



Fire effects on soil biota alter the strength and direction of plant-soil feedbacks between *Schizachyrium scoparium* (Michx.) Nash and *Rudbeckia hirta* L

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Abstract

Background and aims Plant soil feedbacks (PSF) are reciprocal mechanisms through which interactions between plants and soil biota and affect future plant growth. When scaled up to the community level, PSFs are important determinants of above- and belowground community dynamics that influence long-term successional trajectories. Despite over three decades of ecological PSF research, we have a poor understanding of how common environmental processes like fire influence the strength and direction of PSFs. The aim of this study was to evaluate fire effects on PSFs between two common grassland species: *Schizachyrium scoparium* and *Rudbeckia hirta*.

Methods In this work we evaluated how fire effects on *S. scoparium* and *R. hirta* associated soil biota influenced feedbacks on plant growth using a two phase experiment. We tested this by first growing *S. scoparium* and *R. hirta* with the same soil inocula, and then simulating low intensity, grassland fires in a

controlled greenhouse pot experiment (soil training). We then evaluated plant growth responses to burned and unburned inter- and intraspecific soil biota treatments (response phase).

Results Fire effects on inocula neutralized negative feedbacks in *S. scoparium*, and caused negative feedbacks in *R. hirta*. This shows that environmental disturbance like fire can alter the strength and direction of PSFs in ways that modify plant growth and potentially influence plant fuel loads and community dynamics.

Conclusion That fire can alter the strength and direction of PSFs on plant growth suggests that fire effects on soil related processes may influence plant community dynamics and fire-fuel dynamics in fire recurrent grassland ecosystems. Further, this study shows that fire effects on PSFs vary between plant species.

Keywords Plant-soil feedbacks · Fire · Fire-fuel feedback · Plant–microbe interaction · Disturbance

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Introduction

Fire is an ancient and ubiquitous terrestrial disturbance that contributes to long term evolutionary and community assembly patterns in biological communities (Glasspool et al. 2004; Archibald et al. 2013). Over small and large spatial scales, biological responses to fire contribute to changes in diversity

(He et al. 2019; Pausas and Bond 2019), community assembly (Kruger 1983; Harms et al. 2017; Day et al. 2020), and productivity (Pausas and Ribeiro 2013), that influence biogeochemical and ecosystem level processes (Archibald et al. 2018). Given changes in global fire regimes predicted by climate change models (Dale et al. 2001; Moritz et al. 2012; Harris et al. 2016; Jones et al. 2022), it is imperative that we understand how fire influences feedbacks between above- and belowground biota (e.g., plants and soil microbes). Fire favors plant and microbial taxa that can either survive or avoid the harmful effects of fire, and take advantage of post-fire conditions (Keeley and Fotheringham 2000; Pressler et al. 2019; Resco de Dios 2020; Fox et al. 2022). These plant and microbial adaptations to fire in turn can generate variable plant responses to post-fire soils that may influence subsequent seed germination and plant growth (Hopkins et al. 2023a; De Marco et al. 2023). Since plant growth responds to fire effects on soil biota, this implies that fire may modify plant-soil feedbacks through changes to soil biota (Kardol et al. 2023).

The importance of plant-soil feedbacks (PSF) have long been acknowledged in agricultural settings and proven informative of the soil abiotic, biotic, and plant related processes that influence plant-soil interactions (van der Putten et al. 2013). Briefly, PSFs are pathways through which plants modify their soil environment and influence future plant growth (Bever 1994; Bever et al. 1997; Ehrenfeld et al. 2005). Negative feedbacks arise when plants grow less well in soil trained by their own species, while positive feedbacks occur when plants grow larger in conspecific trained soil. More recently, the roles that different soil biota groups play in PSFs have been identified by ecologists (Bever 2002; reviewed in van der Putten et al. 2013; Ke et al. 2015), and demonstrated how reciprocal interactions between plants and soil biota influence above- and belowground community dynamics and successional trajectories (Kardol et al. 2013; Bever 2015; Bauer et al. 2015; Maron et al. 2016). Within the past ten years however, the importance of climate change related impacts on PSFs has received greater consideration since changes in climate patterns are expected to modify soil microbe and plant communities involved in PSFs (Andrew et al. 2016; Bennett and Classen 2020; Bardgett and Caruso 2020; Keeler et al. 2021) through shifts in above-ground processes like fire regimes (Harris et al. 2016;

Hewitt et al. 2022; Kardol et al. 2023; Warneke et al. 2023). Despite over three decades of ecological PSF research, it is unclear how processes like fire alter the strength (magnitude) and direction (positive/negative) of PSFs between plant taxa (Hewitt et al. 2022; Beals et al. 2022; Kardol et al. 2023).

