Organic matter priming by invasive plants depends on dominant mycorrhizal association

Amit Kumar a,*, 1, Richard P. Phillips b, Andrea Scheibe b, Saskia Klink a, Johanna Pausch a

a Department of Agroecology, University of Bayreuth, Universitätsstr. 30, 95440, Bayreuth, Germany
b Department of Biology, Indiana University, 1001 E Third St, Bloomington, IN, 47403, USA

ARTICLE INFO

Keywords:
C natural abundance
CO 2 emission
Flux partitioning
Microbial activation
Rhizosphere priming effects
Mycorrhizal-associated nutrient economy (MANE)

ABSTRACT

While it has long been held that invasive plants alter ecosystem processes, the magnitude and direction of these effects have rarely been quantified in situ. We measured the effects of an invasive C 4 grass ( Microstegium vimineum ) on soil organic matter (SOM) decomposition in a deciduous forest in south-central Indiana, USA. The unique 13 C signature of the C 4 grass relative to the C 3 trees allowed us to partition soil CO 2 fluxes and estimate M. vimineum effects on decomposition. The magnitude and direction of priming effects hinged on the soil characteristics, which related to the mycorrhizal association of dominant trees. In forest plots dominated by ectomycorrhizal trees, with low nitrogen availability and most SOM in particulate (i.e., unprotected) forms, M. vimineum increased SOM decomposition by 58%. In contrast, in plots dominated by arbuscular mycorrhizal trees, characterized by high nitrogen availability and most SOM in mineral-associated (i.e., protected) forms, M. vimineum decreased decomposition by 14%. Collectively, our results demonstrate that invasive species can play a large role in altering ecosystem processes and suggest that the magnitude and direction of such effects depend on the dominant trees and edaphic characteristics of the stand.

Understanding the sensitivity of soil organic matter (SOM) decomposition to environmental change is critical given the massive stores of carbon (C) in soils globally ( Lal, 2008 ). While numerous studies have examined the sensitivity of SOM decomposition to warming, nitrogen (N) deposition, elevated CO 2 and precipitation change ( Song et al., 2019 ), far fewer have investigated the role of invasive plants in altering SOM dynamics. Plant invasions can have strong effects on soil C and N cycling ( Liao et al., 2008 ) and there is a need to quantify and better understand how and why invaders impact SOM within and across ecosystems ( Parker et al., 1999 ; Strayer, 2012 ; Vilà et al., 2011 ; Huíme et al., 2013 ).

Many invasive plants produce fast-decaying litter ( Jo et al., 2017 ) and root-derived products ( Bradford et al., 2012 ; Morris et al., 2016 ) that are presumed to accelerate SOM decomposition via ‘priming effects’. Priming effects occur when soil microbes use energy from leaf ( Chao et al., 2019 ) or root ( Pausch et al., 2013 ; Kumar et al., 2016 ) inputs to synthesize extracellular enzymes in order to mine N from indigenous SOM, resulting in SOM decay ( Cheng and Kuzyakov, 2005 ). While numerous studies have reported smaller SOM stocks in invaded soils vs. uninvaded soils ( Peltzer et al., 2010 ), direct field measurements of priming based on soil CO 2 emissions are exceedingly rare given the challenges of quantifying SOM decomposition in situ. 

 Microstegium vimineum (Japanese stiltgrass) is a non-native C 4 grass that invades forest understories throughout the eastern U.S ( Flory and Clay, 2010 ) and is known to accelerate C and N cycling ( Ehrenfeld et al., 2001 ; Lee et al., 2012 ; Shannon-Firestone et al., 2015 ). Several studies have reported lower SOM in M. vimineum-invaded soils relative to adjacent uninvaded plots ( Strickland et al., 2010 ; Craig and Fraterrigo, 2017 ; Craig et al., 2019 ), leading to speculation that the invader may activate microbes to decay SOM ( Sokol et al., 2019 ). Nevertheless, there is no direct evidence of C fluxes resulting from priming by M. vimineum and the role of tree species and edaphic factors in shaping the magnitude and direction of invader-induced priming effects has not yet been investigated.

The Mycorrhizal-Associated Nutrient Economy (MANE) hypothesis ( Phillips et al., 2013 ) provides a framework for considering variability in invader impacts on SOM dynamics. Forest plots dominated by arbuscular mycorrhizal (AM) trees typically have fast-decaying litters...
Soil Biology and Biochemistry 140 (2020) 107645

Table 1
Soil properties in uninvaded EcM and AM stands in Moore’s creek forest reserve (Phillips et al., 2013; Craig et al., 2019).

