ECOLOGY

Warming and elevated ozone induce tradeoffs between fine roots and mycorrhizal fungi and stimulate organic carbon decomposition

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Climate warming and elevated ozone (eO_3) are important climate change components that can affect plant growth and plant-microbe interactions. However, the resulting impact on soil carbon (C) dynamics, as well as the underlying mechanisms, remains unclear. Here, we show that warming, eO_3, and their combination induce tradeoffs between roots and their symbiotic arbuscular mycorrhizal fungi (AMF) and stimulate organic C decomposition in a nontilled soybean agroecosystem. While warming and eO_3 reduced root biomass, tissue density, and AMF colonization, they increased specific root length and promoted decomposition of both native and newly added organic C. Also, they shifted AMF community composition in favor of the genus *Paraglomus* with high nutrient-absorbing hyphal surface over the genus *Glomus* prone to protection of soil organic C. Our findings provide deep insights into plant-microbial interactive responses to warming and eO_3 and how these responses may modulate soil organic C dynamics under future climate change scenarios.

INTRODUCTION

Global surface temperature has increased by 0.74°C since the Industrial Revolution and is predicted to further increase by another 1.8° to 3.6°C by the year 2100 (*1*). Concurring with climate warming, the tropospheric ozone concentration had more than doubled (*2*). Climate warming may increase plant growth in humid ecosystems (*3*) but often enhances microbial decomposition of organic carbon (C) in soil and thus soil CO_2 emissions into the atmosphere (*4*, *5*), positively feeding back to climate warming (*6*). On the other hand, elevated ozone (eO_3) can damage stomatal function and reduce plant growth and C allocation belowground, thereby reducing detritus inputs into soil and subsequent formation of soil organic matter (*7*–*9*). Warming enhancement of microbial decomposition and O_3 reduction of plant-derived C inputs to soil raise a concern that concurring warming and eO_3 may aggravate losses of soil organic C, the largest active C pool on Earth's surface, and constrain the capacity of terrestrial ecosystems as a C sink. However, experimental evidence in the field is meager.

Warming and eO_3 can affect plant photosynthesis and further photosynthate allocation belowground to roots and their symbiotic microbes, rhizobia, and mycorrhizal fungi in particular (*7*, *10*). Arbuscular mycorrhizal fungi (AMF) form symbiotic associations with most terrestrial plants and acquire their C solely from their host plants in return for mineral nutrients (*11*). Warming has been shown to have positive (*12*, *13*), negative (*14*, *15*), or even neutral effects (*16*, *17*) on plant roots and AMF. In ecosystems with moderate water availability, warming often increases evapotranspiration and water stress to plants, reducing C allocation belowground and suppressing the growth and/or activities of roots and AMF (*14*, *15*). When water is not limiting, however, warming often enhances root cell elongation (*18*, *19*) and promotes root growth, increasing the plant's ability to enhance soil exploration for nutrients (*20*). Warming may also enhance AMF colonization of roots directly through stimulating hyphal growth and/or indirectly by promoting plant growth and subsequent C allocation belowground to roots and AMF (*10*, *13*). In comparison, ozone effects on roots and AMF are mostly indirect through inhibiting plant physiologies and growth, as O_3 is unable to penetrate into the soil to exert direct effects (*7*). Elevated O_3 diffuses into the intercellular air space of the mesophyll and reacts rapidly in the apoplast with a diverse set of molecules to generate reactive oxygen species (ROS) (*21*, *22*). These apoplastic ROS can react with components of the cell wall and plasma membrane and activate several signal transduction pathways that regulate the responses of the cells to the increased oxidative load, leading to chloroplast degradation and damaged plant leaves (*21*, *23*). These responses are modulated by plant hormones such as abscisic acid, salicylic acid, jasmonic acid, and ethylene (*22*, *24*). Damaged leaves not only reduce plant photosynthesis but also require more photosynthates for cell repairing, thereby reducing photosynthate allocation belowground (*7*, *25*) and altering root traits and AMF community composition and activities (*26*, *27*).

Changes in roots and AMF may critically modulate microbial decomposition in the mycorrhizosphere. While roots are a major source of soil organic C (*28*, *29*), labile C derived from live roots also provides the energy for saprophytic microbes that produce extracellular enzymes responsible for organic matter decomposition (i.e., priming effect) (*30*–*32*). However, live roots may also suppress microbial decomposition by outcompeting microbes for soil nutrients and water (*28*, *33*). Effects of AMF on soil organic C can be equally variable. On one hand, AMF may enhance soil C sequestration directly by facilitating the formation and stability of soil aggregates via their secondary compounds (e.g., chitin and glomalin) (*34*) and hyphal enmeshment (*35*, *36*) and indirectly by promoting plant

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Table 1. Daily mean air temperature, ozone concentration (12 hours), air humidity, and soil moisture and temperature during the experimental period for experimental climate treatments. Data are means ± SE ($n = 3$). CF, charcoal-filtered ambient air; W, warming; eO_3, elevated O_3; W + eO_3, warming + eO_3. Significant P values ($P < 0.05$) are shown in bold, ANOVA mixed model.