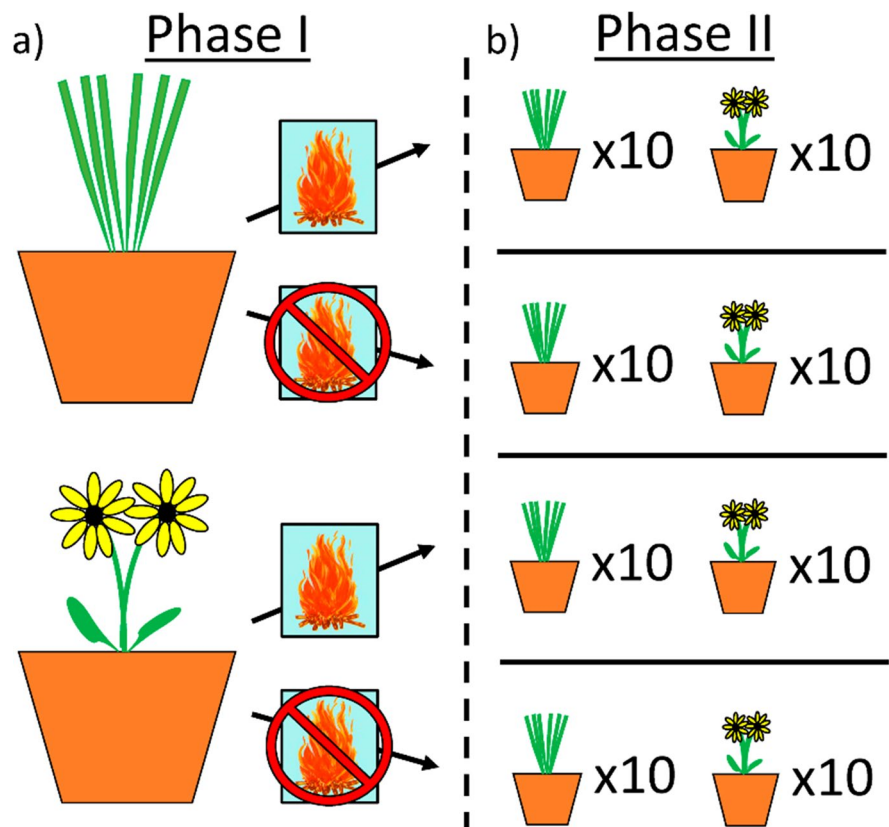
Fire alters plant associated soil microbiota through direct and indirect effects on the soil system. Fire is most commonly associated with direct, heat related mortality (i.e., soil heating) that can reduce microbial abundance and diversity (Hamman et al. 2007; Certini et al. 2021; Jurburg et al. 2021; Fox et al. 2022), and drive changes in soil microbial communities (Dove and Hart 2017; Semenova-Nelsen et al. 2019; Day et al. 2019). The degree of soil heating is a function of soil characteristics (Alcañiz et al. 2018; Pingree and Kobziar 2019); however, even lower severity fires can generate changes in plant associated microbial communities (Hopkins et al. 2021; Hopkins and Bennett 2023). Fire also indirectly influences soil biota through changes to edaphic characteristics such as soil moisture, pH, UV exposure, and the introduction of reactive oxygen species (Certini 2005; Alcañiz et al. 2018; Sigmund et al. 2021). Fire associated changes in soil biota may also differentially effect microbial groups like plant pathogens (Katan 2000; Beals et al. 2022) and mutualists (Hamman et al. 2007; Glassman et al. 2016; Dove and Hart 2017; Hewitt et al. 2022), with important implications for plant growth and reproduction. For example, low severity fires that only affect shallower soil depths may reduce litter layer pathogens while leaving sub-surface mutualists unharmed, thus benefitting plant growth. Therefore, fire driven changes to soil biota have the potential to modify the strength and direction of PSFs.

