al. 2005).

3.2.4 Interactive Effects of eO_3 with Other Pollutants

The co-occurrence of other pollutants in the environment may modify the effects of O_3 as it is for example the cases of SO_2 which has been found to exhibit a synergistic interaction effect with O_3 on roots biomass of yellow poplar seedlings (Chappelka et al. 1985). On the other hand, no interaction effects between eO_3 with air NH_3 (Dueck et al. 1998) or NO_2 (Kress and Skelly 1982) on root biomass of several species was found. However, studies dealing with SO_2, NH_3, or NO_2 are extremely limited and not enough to lead to generalizations.

The most interesting and most studied interactions are those of eO_3 with elevated CO_2 (eCO_2) or acid rain.

eO_3 Interaction with eCO_2 The nature of O_3 and CO_2 impose their simultaneous presence. eCO_2 may play a role in the O_3-plants interaction. It is also possible eCO_2 to ameliorate the impact of eO_3 by providing extra C and energy via higher net assimilation (Noble et al. 1992; Dickson et al. 1998; Broadmeadow and Jackson 2000; Gaucher et al. 2003; Riikonen et al. 2004), or, from another point of view, it is possible eO_3 to reduce the positive effects of eCO_2 (Dickson et al. 1998; King et al. 2005). It has been reported that eCO_2 along with elevated eO_3 have a positive synergistic effect on coarse and fine roots, as the differences are higher than those caused by eCO_2 (Watanabe et al. 2010; Koike et al. 2015) or eO_3 (Kytoviita et al. 1999) alone. In many cases included in this study, eCO_2 has no interaction with eO_3 at all (e.g., Mortensen 1995; Loats and Rebbeck 1999; Broadmeadow and Jackson 2000; Dickson et al. 2001; Utriainen et al. 2000; Kasurinen et al. 2005; Kozovits et al. 2005a). In some cases (Vanhatalo et al. 2003), there was an insignificant response of plants to the combination of eO_3 with eCO_2, compared to the control (charcoal-filtered air). *P. tremuloides* Michx. seedlings had O_3-induced reduced RbM ratio only under ambient CO_2 and low N availability but not under eCO_2 or high N availability (Volin and Reich 1996).

eO_3 Interaction with Acid Rain The RbM response to eO_3 seems to be influenced when exposure to O_3 is conducted under simultaneous exposure to SAR: RbM is decreasing with decreasing (Chappelka et al. 1985) or increasing (Keane and Manning 1988) rain pH. Also, with pH 3.5, there was no eO_3 effect on RbM of Paper birch seedlings but with pH 5.6 RbM decreased by eO_3 (Keane and Manning 1988). In a study by Temple (1988) with Jeffrey pine and giant sequoia treated with O_3 (200 nmol mol^{-1}) and/or acidic mist (pH 2.0), it was found that O_3 and acidic mist can interact to exacerbate their single effect by greater-than-additive inhibition of root growth observed on giant sequoia, but there was a lack of interactive effects on Jeffrey pine. However, there are several other investigations supporting no interaction between eO_3 and SAR (Chappelka et al. 1988; Edwards et al. 1990, 1991, 1992a; Davis and Skelly 1992; Kelly et al. 1993) or mist (Taylor et al. 1986; Temple 1988; Matsumura 2001) on RbM production.

Interaction of simulated acidic rain with eO_3 on chemical composition of roots is hardly observed (Friend et al. 1992). Chronic acidic rain may not alter alter the N, S, P, K, Ca, Mg content but may decrease the NH_4 and SO_4 of soil (*priming effect* of fertilization); its effects are not influenced by eO_3 (Edwards et al. 1992b).

It is recommended future experiments with acidic rain include chronic rather than acute levels of acidity in order to be acidic enough to elicit foliar or soil nutrient leaching of plants (Edwards et al. 1992b).

3.2.5 Light Condition

Evidence shows that there is a differential response of RbM to eO_3 between seedlings grown under closedcanopy versus clearing environments, and this seems to be species specific: RbM reduction due to O_3 was higher in some taxa, e.g., sugar maple (Tjoelker et al. 1993; Topa et al. 2001) and silver birch (Landolt et al. 2000), when plants were shaded but in some other taxa, e.g., hybrid poplar (Tjoelker et al. 1993), the RbM reduction was higher in unshaded plants.