Climate treatments				Mixed ANOVA		
CF	**W**	**eO_3**	**W + eO_3**	**Warming**	**O_3**	**Warming × O_3**
Air temperature (°C)						
24.7 ± 0.1	27.4 ± 0.3	24.7 ± 0.0	27.8 ± 0.4	**<0.001**	0.353	0.482
O_3 (ppb)						
18.1 ± 0.3	20.8 ± 0.1	66.4 ± 0.8	65.2 ± 0.1	0.140	**<0.001**	**0.002**
Air humidity (%)						
72.0 ± 0.1	67.6 ± 0.8	71.5 ± 0.2	66.3 ± 0.9	**<0.001**	0.149	0.496
Soil moisture (V%)						
24.7 ± 0.6	23.9 ± 0.4	23.4 ± 0.5	23.7 ± 0.2	0.380	**0.047**	0.123
Soil temperature (°C)						
22.2 ± 0.0	24.2 ± 0.1	22.1 ± 0.0	24.1 ± 0.2	**<0.001**	0.509	0.959

growth and C inputs (*11*). On the other hand, increasing evidence has shown that AMF may enhance soil organic C decomposition likely by stimulating saprophytic microbes and contributing to the priming effect (*30*, *37*). A decrease in photosynthate allocation belowground under warming and/or eO_3 may promote plants to construct roots with high specific root length (SRL) and low root diameter or root tissue density (RTD) and reduce AMF colonization of roots and/or favor AMF species with lower C requirements (*38*, *39*). However, roots with high SRL and/or low RTD are often associated with high root turnover or short life span (*40*, *41*), and reduced AMF may decrease their contribution to soil aggregation and subsequent protection of soil organic C (*35*, *36*, *42*), favoring soil saprotrophs and their decomposition of soil organic C. However, very few field experiments have investigated how concurring warming and eO_3 may modulate root and AMF mediation of organic C decomposition in the field, although various observational studies have examined the responses of plant roots and AMF to climate warming (*10*, *20*, *43*) or eO_3 (*7*, *44*, *45*).

Taking advantage of an existing long-term field manipulation experiment, we investigated the effects of warming, eO_3, and their combination on soybean roots and their associated AMF as well as the resulting impact on residue decomposition. In particular, we integrated field temperature and O_3 manipulations with the Illumina MiSeq sequencing and stable isotope tracing to explore the linkages among root traits, AMF community composition, and microbial decomposition of organic C in soil. We hypothesized that (i) both warming and eO_3 would increase SRL, reduce RTD, and shift AMF community composition in planta; (ii) warming- and eO_3-induced changes in root traits and AMF would promote root-mediated microbial decomposition of organic C in soil; and (iii) concurring warming and eO_3 would aggravate their effects on plant roots and organic C decomposition.

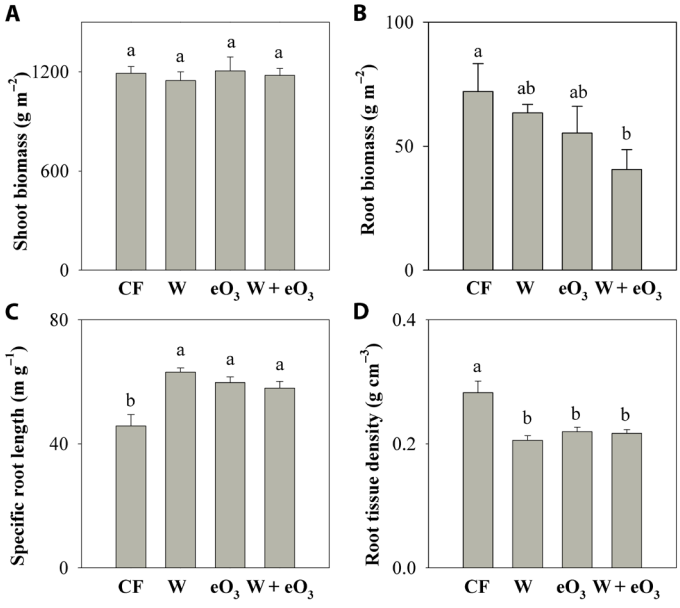

Fig. 1. Effects of warming and eO_3 on plant traits. Shoot biomass (**A**), root biomass (**B**), SRL (**C**), and RTD (**D**). Data are means ± SE ($n = 3$). The four treatments are as follows: CF, charcoal-filtered ambient air; W, warming; eO_3, elevated O_3; W + eO_3, warming + eO_3. Different letters mean significant differences at $P = 0.05$ level under different treatments.

RESULTS AND DISCUSSION

Field manipulations of temperature and O_3 concentration were achieved through the air exclusion system (AES) (fig. S1), leading to an average temperature across the growing season at 24.7° and 27.6°C in the ambient temperature and warming plots, respectively, and O_3 concentrations at 19.5 and 65.8 parts per billion by volume (ppbv) in the low (CF and W) and elevated O_3 (eO_3 and W + eO_3) plots, respectively (Table 1).