Fire effects on soil microbiota have the potential to alter biotic feedbacks that control plant growth. Under agricultural and natural conditions, pathogen buildup can drive negative intraspecific feedbacks that regulate the dominance of plant taxa (Flory and Clay 2013; Maron et al. 2016; Mariotte et al. 2018). Since fire kills plant-associated pathogens (Mooney and Conrad 1977; Katan 2000; Beals et al. 2022), fire may reduce or neutralize negative feedbacks. If fire kills mutualists like mycorrhizal fungi or rhizobia however (severe fire in particular; Klopatek et al. 1988; Taudière et al. 2017; Hewitt et al. 2022), then this could reduce the strength of positive feedbacks.

Therefore, any fire associated changes to PSFs (particularly negative PSFs) could alter the dominance of plant taxa, reduce diversity, change plant fuel loads, and facilitate invasion by fire tolerant plant species (Brooks 2002). Plant responses to soil biota also vary between plant species and successional stage (Kozioł and Bever 2015; Bauer et al. 2015, 2018; Cheeke et al. 2019), thus it is likely that plants also display species specific responses to fire effects on PSFs that modify their interactions with other plant species and post-fire above- and belowground community dynamics. Fire effects on PSFs are likely regulated by fire regime, as the severity, intensity, and frequency of fires can determine the strength of fire's effects on soil microbiota (Glassman et al. 2016; Bruns et al. 2020; Certini et al. 2021). Thus, understanding fire effects on PSFs can help us understand the processes that structure above- and belowground communities and fire-fuel feedbacks of fire frequented ecosystems.

We tested how fire altered the strength and direction of PSFs between two grassland plant species (*Schizachyrium scoparium* (Michx.) Nash & *Rudbeckia hirta* L.), and their soil communities in a greenhouse pot experiment (Fig. 1). Soil biota collected from a tallgrass prairie restoration were first allowed to differentiate in response to the two plant host species. Following the initial soil training period, low intensity fires were ignited in half of the pots. Soils from the burned and unburned pots were then used to inoculate a second generation of the *S. scoparium* and *R. hirta*. Growth responses of the two plant species to fire and prior host plant effects on soil biota were then evaluated. This allowed us to test two questions: does fire alter the strength (magnitude of effect) and direction (positive vs. negative) of 1) intraspecific and 2) interspecific PSFs? We hypothesized that fire's effect on PSFs would vary based on plant species. We predicted that fire would reduce negative, intraspecific PSFs, and neutralize positive, interspecific PSFs.

Fig. 1 Experimental design for testing fire effects on intra- and interspecific plant-soil feedbacks (PSFs). a) In phase 1, *S. scoparium* (n = 10) and *R. hirta* plants (n = 10) were grown for three months, after which half were subjected to low-intensity fires. b) In phase 2, soil from Phase 1 was used to inoculate a second generation of *S. scoparium* (n = 40) and *R. hirta* (n = 40) plants. This allowed us to test how fire altered the strength and direction of intra- and interspecific PSFs between *S. scoparium* and *R. hirta*



Materials and methods

Study system: We conducted field components of our study at the Larry R. Yoder Prairie Learning Laboratory in Marion, Ohio (40° 34'N, -83°5'W). This site in central Ohio has a five to six month growing season and an average annual precipitation of 998 mm. Soils are Pewamo silty clay loams with 0 to 1 percent slopes (USDA NRCS 2023a). The Larry R. Yoder Prairie is a 47-year-old tallgrass prairie restoration of ~4.45 hectares, characterized by *Monarda fistulosa* L., *Ratibida pinnata* (Vent.) Barnhart, *Andropogon gerardii* Vitman, *Schizachyrium scoparium* (Michx.) Nash, *Echinacea purpurea* (L.) Moench, *Solidago juncea* Aiton, and *Chamaecrista fasciculata* (Michx.) Greene, and *Rudbeckia hirta* L.. This restoration has been managed with triennial prescribed ground-layer fires during the past decade.

In both phase 1 (inocula training) and phase 2 (growth assay) of this work, *S. scoparium* and *R. hirta* were used as representative prairie plants. Both species are common in fire recurrent grasslands of the Midwestern United States (USDA NRCS 2023b). *S. scoparium* is a perennial, C4 grass, and *R. hirta* is an annual/biennial forb. Both plants are considered to have “medium” fire tolerance (scale: none, low, medium, high; Abrahamson 2023), meaning they can either resprout, regrow, or reestablish from residual seed following fire. Seeds for *S. scoparium* and *R. hirta* were purchased from Prairie Moon Nursery (Winona, MN), started in sterile potting soil (autoclave: 2 h, 120 °C), and grown for 3 weeks.