3.3 Ecological Implications

In nature, everything interacts with everything else. If an ecosystem change due to the O_3 effects on plants, then, numerous other facts are expected to occur. Although several ecological consequences of the eO_3 effects on forest ecosystems have been suggested, we here focus only to those ecological consequences expected from the eO_3 effects on the roots and the rhizosphere of forest trees.

Carbon is cycling through CO_2 fluxes among vegetation, soil, and atmosphere (Cao and Woodward 1998; Valentini et al. 2000; Heimann and Reichstein 2008). CO_2 efflux is therefore important for C cycling and sequestration (Hanson et al. 2000; Kim 2013) and changes in it, along with C allocation to roots, could be critical in C cycle and should be taken into account in greenhouse effects and climate change modeling. Terrestrial biosphere can act as a sink of atmospheric CO_2 and simultaneously as a source (Piao et al. 2009; Munoz et al. 2010; Ahlstrom et al. 2012) through the two core plants functions: photosynthesis and respiration. As it has been discussed before, eO_3 negatively affects photosynthesis, leading to a reduced amount of carbon stored to roots reducing, thus the ability of forests to act as carbon sinks. On the other hand, root respiration seems to be quite complex: (a) reduced root biomass means reduced respiratory root biomass and thus reduced CO_2 efflux (Edwards et al. 1994); (b) the root respiration has been found either to be enhanced by eO_3 (Andersen and Scagel 1997; Scagel and Andersen 1997) and as such to enhance CO_2 efflux from roots; or (c) to be reduced (Kelly et al. 1993; Shan et al. 1996) by eO_3 and thus to reduce CO_2 efflux from roots, depending on the genetic profile of the trees. The worst scenario would be if the C allocation to roots is reduced while the CO_2 efflux is increased. This would indicate forests acting more as sources than sinks. CO_2 efflux under eO_3 not only should not be overlooked but it should be also considered essential to be accounted in predictive modeling of future atmospheric C levels.

It has been suggested that altered S/R may indicate acclimation of plants to eO_3 as well (Matyssek et al. 1995). However, the disproportional reductions or roots in comparison to shoots (increase in S/R), in a long-term negative feedback, may lead to reduced water and nutrient supply from roots to the canopy (Koike et al. 2003). Furthermore, they may lead to reduced net ecosystem production, inability to maintain rhizosphere organisms, and increased susceptibility to drought, nutrient deficiency (Horton et al. 1990), or diseases and pests. Much worse, the outbreaks of forest diseases are foreseen to become more frequent and intense with increased drought and the presence of other stressors (Sturrock et al. 2011). Thus, dry periods in future scenarios of drought combined with predicted increased levels of O_3 could be critical for ecosystems functioning.

Such effects may be further amplified at plant community level because the competition of O_3-sensitive versus O_3-insensitive plants will change, with the latter dominating. When some species grow under competition for nutrients, they may become more susceptible to O_3, leading to high alterations of the root chemical composition (Andersen et al. 2001). Competition of trees with grasses seems to have no interaction with eO_3 on RbM production (Andersen et al. 2001), showing that there could be no changes between mono cotyledonous and dicotyledonous.

Species-specific differences in root system are related with species successional characteristics: “large proportions of shoot production are characteristic of vegetation in early successional phases, while high proportions of root production are characteristic of climax vegetational phases” (Antos and Halpern 1997). As such, the eO_3-induced reduction of the proportion of root production at different extend among different taxa may result in crucial ecological consequences during ecological succession process. Therefore, in order to understand species replacement during secondary succession (Antos and Halpern 1997), long-term community-level studies are needed. Such studies, albeit, are practically impossible to be conducted, since succession happens in ecological time (i.e. it takes dozens or hundreds of years). Only modeling approaches can reveal such long-term potential effects of O_3 in ecological succession.

As it has been already discussed, aboveground O_3 impact is directly related to the stoichiometry of roots. However, foliar stoichiometry is indirectly related to the soil stoichiometry through litter decomposition. Altered soil stoichiometry and decomposition process might point out several ecological consequences. For example, an increased availability of K in soil which might be induced by eO_3 (through root turnover with increased K content) can enhance plant invasive success (Sardans and Penuelas 2015), although such consequences of potential changes under eO_3 remain to be elucidated. Moreover, changes in the ratios between soil elements may influence the heterotrophic microbial communities (Zechmeister-Boltenstern et al. 2015). Fungi may show a slower and delayed direct respond to climate change than plants do (Damialis et al. 2015), but it seems that there is an indirect response to climate change (e.g., eO_3) as well. As such, there is an ecological "emergency call" due to their notable role in sustaining life on earth (Ahad et al. 2014). Taking into account the alterations in organisms' gene expression and metabolism under climate change (Penuelas et al. 2013) and changes in root and soil chemical composition along with ecological effects on soil fungi, it is unknown what the effects will be on forest floor mushrooms. Agathokleous et al. (2015b) stressed the ecological and anthropocentric need for wild species protection against O_3 deleterious effects.