<table>
<thead>
<tr>
<th>Soil properties</th>
<th>EcM soil</th>
<th>AM soil</th>
</tr>
</thead>
<tbody>
<tr>
<td>Soil pH</td>
<td>4.27 ± 0.09</td>
<td>5.23 ± 0.24</td>
</tr>
<tr>
<td>DOC</td>
<td>0.64 ± 0.06</td>
<td>0.32 ± 0.04</td>
</tr>
<tr>
<td>Organic N/Inorganic N</td>
<td>255 ± 50</td>
<td>159 ± 28</td>
</tr>
<tr>
<td>Nitrification rates</td>
<td>∼0.001</td>
<td>1.05 ± 0.21</td>
</tr>
<tr>
<td>Decomposition rates</td>
<td>9.8 ± 1.6</td>
<td>17.7 ± 2.8</td>
</tr>
<tr>
<td>POM-N: MAOM-N</td>
<td>1.57 ± 0.76</td>
<td>0.96 ± 0.38</td>
</tr>
<tr>
<td>POM-C: MAOM-C</td>
<td>2.16 ± 0.93</td>
<td>1.36 ± 0.50</td>
</tr>
</tbody>
</table>

DOC: mg organic C g⁻¹ soil; nitrification rates: µg NO3⁻ N g⁻¹ soil d⁻¹; decomposition rates: % litter mass loss; POM-N (C): particulate organic matter-nitrogen (carbon); MAOM-N (C): mineral associated organic matter-nitrogen (carbon).

DOE and EEM represents uninvaded plots whereas AM_Mv and EcM_Mv represents plots invaded by M. vimineum. Total CO2 emission was partitioned into SOM-derived and M. vimineum-derived (M.v.-derived). Different letters indicate significant differences (Tukey’s post-hoc test, P < 0.05) of total CO2 emission between invasion and type of mycorrhizal association.

Fig. 1. Miller/Tans model for purification of the δ¹³C value of soil CO2 from atmospheric admixture. The slope of the regression line (OLS) represents the isotopic composition of pure soil CO2. A reference plot without invasion (grey diamonds) and a plot with M. vimineum invasion (green diamonds) are shown exemplarily. With invasion, soil CO2 shifts towards more positive δ¹³C values due to an influence of the C4 signal from M. vimineum. EcM represents uninvaded plots whereas EcM_Mv represents the plots invaded by M. vimineum. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Fig. 2. Total CO2 emission (µmol CO2 m⁻² s⁻¹ ±SE) from AM and EcM plots. AM and EcM represents uninvaded plots whereas AM_Mv and EcM_Mv represents plots invaded by M. vimineum. Total CO2 emission was partitioned into SOM-derived and M. vimineum-derived (M.v.-derived). Different letters indicate significant differences (Tukey’s post-hoc test, P < 0.05) of total CO2 emission between invasion and type of mycorrhizal association.

(Midgley et al., 2015; Keller and Phillips, 2019), high inorganic N availability (Midgley and Phillips, 2016; Mushinski et al., 2019), lower standing fungal biomass and fungal to bacterial ratio (Cheeke et al., 2017), and large stocks of mineral-associated (i.e., protected) organic matter (Craig et al., 2018, 2019). In contrast, plots dominated by ectomycorrhizal (EcM) trees have slow-decaying litters, low inorganic N availability, and large stocks of particulate (i.e, unprotected) organic matter. Given that priming depends on the chemical quality of plant inputs, nutrient availability, structure and functioning of microbial communities, and the degree to which the SOM is protected from decay (Cheng et al., 2014), priming effects are believed to be greater in EcM-dominated plots relative to AM-dominated plots (Fontaine and Barot, 2005; Brzostek et al., 2015; Sulman et al., 2017). However, the degree to which priming by invasive plants differs between AM- and EcM-dominated plots is unknown.

We quantified invader-induced SOM priming effects in adjacent AM- and EcM-dominated plots at Indiana University’s Moores Creek Research and Teaching preserve in the south-central Indiana, USA. The forest plots are classified into AM- and EcM-plots based on known mycorrhizal associations of dominant tree species, in which, trees associated with dominant mycorrhizal type represented more than 80% of the basal area of the plot. The AM plots mainly contained a mixture of tulip poplar (Liriodendron tulipifera), sugar maple (Acer saccharum), and sassafras (Sassafras albidum), whereas, American beech (Fagus grandifolia), pigmut hickory (Carya glabra), black oak (Quercus velutina), white oak (Q. alba), and red oak (Q. rubra) are the predominant species at the EcM plots (see Phillips et al., 2013; Mushinski et al., 2019 for detailed site description). Four M. vimineum-invaded and four uninvaded plots (80 x 80 cm) within EcM- and AM-dominated plots were identified and trenched to a depth of 30–35 cm. After trenching, three PVC collars (inner diameter 5 cm) were installed randomly to a depth of 3 cm within each plot. Extra care was taken during trenching and PVC collar installation to minimize the soil disturbance and allowed to establish for c. 3 weeks. Both the plots had similar abundances of M. vimineum, but differed in a number of soil characteristics (Table 1).