Phase 1 – inocula training: Soil inoculum was collected from the upper 15 cm of the Larry R. Yoder Prairie in September 2022 and sieved (2 cm) to remove large roots. Soil was stored in sterilized buckets until use as inocula. Sieved background soil (2 cm) was collected in Columbus, OH and combined 1:1 with sand, then autoclaved twice for 2 h at 120 °C. Abiotic characteristics for the sand:soil mix are as follows: pH=8, total carbon=18.8 ppm, N<10 ppm, P=40 ppm, and K>800 ppm. In October 2022, 500 mL of sterilized sand:soil mix was added to 15 cm clay pots (depth of 8 – 10 cm), followed by 100 mL of prairie soil inoculum (depth range 1 – 2 cm), then inoculum was covered with 200 mL of sterilized sand:soil mix (depth of 0 – 1 cm). Using sterile soil at the bottom and top of the pot helps prevent contamination between pots. One *S. scoparium*

(n=10) or *R. hirta* (n=10) plant was planted in the center of each pot. Plants were grown for 3 months in a greenhouse under extended day lighting. Plants were watered 4 times daily using a drip irrigation system with 7.6 L/hr emitters for 1 min intervals. Use of drip irrigation reduces inter-pot contamination during watering. Plants were fertilized monthly with 200 mL of 200 ppm 15–0–15 (N–P–K) water soluble fertilizer.

Experimental fires: Tallgrass prairie fuel loads described in Leis and Hinman 2015 were used to design experimental fuel loads. Briefly, average prairie fuel loads of 0.7 kg/m² were scaled down to a 176 cm² pot soil surface area (12.36 g of fuels per pot). Experimental fuel loads consisted of wheat straws that were arranged on the soil surface of five *S. scoparium* and five *R. hirta* pots. Prior to fire, plant aboveground biomass for each pot was clipped and removed to further standardize fuel loads. Fires were ignited using a propane hand torch along the edge of the pot rim. Each fire burned for an average of 6 min with pot fires falling within ± 15 s of this time, and following fire, ash was removed from top of each pot. Fires in this experimental pot system reliably elevate soil temperatures at depths of 1 cm to 50.5 °C (a 22.7 °C increase over ambient soil temperatures), and maintain temperatures of greater than 40 °C at this depth for around 3.6 min (for more details, see Supplementary Section S1). Further, fire effects on soil temperature do not differ between *S. scoparium* and *R. hirta* host plants in this system ($F_{1,8}=0.06$, $p=0.82$; Supplementary Section S1: Fig. S1, Table S1). Ash was removed to ensure that treatment effects were due to fire effects on soil microbiota rather than combustion associated nutrient pulses and changes in soil pH. All soils (including roots) from each pot were collected in separate sterile bags, then soil in each bag was evenly chopped and homogenized, followed by storage at 4 °C for 2 weeks.

Phase 2 – growth assay: To assess fire effects on plant-soil feedbacks, *S. scoparium* and *R. hirta* plants were grown in soils trained in phase 1. Seeds of both species obtained from Prairie Moon Nursery (Winona, MN) were started identically to those in phase 1. In January 2023, 500 mL of sterilized sand:soil mix was added to 15 cm clay pots, followed by 100 mL of trained soil inocula from phase 1, then inoculum was covered with 200 mL of sterilized sand:soil mix. One *S. scoparium* (n=40) or *R. hirta* (n=40) plant was planted in the center of each pot and starting plant