Warming and eO_3 significantly influenced root biomass, although they did not affect shoot biomass (Fig. 1, A and B, and table S2). Effects of warming and eO_3 in the combined treatment appeared to be additive with no warming-ozone interaction observed (table S2). In particular, eO_3 alone reduced root biomass by 23%, and its combination with warming additively reduced root biomass by 44% (Fig. 1B and tables S2 and S4). Warming, eO_3, and their interaction

significantly increased SRL by 38, 31, and 27% (Fig. 1C and table S2) and root surface area by 30, 25, and 22% (fig. S4C and table S2), respectively. In contrast, they significantly reduced RTD by 27, 22, and 23%, respectively (Fig. 1D and table S2). These tradeoffs between root length/surface area and root density indicate that warming and eO_3 prompted plants to construct long, less dense roots with limited biomass investment and increase root surface that would allow to optimize belowground resource acquisition.

We then examined how warming and eO_3, alone or in combination, affected mycorrhizal colonization of host plant roots. Warming and eO_3, alone or in combination, all significantly reduced the proportion of root length colonized by AMF (Fig. 2A and table S2), which contrasted with the positive effects of warming, eO_3, and their combination on SRL (Fig. 1C). Regression analysis showed that root specific length was significantly negatively related with the AMF colonization rate of roots, indicating a tradeoff between fine roots and AMF (Fig. 2B). Plant species with long, narrow-diameter roots tend to have low dependence on mycorrhizal fungi at both local and global scales (*38*, *39*). These results, together with reduced root density (Fig. 1D), suggest that plants may optimize their C allocation for resource acquisition through developing roots with higher SRL and surface area over AMF under future climate warming and eO_3 conditions.

Warming- and eO_3-induced changes in plant photosynthate allocation belowground to roots may differentially affect AMF species as they have distinct life history strategies and C requirements (*43*, *44*). To examine whether warming and eO_3 may also lead to shifts in the AMF composition in roots, we characterized the AMF community composition via MiSeq sequencing. Our results showed that across all treatments, *Glomus* (46.6%) and *Paraglomus* (48.2%) were the most abundant, followed by *Claroideoglomus* (3.7%) and *Gigaspora* (1.0%) (Fig. 3A, fig. S5, and table S5). Nonmetric multidimensional scaling (NMDS) ordination and permutational multivariate analysis of variance (PERMANOVA) revealed a significant effect of warming and eO_3 on the taxonomic composition of AMF communities, leading to a clear separation in the AMF communities between the control and warming, eO_3, or their combination treatment (Fig. 3B). In particular, warming reduced *Glomus* but increased *Paraglomus* (Fig. 3A and table S2). *Paraglomus* or *Gigaspora* species often have more extensive extraradical hyphal network than *Glomus* ones (*46*, *47*). As soybean plants mainly rely on N fixation by symbiotic rhizobia for N nutrient (*48*), eO_3 may negatively affect the level of root nodulation and reduce the rate of N fixation (*49*). Also, warming and eO_3 may significantly affect soybean N fixation through affecting the tripartite association of plant, rhizobia, and AMF (*50*), although these effects were not the focus of this study. Soybean plants can also better obtain N through water uptake under warming, and an increase in *Paraglomus* species may help plant acquisition of less mobile nutrients such as phosphorus (P) (*51*, *52*). We also observed that eO_3 reduced *Glomus* abundance but increased *Paraglomus* abundance (Fig. 3A and table S2), providing direct evidence of O_3-led alteration of in planta AMF community composition.

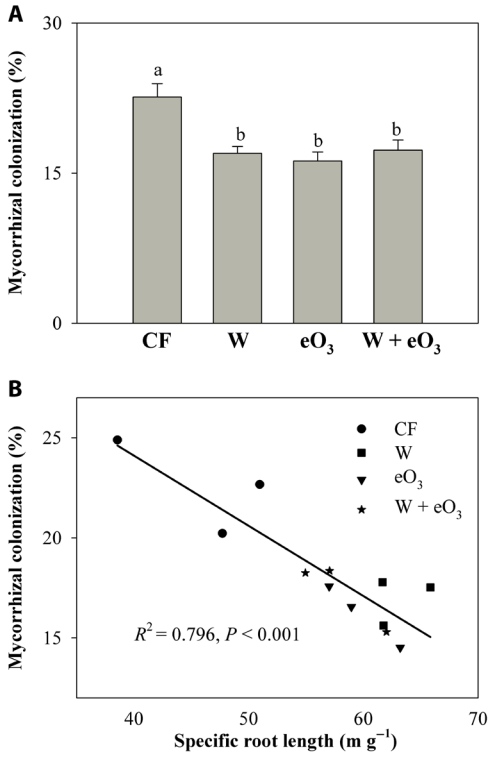

Fig. 2. Effects of warming and eO_3 on mycorrhizal colonization of soybean roots. Mycorrhizal colonization rates (**A**) and the relationship between mycorrhizal colonization of soybean roots and SRL (**B**) Data are means ± SE ($n = 3$). The four treatments are as follows: CF, charcoal-filtered ambient air; W, warming; eO_3, elevated O_3; W + eO_3, warming + eO_3. Different letters mean significant differences at $P = 0.05$ level under different treatments. Relationship was considered significant if $P < 0.05$.