We hypothesized that M. vimineum accelerates SOM decomposition in EcM-dominated plots more than AM-dominated plots owing to the lower N availability and greater fraction of unprotected SOM in the EcM-relative to the AM-dominated plots. To test our hypothesis, we took advantage of differences in the δ¹³C natural abundance between sources of soil CO2 emission (native SOM-derived vs. M. vimineum-derived) as a proxy for SOM decomposition. Trees with C4 photosynthetic pathways have unique δ¹³C values (~27.6% in EcM trees and ~27.1% in AM trees) relative to the δ¹³C signature of the C4 grass M. vimineum (~14.39%). This enabled us to partition the source of soil CO2 emission and to calculate SOM priming under natural conditions. The δ¹³C of pure soil CO2 efflux was calculated after correcting the measured δ¹³C value for the atmospheric CO2 admixture based on the Miller/Tans model (Miller and Tans, 2003; Pausch and Kuzyakov, 2012) (Fig. 1). Priming effects (PE) were calculated as the difference of SOM-derived CO2 between M. vimineum-invaded (C4 (M.vimineum-invaded)) and uninvaded plots (C4 (uninvaded)):

\[ PE = C4 (M.vimineum-invaded) - C4 (uninvaded) \]

Where C4 (uninvaded) is the total CO2 efflux from the uninvaded plots (see supplementary material for detailed site description, measurements and calculations).

Rates of soil CO2 emission between the uninvaded AM and EcM plots remained similar whereas recent invasion by M. vimineum resulted in increased rates of soil CO2 emission in EcM plots only (Fig. 2). On average, M. vimineum increased rates of CO2 emission by 41% compared to uninvaded plots. In invaded plots, a linear two-source isotopic mixing model was used to partition the total CO2 to its sources (SOM-derived and M. vimineum-derived CO2). M. vimineum resulted in a net positive SOM priming in EcM plots of 2.26 µmol CO2 m⁻² s⁻¹ - a 58% increase.
compared to uninvaded plots (Fig. 3). In contrast, invasion resulted in a 14% reduction in SOM-derived CO2 in AM plots resulting in a negative SOM priming (Fig. 3).

Previous studies have reported links between invasive plants, microbial activities and accelerated SOM loss (Strickland et al., 2010; Bradford et al., 2012; Sokol et al., 2019; Craig et al., 2019); however, direct measurements of invader-induced priming effects in situ are rare. Our results showed that invader-induced priming can be appreciable (58% increase in SOM loss), and that site level factors (ository community and edaphic characteristics) mediate this effect. Trace amounts of exudates can boost microbial metabolism and activity (De Nobili et al., 2001). Given the strong competition for N in Ecm plots at this site (Midgley and Phillips, 2016), microbes stimulated by invader inputs may need to mine SOM for N (Craine et al., 2007). Moreover, higher fungal to bacterial ratios, and a shift in enzymatic stoichiometry to higher investment in extracellular enzyme production for nutrient rather than C acquisition in EcM than AM plots (Cheeke et al., 2017), can be directly linked to accelerated SOM decomposition through nutrient mining (Fontaine and Barot, 2005). This finding highlights the role of soil microbial communities as drivers of priming effects (McGuire et al., 2010; Taylor et al., 2016; Cheeke et al., 2017). In AM-dominated plots where N is abundant and competition for N is reduced (Midgley and Phillips, 2016), microbes may preferentially use C exuded by the invaders, resulting in reduced metabolic costs and less SOM decomposition leading to negative priming effects. Additionally, the accumulation of unprotected SOM in EcM soils owing to the slow decomposition of EcM tree litter was likely more vulnerable to priming than the protected SOM in AM soils that was formed from fast-decaying litter (Cotrufo et al., 2013; Averill and Hawkes, 2016; Salman et al., 2017). Furthermore, recent studies that have tracked the flow of M. vimineum litter into soil pools have found that as particulate organic matter decays, it leads to more mineral-associated OM formation (Sokol et al., 2019; Craig et al., 2019). Thus, it is important to consider that while our study focused on priming effects, some fraction of fast-decaying litter from the invader likely moved into the mineral-associated SOM pool (Sokol et al., 2019; Craig et al., 2019). This could offset some of the losses from priming, though more work is needed to better evaluate the net effects of invaders on SOM pools.

Collectively, our results demonstrate that the impact of fast-growing invasive species on priming effects depends on the edaphic characteristics and highlight the importance of considering invasive plants as drivers of SOM change. Future studies should also consider soil mineralogy as a mediator of invasion-induced organic matter priming effects.

Acknowledgements

The authors would like to thank Robin Johnson, Elizabeth Huenupi, and Katie Beidler for their field assistance. Elizabeth Huenupi’s help is laboratory analyses is highly appreciated. We would also like to thank Peter E. Sauer at the Stable Isotope Research Facility (SIRF) in the Department of Geological Sciences, Indiana University, Bloomington, U. S.A. for isotopic analyses. Authors would like to thank Andreas Fichtner and Benjamin M. Delory at the Institute of Ecology, Leuphana University Lüneburg, Germany for statistical consultancy. Authors gratefully acknowledge the German Academic Exchange Service (DAAD) for scholarship award (PPP-7020289). This study was supported by the German Research Foundation (DFG) within the project PA2377/2-1. We would like to thank the editor and two anonymous reviewers whose comments significantly improved the quality of this publication.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.soilbio.2019.107645.

References

A. Kumar et al.