heights were recorded. This produced 80 total pots, with 10 replicates for each phase 1 species x phase 2 species x fire (burn/no burn) combination. While soil microbial community composition was not assessed prior to or following burn treatments, the use of identical fuel loads and similar burn times across all pots ensures fire effects on soil biota were as uniform as possible. Further, inoculating pots with 100 mL of soil (~10% pot volume) ensures that inoculum effects are due to differences in soil microbiota rather than abiotic differences (Pernilla Brinkman et al. 2010). Inoculum origin was recorded for each pot to account for background variation in phase 1 inocula, and included in all statistical analyses. Note that sterile inoculum treatments were not required in this study as comparing conspecific and heterospecific trained soil is preferable when comparing plant-soil feedbacks between multiple plant species (Pernilla Brinkman et al. 2010). Plants were grown under conditions identical to phase 1. Each month of the growing period (3), plant height and tiller number (*S. scoparium*), as well as longest leaf length and flower number (*R. hirta*) were recorded. Following 3 months of growth, plant above- and belowground biomass was harvested and dried for 3 days at 60° C, then aboveground, belowground, and flower biomass (*R. hirta* only) were recorded. Aboveground biomass values were considered in addition to total biomass since aboveground biomass represents the actual fuel loads for fire. Root:shoot ratios were calculated for each plant by dividing above- by belowground biomass values. Phase 2 pots were then randomly assigned to pairs of home and away soil treatments within Phase 2 plant species and fire treatments (as in Pernilla Brinkman et al. 2010), these pairs were then used to calculate the following plant-soil feedback metric (Klironomos 2002; Petermann et al. 2008):

$$Feedback_i = \log \left[\frac{biomass_i(home)}{biomass_i(away)} \right]$$

where $biomass_i(home)$ is plant biomass of species i in soil trained by species i , and $biomass_i(away)$ is plant biomass of species i in soil trained by species j . This feedback metric was chosen as we were specifically interested in testing how plant responses to home and away soil inocula varied between fire treatments. Separate feedback metrics were calculated for both total plant biomass and aboveground biomass.

Feedback values greater than 0 denote positive feedbacks (i.e., larger growth in soil trained by own species), and values less than 0 denote negative feedbacks (i.e., larger growth in soil trained by their other species).

Statistical analyses: Analyses were conducted in R version 4.2.2 (R Core Team, 2022). To test fire and phase 1 plant ID effects during the phase 2 growth period we used type III multivariate analyses of variance (MANOVAs) using the base MANOVA() function and the joint_tests() function in the emmeans package (Lenth 2018). MANOVAs are omnibus tests that allow for the consideration of multiple response variables and prevent the need for multiple ANOVA tests. Using a single MANOVA reduces type I error that arises with multiple testing (e.g., multiple ANOVA tests) and allows for the use of Type III sums of squares required when analyzing interactions between variables. The MANOVA model included tiller/leaf lengths for plants in months 1 and 3 as response variables, in addition to fixed effect terms for fire, phase 1 species (i.e., “trainer” species), and phase 2 species. Month 2 tiller/leaf lengths were not included due to high collinearity with month 3 measurements ($r < 0.81$). The MANOVA model also controlled for starting plant heights, greenhouse row (i.e., location in greenhouse), and inocula source pot. Model residuals were visually assessed for normality and met model assumptions. Following significant main effects, custom contrasts were applied testing fire effects on phase 2 plant growth in inter- and intraspecific soil treatments (e.g., *S. scoparium* growth with burned or unburned *S. scoparium* vs. *R. hirta* trained inocula) using the contrast() function.

To test fire and phase 1 plant ID effects on phase 2 plant biomass, a separate MANOVA that included aboveground mass, total mass, flower mass, and root:shoot ratios as response variables was used. All fixed effect and covariate terms were identical to the growth MANOVA described above. Due to high collinearity between belowground and total biomass ($r < 0.81$), belowground biomass was omitted from the model. Model residuals were visually assessed for normality and met model assumptions. Then, custom contrasts similar to those described above were applied.

To test fire and plant species effects on plant-soil feedbacks we used type III analyses of variance (ANOVA) that included feedback metrics as response

variables, and phase 1 plant ID and fire treatment as fixed effects, as well as their interaction term. Model residuals were assessed as above,

Results

Fire alters plant-soil feedback effects on plant growth: Plant growth (i.e., height and leaf length) varied in response to fire. Throughout the 3-month growing period, *S. scoparium* plants were shorter when grown with *S. scoparium* versus *R. hirta* trained

inocula ($F_{1,40}=21.5$, $p<0.0001$; Table 1, 2; Fig. 2) and taller when grown with any type of burned inocula ($F_{1,40}=6.6$, $p=0.01$). This negative feedback effect was modified by fire however ($F_{1,40}=4.7$, $p<0.04$; Fig. 2), with burned *S. scoparium* ($p=0.07$) and *R. hirta* ($p<0.0001$) trained inocula promoting *S. scoparium* growth relative to unburned inocula treatments. While *R. hirta* did not demonstrate overall positive or negative feedbacks ($p=0.11$) or responses to fire ($p=0.67$), *R. hirta* did display fire dependent responses that varied with phase 1 plant species. When *R. hirta* plants were grown in burned *R.*