Along with directly human-induced threats to forest soil ecology and forest productivity (Cambi et al. 2015). eO_3 seems to be a vital threat. Ecological consequences of changes in chemical composition of root and soil and soil microbial composition under eO_3 are poorly understood. Such changes may affect the structure and function of heterotrophic microbial communities, microbial interactions, and community dynamics, leading to feedbacks in nutrient availability, decomposition process, and finally soil fertility (Zechmeister-Boltenstern et al. 2015). In a study by Scagel and Andersen (1997) with Ponderosa pine seedling growing in a low-nutrient soil or a fertilizer-amended organic potting media, eO_3 decreased C allocation to roots, disrupted root metabolism and affected (nonlinearly) the biomass of active soil fungi and active bacteria in rhizosphere. When compared with controls, total fungal and bacterial biomass increased at low O_3 levels and decreased at increased O_3 level. In both substrates, the fungal/bacterial biomass ratio increased by eO_3. It is apparent that eO_3 impairs not only the ectomycorrhizae colonization but also the species richness, with shifts in specialists/generalists composition (Wang et al. 2015b). On a larger scale, the response of trees, in terms of RbM reduction, to eO_3 does not depend on the species composition of the community (King et al. 2005; Kozovits et al. 2005a).

4 Conclusions

We reviewed published literatures dealing with the belowground response of woody plants to elevated O_3. The most reported O_3-induced responses were reduction of root biomass and alteration in the root/shoot ratio, via different strategies of plants to cope with O_3 stress. The imbalance in carbon allocation toward roots leads to a relatively greater reduction on root mass compared with shoot biomass. Such a reduction in root biomass of urban trees may result in tree failure under strong winds, and may, thus, cause severe risks to citizens (Lorenzini and Nali 2014). This is a risk that needs to be taken into account by urban plant pathologists.

The imbalance in root/shoot ratio further leads to reduced supply of nutrients and water from roots to canopy, which, as a negative feedback effect, may amplify the O_3 direct effects on the leaves and enhance the plant susceptibility to other biotic or abiotic stressors. In addition, negative O_3 effects on the root nutrient quantity (and probably quality) may have unknown implications to soil biodiversity. The O_3-induced belowground effect may—in long term—reduce the net productivity of ecosystems.

We highlight the necessity for long-term open-field studies (>3 growing seasons) and, at the same time, we encourage studies at molecular level to give a clear image of what is actually happening to the roots of woody plants under eO_3. We suggest plant response to O_3 to be considered from the view point of Soil-Plant-Atmosphere Continuum (SPAC) with emphasis being paid to what happens in rhizosphere as a result of elevated O_3 in the atmosphere, instead of emphasizing to O_3 effects at canopy level and yield. All belowground disturbances occurring due to elevated O_3 and its interactions not only may have an impact on atmosphere in turn but also on hydrosphere, lithosphere, and biosphere (Earth) in long term.

Acknowledgments The authors acknowledge the authors of the original publications for significant contributions and apologize to authors whose articles may not have been cited. Constructive comments of the reviewers are appreciated. The senior author (E.A.) would like to thank Dr. Matsumoto Naoyuki of the Research Faculty of Agriculture, Hokkaido University, Japan, for useful discussions on soil microbiology. He is also thankful to the Japanese Ministry of Education, Culture, Sports, Science and Technology and the Japan Society for the Promotion of Science (JSPS) for funding (no. 140539). Part of the findings of this study was presented by E.A. at the 6th International Symposium on Physiological Processes in Roots of Woody Plants which was held in 2014 at Nagoya, Japan. This study was financially supported in part by the JSPS research funds to T.K. (Type B 26292075).

Author Contribution E.A. planned the study and surveyed, managed and reviewed the literature. E.A. synthesized and produced the manuscript with authorial contributions from C.J.S., X.W., M.W., and T.K. All the contributions were significant to carry out the study.

Compliance with Ethical Standards

Conflict of Interest The financial source support of this study (Japan Society for the Promotion of Science) is a nonprofit organization. We declare that our research has no conflict of interest.

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