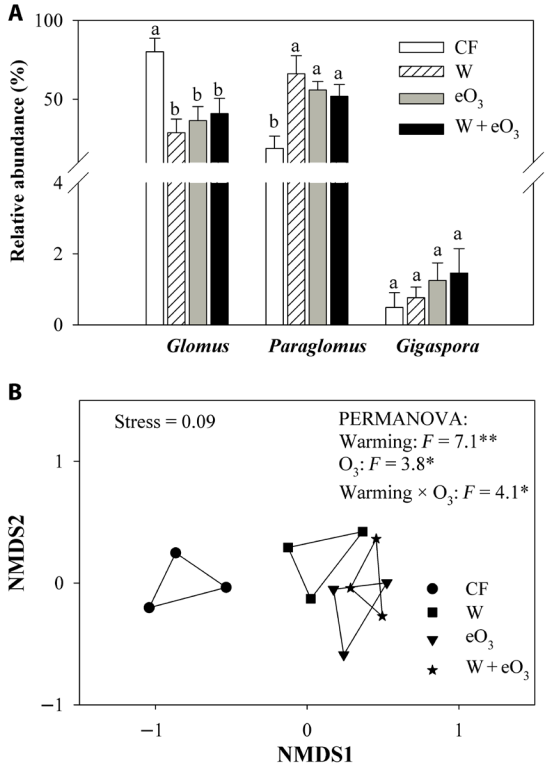

Fig. 3. Effects of warming and eO_3 on AMF community composition in soybean roots. Relative abundance of *Glomus*, *Paraglomus*, and *Gigaspora* (**A**) and NMDS of community composition of AM fungal VT colonizing soybean roots among different treatments (**B**). Data are means ± SE ($n = 3$). The four treatments are as follows: CF, charcoal-filtered ambient air; W, warming; eO_3, elevated O_3; W + eO_3, warming + eO_3. In (A), different letters denote significant differences at $P = 0.05$. In (B), *$0.01 < P \leq 0.05$; **$0.001 < P \leq 0.01$.

Previously, Cotton *et al.* (*44*) observed no significant eO_3 effects on AM fungal community composition, richness, and evenness from the SoyFACE experiment at the University of Illinois, but their plants sampled may be too young (around 8 weeks) to fully reflect the eO_3 impact on AMF. In comparison, Wang *et al.* (*53*) found that eO_3 significantly altered the general soil microbial community under a hybrid maize but did not assess the impact on the AMF composition. The warming- and O_3-induced shift in favor of *Paraglomus* over *Glomus* observed in our study (Fig. 3A) likely stems from their different C requirements. Since *Paraglomus* in general form smaller spores and have smaller C demand than *Glomus* species (*46*, *51*, *54*), they may likely more efficiently use scarce C resources under environmental stresses while obtaining nutrients at lower energy costs.

To examine the potential impact of warming- and/or eO_3-induced changes in roots and AMF on ecosystem functioning, we assess microbial decomposition of organic C in the mycorrhizosphere. Given that AMF are obligately biotrophic, we used different sizes of mesh to isolate the effect of AMF from their host roots (*30*). While the hyphae-ingrowth chambers (mesh size at 20 μm) only allow AMF hyphal penetration, the root-ingrowth chambers (mesh size at 1.8 mm) permit both roots and AMF to grow inside (fig. S2). Exact 1.80 g of ^{13}C-enriched materials [aboveground residues of switchgrass, a C_4 plant with $\delta^{13}C = -11.51‰$ (per mil)] was thoroughly mixed with 180.0 g of the field soil (with $\delta^{13}C = -23.79‰$), and the soil-residue mixture was then introduced into each chamber to trace the C dynamics. Thirteen weeks after the placement of hyphae- or root-ingrowth chambers, the presence of AMF alone or AMF with roots significantly stimulated soil C decomposition within hyphae- and root-ingrowth chambers (Fig. 4A and table S3; also see ^{13}C in fig. S6). Neither warming nor eO_3 had any significant impact on soil C in the no-AMF control (Fig. 4A and table S3; also see ^{13}C in fig. S6). In the presence of AMF alone, however, warming, eO_3, and their interaction significantly reduced total soil C by 8, 7, and 9%, respectively (Fig. 4A and table S3). In the presence of both plant roots and AMF, warming, eO_3, and their interaction reduced total soil C more significantly by 11, 14, and 12%, respectively (Fig. 4A and table S3). Also, mycorrhizal colonization rate was positively correlated with total C remaining in the AMF- and root-ingrowth chambers (Fig. 5, B and C). Further, the relative abundance of *Glomus* was positively correlated with total C remaining in the AMF- and root-ingrowth chambers (Fig. 6, C and E). In contrast, the relative abundance of *Paraglomus* was negatively correlated with total C remaining in the AMF- and root-ingrowth chambers (Fig. 6, D and F). Through quantifying ^{13}C remaining within hyphae- and root-ingrowth chambers, we further found that warming, eO_3, and their interaction significantly enhanced the loss of the residue-derived organic C in the presence of AMF alone and roots with AMF (Fig. 4B and table S3).