Table 1 MANOVA results for fire and soil biota treatment effects on plant height and leaf length during months 1 and 3. Note the repeated measures correspond to month 1 and month 3 growth metrics

Model term	d.f.1	d.f.2	F-test	p-value
<i>fire treatment</i>	1	40	16.63	0.0002**
<i>training species</i>	1	40	3.75	0.06
<i>plant species</i>	1	40	22.60	<0.0001***
<i>starting height</i>	1	40	6.58	0.01**
<i>greenhouse row</i>	19	40	1.58	0.11
<i>repeated measure</i>	1	40	356.38	<0.0001***
<i>fire x training species</i>	1	40	0.39	0.54
<i>fire x plant species</i>	1	40	6.59	0.01**
<i>fire x rep. meas</i>	1	40	9.45	0.004**
<i>trainer x plant species</i>	1	40	21.53	<0.0001***
<i>trainer x rep. meas</i>	1	40	1.11	0.30
<i>plant x rep. meas</i>	1	40	60.71	<0.0001***
<i>starting height x rep. meas</i>	1	40	0.91	0.35
<i>row x rep. meas</i>	19	40	1.70	0.08
<i>fire x trainer x plant</i>	1	40	4.56	0.04**
<i>fire x trainer x rep. meas</i>	1	40	1.25	0.27
<i>fire x plant x rep. meas</i>	1	40	0.19	0.66
<i>trainer x plant x rep. meas</i>	1	40	3.68	0.06
<i>inocula source (within fire x trainer x plant)</i>	11	40	1.95	0.06
<i>fire x trainer x plant x rep. meas</i>	1	40	0.16	0.70

$p \leq 0.1$, *: $p \leq 0.05$, **: $p \leq 0.01$, ***: $p \leq 0.0001$

Table 2 A priori contrasts for plant height/leaf length MANOVA

Contrast	Estimate	S.E	d.f	t-test	p-value
<i>S. scoparium</i> : fire (+ vs. -)	26.41	5.59	40	4.70	<0.0001***
<i>R. hirta</i> : fire (+ vs. -)	2.42	5.54	40	0.40	0.67
<i>S. scoparium</i> feedback	-30.45	5.61	40	-5.43	<0.0001***
<i>R. hirta</i> feedback	-9.65	5.96	40	-1.62	0.11
<i>S. scoparium</i> in <i>S. scoparium</i> soil: fire (+ vs. -)	8.42	4.44	40	1.89	0.07
<i>S. scoparium</i> in <i>R. hirta</i> soil: fire (+ vs. -)	18.00	4.07	40	4.43	<0.0001***
<i>R. hirta</i> in <i>R. hirta</i> soil: fire (+ vs. -)	-7.12	3.80	40	-1.87	0.07
<i>R. hirta</i> in <i>S. scoparium</i> soil: fire (+ vs. -)	9.54	4.30	40	2.22	0.03*