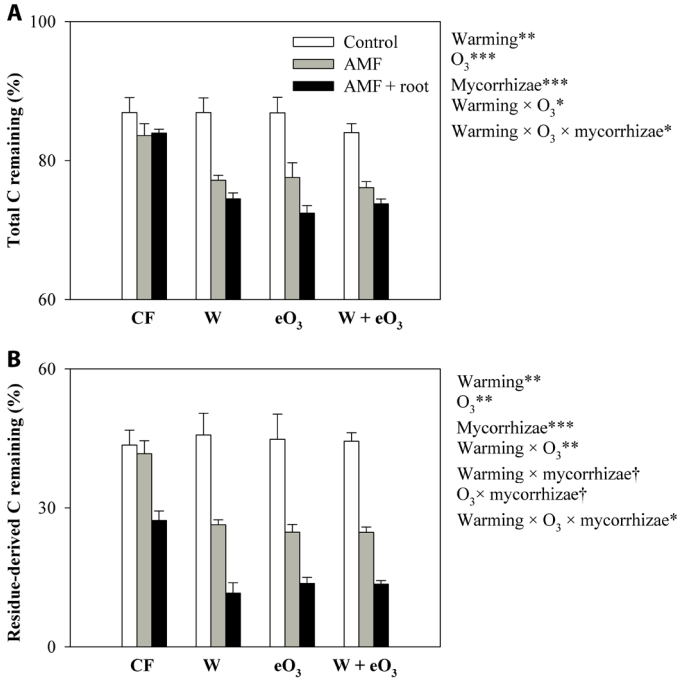

Fig. 4. Warming and eO_3 modulated the effects of plant roots and their associated AMF on organic C decomposition. (**A**) Effects on total soil C remaining (%) and (**B**) effects on the residue organic C remaining (%) as determined by ^{13}C remaining within no-hyphae–, hyphae-, and root-ingrowth chambers. Data are means ± SE ($n = 3$). Control, neither AMF nor roots growing into the chamber; AMF, AMF hyphae but not roots growing into the chamber; AMF + root, both AMF hyphae and roots growing into the chamber. The significance levels are labeled with †$0.05 < P \leq 0.10$; *$0.01 < P \leq 0.05$; **$0.001 < P \leq 0.01$; ***$P \leq 0.001$.

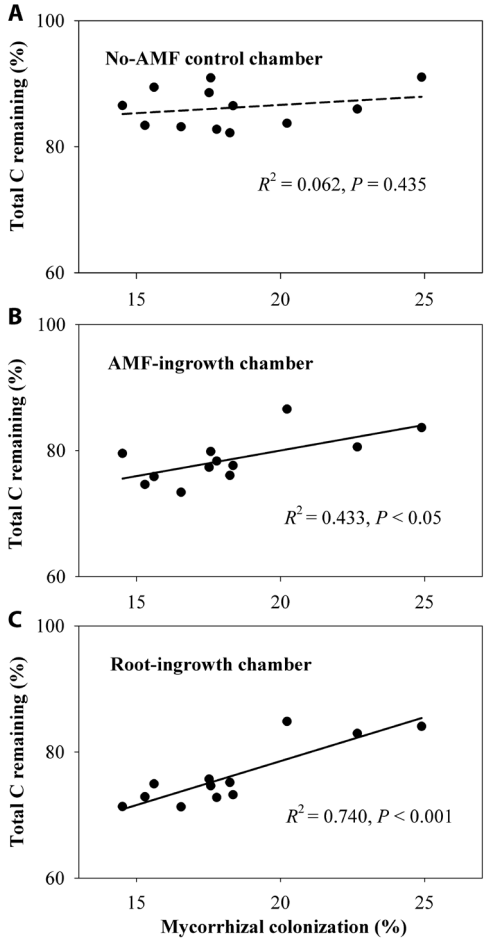

Fig. 5. Warming and eO_3 modulated the relationships between AMF colonization rates of soybean roots and total C remaining. Relationships between mycorrhizal colonization of soybean roots and total C remaining (%) within (**A**) no-hyphae–, (**B**) hyphae-, and (**C**) root-ingrowth chambers across different climate change treatments. Relationships were considered significant if $P < 0.05$.

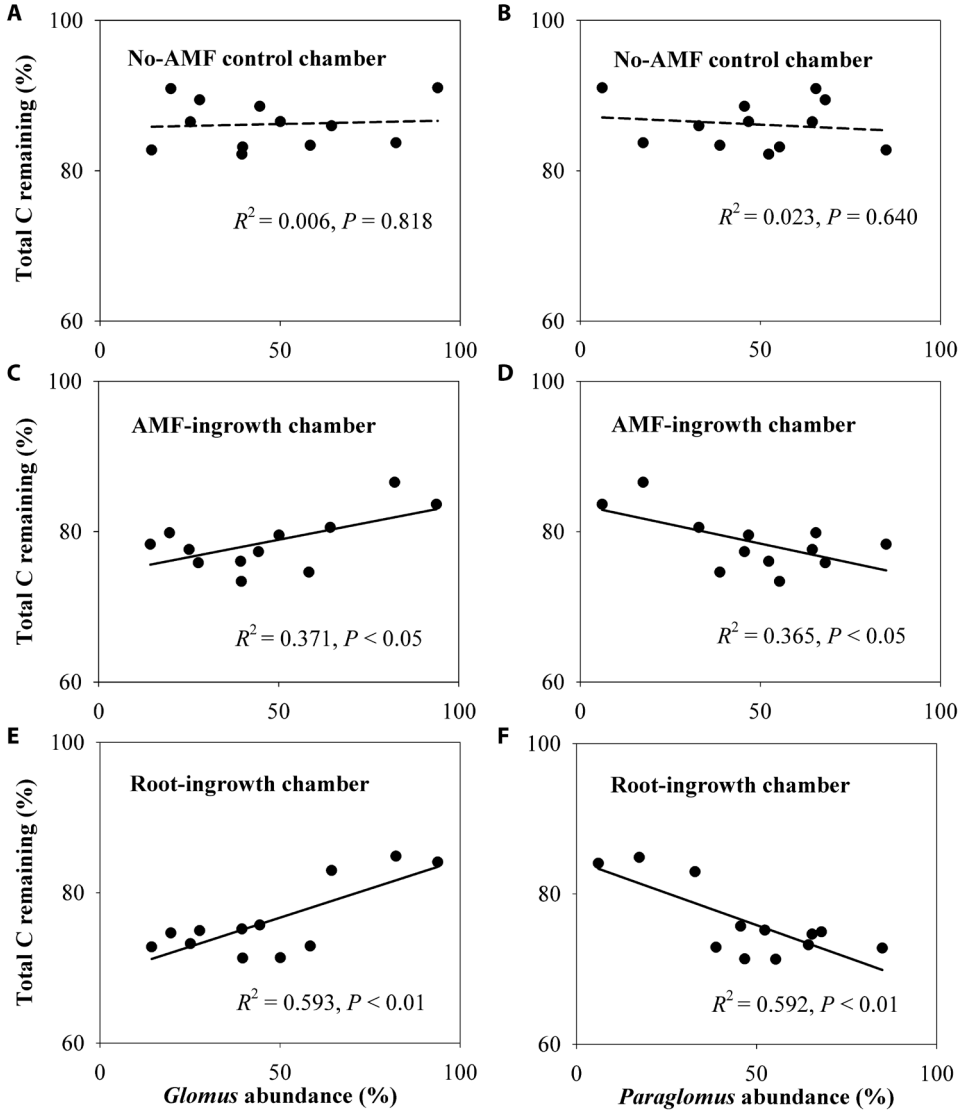

Fig. 6. Warming and eO_3 modulated the relationships between AMF composition and total C remaining. Relationships between the relative abundance of *Glomus* (**A**, **C**, and **E**) or *Paraglomus* (**B**, **D**, and **F**) in soybean roots and total C remaining (%) within no-hyphae–, hyphae-, and root-ingrowth chambers across different climate change treatments. Relationships were considered significant if $P < 0.05$.

The significantly increased organic C decomposition in the presence of AMF or roots (Fig. 4) indicated that changes in roots and AMF under warming and eO_3 can modify C and N dynamics. The changes in root traits (increased SRL and reduced RTD), decreased colonization of roots by AMF, and shifts in the AMF community composition may cascade up to affect ecosystem C dynamics through several mechanisms. First, roots with lower density are more fragile and turn over faster, as root life span often correlates negatively with SRL and positively with RTD (*40*, *41*). Second, reduced AMF colonization under warming and eO_3 (Fig. 2A) may increase root exudation (*55*). Significantly increased microbial biomass C and N under warming, despite having no effects on plant root biomass and decreased AMF colonization (Figs. 1B and 2A and table S1), provide direct evidence indicating increased labile C availability for saprophytic microbes, which likely prime the decomposition of organic C in soil. Third, plant roots and AMF are major binding agents for soil aggregating through enmeshing microaggregates into macroaggregates (*35*, *36*), and decreased RTD and AMF under warming and eO_3 (Figs. 1D and 2A) would reduce the capacity of roots and AMF for aggregation (*36*, *42*). Last, AMF produce secondary compounds such as polysaccharides that function as important binding agents and can protect organic C from microbial decomposition (*35*, *56*). In particular, *Glomus* species can produce glycoprotein-type compounds (e.g., glomalin) that likely enhance soil organic C stability (*34*), as supported directly by the positive correlations between organic C remaining and AMF colonization rate (Fig. 5, B and C) or *Glomus* abundance (Fig. 6, C and E) and indirectly by the negative correlations between the organic C remaining and *Paraglomus* abundance (Fig. 6, D and F). Consequently, enhanced C availability for saprophytic microbes due to increased root turnover and reduced protection of soil organic materials due to decreases in root strength and AMF colonization may jointly facilitate the microbial turnover of soil organic C.