∴ $p \leq 0.1$, *: $p \leq 0.05$, **: $p \leq 0.01$, ***: $p \leq 0.0001$

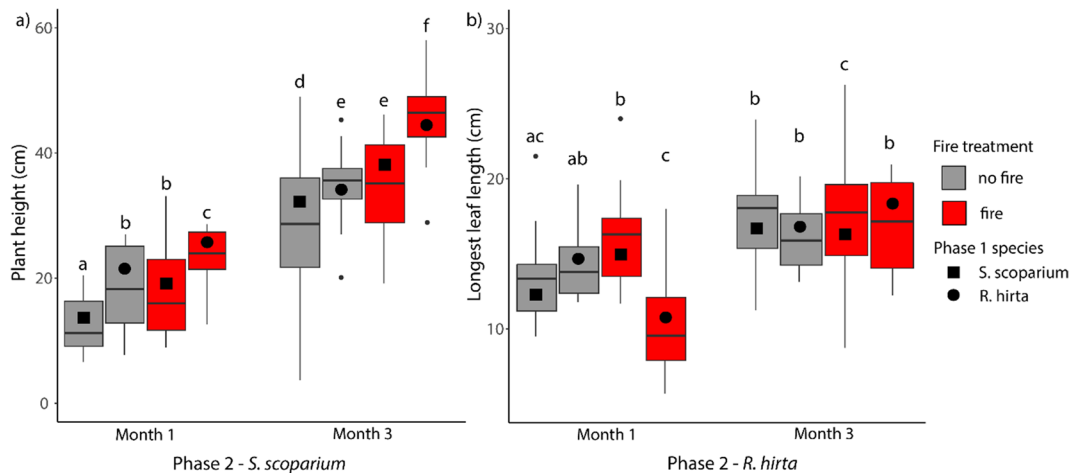


Fig. 2 Plant height and leaf length responses to fire and soil biota treatments. a) *S. scoparium* displayed negative PSFs that were neutralized by burned inocula, with *S. scoparium* plants being the largest in burned soil trained by *R. hirta*. b) *R. hirta*

hirta trained inocula, leaf lengths were shorter relative to plants grown with unburned *R. hirta* inocula ($p=0.07$), whereas leaf lengths were longer with burned *S. scoparium* trained soil ($p=0.03$). Treatment effects on growth did not vary between months 1 and 3 for either plant species ($P<0.05$). In summary, fire effects on inocula modified the strength and direction of feedbacks on plant growth.

Fire alters plant-soil feedback effects on plant biomass: Plant species biomass production was influenced by phase 1 plant species and fire. After the 3-month growth period, *S. scoparium* plants were lighter (both aboveground and total biomass metrics) in *S. scoparium* trained soil ($F_{1,59}=13.4$, $p=0.0005$; Table 3, 4) and heavier with any type of burned inocula ($F_{1,59}=7.03$, $p<0.01$; Fig. 3a-b). Fire also modified the strength and direction of feedback effects on *S. scoparium* plants ($F_{3,59}=21.5$, $p=0.001$; Fig. 3). Specifically, *Scoparium* plants were larger (aboveground and total biomass) when grown in burned vs. unburned *R. hirta* soil ($p<0.0001$, $p<0.0001$). *R. hirta* biomass did not vary with phase 1 training species ($p=0.16$) or with burned inocula ($p=0.99$); however, *R. hirta* responses to phase 1 plants were modified by fire ($F_{3,59}=21.5$, $p=0.001$). *R. hirta* plants were heavier (aboveground biomass: $p=0.05$, total biomass: $p=0.001$) and produced more flowers ($p=0.001$) when grown with unburned vs. burned *R. hirta* inocula (Fig. 3a-c). Root:shoot ratios were not

leaf lengths were shorter when grown with burned *R. hirta* soil biota, and longer when grown with burned *S. scoparium* soil biota

modified by fire effects on PSFs ($p>0.05$). In summary, fire modified plant-soil feedback effects on *S. scoparium* and *R. hirta* biomass production.

Fire and plant species modify plant-soil feedbacks: Plant soil feedback metrics were modified by plant species and fire treatment. Plant-soil feedback effects on total plant biomass were primarily determined by plant species ($F_{1,35}=7.2$, $p=0.01$; Table 5, Fig. 4a), with *S. scoparium* displaying strong negative feedbacks and *R. hirta* displaying no feedback effects. Plant-soil feedback effects on aboveground biomass were marginally impacted by fire ($F_{1,35}=2.9$, $p=0.09$; Table 5, Fig. 3b), with fire driving positive feedback effects on both species. Fire associated reductions in feedbacks were larger in *S. scoparium* relative to *R. hirta* however (Fig. 4b).

Discussion

Fire effects on soil biota altered plant growth and plant-soil feedbacks between *S. scoparium* and *R. hirta*. Fire effects on PSFs drove changes in plant height, leaf lengths, biomass, and flowering that varied between plant taxa. Specifically, *S. scoparium*, a common grassland graminoid species, grew taller and produced more biomass when grown with burned soil biota. Conversely, growth of *R. hirta*, a common grassland forb species, was lower with burned, *R.*