Our findings illustrate that concurring climate warming and eO_3 under future climate change scenarios may elicit a cascade of events

that alter root traits and AMF communities, thereby stimulating root turnover and organic C decomposition. What is interesting is that these two different factors converged in driving similar effects on plant traits and root symbionts. This convergence may likely occur because both factors function as a stress to plants that often reduces plant C fixation and/or plant carbohydrate allocation belowground (*25*, *57*). A reduction in plant photosynthate supply likely prompts changes in root traits and root symbionts that allow to optimize resource acquisition at the minimum energy cost. Warming and O_3 enhancement of soil organic C decomposition as a result of the root-AMF tradeoffs observed in our study may have some important implications for soil C dynamics. A meta-analysis found that ambient O_3 concentration (ca. 40 ppb on average) in the Northern Hemisphere may have reduced the total biomass of trees in the temperate forests by 7%, compared with trees grown in charcoal-filtered controls (*26*). A further increase of O_3 concentration to 64 ppb would reduce total biomass by 11%, compared with trees grown at the current ambient concentration (*26*). In agroecosystems, model analyses estimated that ozone (mean concentration of 2010 to 2012) reduced global yield annually by 12.4, 7.1, 4.4, and 6.1% for soybean, wheat, rice, and maize, respectively (*58*). Results from meta-analyses showed that compared to their respective controls in charcoal-filtered air, chronic exposure to ozone of 62 ppb, on average, reduced rice yield by 14% (*59*), and an increase to 70 ppb reduced soybean shoot biomass by 34% (*60*). Moreover, soybean plants exposed to warming (*57*, *61*) and eO_3 (*49*, *60*) may reduce the level of root nodulation and/or the rate of nitrogen fixation, negatively feeding back to plant production. Reduced detritus inputs and warming and O_3 stimulation of the priming effect may likely affect soil C dynamics. For example, Loya *et al.* (*8*) documented that a 50% increase in the ozone concentration for 4 years caused a 6.5% decrease in total soil C in the aspen and mixed aspen-birch forests. O_3 stimulation of decomposition may have contributed to this decrease as reduced litter input alone cannot fully explain the observed total soil C loss (*8*). In agroecosystems, O_3 suppression of biomass production and/or yield likely occurs with reduced return of crop residues, the primary organic matter source of soil organic C (*62*). Together, O_3 suppression of residue inputs, combined with warming and O_3 stimulation of root turnover and organic C decomposition, may exacerbate soil C losses, constraining the capacity of terrestrial ecosystems for C sequestration in a warmer world.

MATERIALS AND METHODS

The study site and experimental manipulations

This study was a component of a long-term field manipulation experiment at the Lake Wheeler farm of North Carolina State University, Raleigh, NC, USA (35°43′N, 78°40′W; elevation, 120 m) (*63*). The field experiment was established in June 2013. The field manipulation experiment had a 2 × 2 factorial design with two levels of temperature (ambient versus elevated +3°C) and two targeted concentrations of O_3 (low at 20 ppbv versus high at 60 ppbv) in a soybean agroecosystem (*63*, *64*). This led to a total of four treatment combinations: (a) charcoal-filtered air and ambient temperature (CF); (b) charcoal-filtered air plus 3.0°C increase in temperature (W); (c) charcoal-filtered air plus ambient temperature and 1.3 times ambient ozone (eO_3); (d) charcoal-filtered air + warming + 1.3 times ambient ozone (W + eO_3). AESs (fig. S1) (3 m by 10 m each) were used to control the temperature and O_3 concentration, and all AESs were laid out in a randomized block design with three replicates of each treatment. Each AES consisted of two double-walled, open-top chamber panels attached to aluminum frames and placed in parallel. The warming treatments (W and W + eO_3) were achieved by addition of warming, humidified air to increase the ambient air temperature by 3.0°C, taking the control (CF) as the baseline (*63*). In this system, electrical resistance heaters and solar-heated water were used to warm the air. O_3 was generated from oxygen (O_2) by corona discharge (model TG-20, Ozone Solutions, Hull, IA, USA) and dispensed 12 hours daily to each plot in proportion to ambient O_3 concentrations. Air temperature and relative humility and O_3 concentration were constantly monitored (by HOBO Pro V2 Temp/RH Datalogger and an ultraviolet photometric O_3 analyzer, respectively) by an automatic system in an adjacent trailer. On the basis of these results, the feedback system automatically regulated the heat release or O_3 release (please see Supplementary Materials and Methods for details). All plots were planted with a soybean cultivar Asgrow AG5232 in 2013, Asgrow AG5633 in 2014, and with soybean cultivar "Jake" in 2015 and 2016 (*63*, *64*).

Plant and soil sampling

In September 2016, soybean plants (cultivar Jake) of approximately the same age at the pod filling stage were harvested at the soil surface from each plot to determine shoot biomass (*63*). Three plant roots were sampled from each plot to determine root biomass and characterize root morphological parameters and their associated AMF (see Supplementary Materials and Methods for details). Three soil cores (5 cm diameter, 0 to 10 cm depth) from each plot were randomly taken and mixed to form one composite sample.

Determinations of soil chemical and microbial properties, root morphologies, mycorrhizal colonization of roots, and AMF community composition in roots

Soil ammonium (NH_4^+) and nitrate (NO_3^-), extractable organic C, and microbial biomass C and N were measured (see Supplementary Materials and Methods for details). Each root sample was scanned on a desktop scanner, and images were processed with WinRHIZO (Regent Instruments Inc.) to determine root morphological parameters (root diameter, length, surface area, and volume). SRL was determined by dividing root length by the dry biomass weight. RTD was calculated by dividing dry mass by volume. Mycorrhizal colonization of plant roots was microscopically determined after roots were stained with acidic glycerol–trypan blue solution at 90°C for 30 min (*65*) and scored using gridline intersection (*66*).

Mycorrhizal fungal DNA was extracted from a 0.05-g (freeze-dried) subsample of fine roots with a PowerPlant DNA Isolation Kit (MoBio Laboratories Inc., Carlsbad, CA, USA). The quantity and purity of DNA samples were determined using a NanoDrop ND-1000 spectrophotometer (Thermo Fisher Scientific, Wilmington, DE, USA). The primer set AMV4.5NF (5′-AAGCTCGTAGTTGAATTTCG-3′)/AMDGR (5′-CCCAACTATCCCTATTAATCAT-3′) was used to amplify the 18*S* ribosomal RNA (rRNA) gene (*67*). The polymerase chain reaction products were purified with an agarose gel DNA purification kit (AP-GX-250G; Axygen, Union City, CA, USA) and quantified using a NanoDrop ND-1000 spectrophotometer. The purified products were pooled in equimolar amounts and then sequenced on the Illumina MiSeq platform (Shanghai Personal Biotechnology Co. Ltd., Shanghai, China) (see Supplementary Materials and Methods for details).

Raw high-throughput sequencing data were processed by using the Quantitative Insights Into Microbial Ecology (QIIME) toolkit (*68*). Potentially similar sequences were clustered into operational taxonomic units (OTUs) using the seed-based UCLUST algorithm at a 97% identity threshold. The most abundant sequence from each OTU was selected as the representative sequence. To compare our results with other studies, the representative sequences were checked against the MaarjAM database and defined in virtual taxa (VT), roughly corresponding to species-level taxa for further analysis (*69*). The MaarjAM database classifies the central part of Glomeromycotina small subunit rRNA gene sequences into phylogenetically delimited sequence clusters, VT (*69*).

Determination of root and mycorrhizal priming of organic C decomposition

One week after soybeans were planted in June 2016, three ingrowth chambers (a no-hyphae chamber, pore size: 0.45 μm; a hyphae-ingrowth chamber, pore size: 20 μm, and a root-ingrowth chamber, pore size: 1.8 mm) (fig. S2) were randomly buried into each AES plot to assess the impacts of AMF hyphae and roots on organic C decomposition, respectively. Each chamber was filled with 1.80 g of residues of switchgrass (a C_4 plant with $\delta^{13}C = -11.51‰$) and 180.0 g of the field soil (with $\delta^{13}C = -23.79‰$) to trace the C dynamics. After incubation for 13 weeks, all the chambers were retrieved on the same day. Total C and ^{13}C of sample were measured using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK) at the University of California, Davis (*30*). To estimate the net losses of residue-derived C by the mycorrhizal effect, we calculated the mean proportion (f_R) of the residue C in the incubated samples using the equation $f_R = (\delta^{13}_M - \delta^{13}_S)/(\delta^{13}_R - \delta^{13}_S)$, where δ_M, δ_R, and δ_S denote the mean isotopic signatures ($\delta^{13}C$) for the mixture M (incubated samples of soil/residue mixture), source R (residue, which is −11.51‰), and source S (soil, which is −23.79‰), respectively. Although this two-pool model did not allow us to quantify the exact amounts of the organic C derived from root exudates and AMF, it allowed us to estimate the impacts of AMF and roots on organic C decomposition inside the growth chambers (see Supplementary Materials and Methods for details).

Statistical analysis

All statistical analyses were performed using R 3.6.2 (*70*). We used linear mixed-effects models (LMMs) to examine the effects of warming, ozone, and their interactions on plant biomass, soil chemical and microbial parameters, AMF colonization of roots, and root morphological parameters. We also used LMMs to examine the effects of warming, ozone, mycorrhizae, and their interactions on C remaining within hyphae- and root-ingrowth chambers. Treatment was used as a fixed effect and block as a random effect. Linear regression was performed to examine the relationship between SRL and AMF colonization of roots.

The structure of AMF communities was compared using the proportion of different VT reads as a proxy for the relative abundance of AMF taxa per sample (*69*). To visualize variation in AM fungal communities across experimental treatments, NMDS ordination analysis based on the Bray-Curtis distance matrix was performed, using function "metaMDS" from R package vegan (*71*). To test the effects of the experimental treatments on AM fungal composition, we performed two-way PERMANOVA using the default settings, with the function "adonis" from R package vegan (*71*). For all tests, $P < 0.05$ was considered a statistically significant difference.

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at http://advances.sciencemag.org/cgi/content/full/7/28/eabe9256/DC1

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