Table 3 MANOVA results for plant biomass and root:shoot ratio model

Model term	d.f.1	d.f.2	F-test	p-value
<i>plant species</i>	1	59	64.79	<0.0001***
<i>training species</i>	1	59	2.55	0.12
<i>fire treatment</i>	1	59	6.62	0.01**
<i>starting height</i>	1	59	4.48	0.04*
<i>greenhouse row</i>	1	59	7.12	0.01**
<i>repeated measure</i>	3	59	355.98	<0.0001***
<i>trainer x plant species</i>	1	59	13.37	0.0005**
<i>fire x plant species</i>	1	59	7.03	0.01**
<i>plant x rep. meas</i>	3	59	21.46	<0.0001***
<i>fire x training species</i>	1	59	0.12	0.73
<i>trainer x rep. meas</i>	3	59	7.34	0.0003**
<i>fire x rep. meas</i>	3	59	8.78	0.0001***
<i>starting height x rep. meas</i>	3	59	2.38	0.08
<i>row x rep. meas</i>	3	59	3.59	0.02*
<i>fire x trainer x plant</i>	1	59	7.88	0.007**
<i>trainer x plant x rep. meas</i>	3	59	14.52	<0.0001***
<i>fire x plant x rep. meas</i>	3	59	7.26	0.0003**
<i>fire x trainer x rep. meas</i>	3	59	2.90	0.04*
<i>inocula source (within fire x trainer x plant)</i>	11	59	2.89	0.004**
<i>fire x trainer x plant x rep. meas</i>	3	59	6.10	0.001**

∴ p ≤ 0.1, *: p ≤ 0.05, **: p ≤ 0.01, ***: p ≤ 0.0001

hirta soil biota and higher with burned, *S. scoparium* soil biota. The PSF responses to fire demonstrated in this work may reflect the general positive effect of fire on C4 grass dominance (particularly Spring and dormant season burns; Archibald et al. 2013; Simpson et al. 2020; Hopkins et al. 2023a, b) relative to non-graminoid taxa (Howe 1994, 1995; Beckage et al. 2011), and suggest that PSF responses to fire may be specific to plant functional group. PSF responses of more species are required to thoroughly test functional group responses to fire though.

Fire effects on plant growth and PSFs varied between plant species. *S. scoparium* displayed a negative PSFs that were modified by fire. Burned soil biota reduced negative feedback effects on *S. scoparium* and promoted *S. scoparium* growth in *S. scoparium* trained soil. This trend matches observations that fire benefits C4 grass reseeding and dominance in fire frequented grassland and savanna ecosystems (Robinson et al. 1979; Tix and Charvat 2005; Ratnam et al. 2011; Ripley et al. 2015; Simpson et al. 2020). The observed fire driven reduction of negative PSFs on *S. scoparium* suggest that fire may remove harmful pathogens known to build-up in grass trained soil (Bauer et al. 2017). *R. hirta* however did not

display strong PSFs, but fire did alter *R. hirta* growth responses to con- and heterospecific trained soils. As with *S. scoparium*, burned inocula promoted *R. hirta* growth with *S. scoparium* trained soil biota. In *R. hirta* trained soil however, burned inocula harmed *R. hirta* growth and flower production. *R. hirta* is known to promote plant associated soil biota that benefit plant community productivity (e.g., mycorrhizae and rhizobia; Koziol and Bever 2015; Bauer et al. 2017). The negative effects on *R. hirta* growth that arise with burned, *R. hirta* soil biota suggests that fire kills beneficial plant symbionts and results in decreased growth. While it is unclear how soil microbial communities changed in this study, the fire treatments in this study were based on tallgrass prairie fuel loads and reliably heated soils to 50 °C (depth of 1 cm). Low intensity fires such as those in grasslands are known to reduce the abundance of plant pathogens (Katan 2000), drive changes in microbial community composition (Carson et al. 2019; Hopkins et al. 2021, 2023b), and alter the growth of *S. scoparium* through changes in arbuscular mycorrhizal community composition (Hopkins and Bennett 2023). Future work can identify how fire driven changes in soil microbe functional groups correspond with altered plant

Table 4 A priori contrasts for plant biomass MANOVA. The overall growth response represents the combined responses of measured variables to treatment effects. A significant overall

effect means that all response variables responded similarly (e.g., all biomass metrics increased in burned treatments)

Level	Contrast	Estimate	S.E	d.f	t-test	p-value
Overall growth	Fire (+ vs. -)	5.99	2.33	59	2.57	0.01**
	<i>S. scoparium</i> feedback	-5.92	1.60	59	-3.69	0.0005**
	<i>R. hirta</i> feedback	-2.27	1.60	59	-1.42	0.16
	<i>S. scoparium</i> : fire (+ vs. -)	5.96	1.62	59	3.67	0.0005**
	<i>R. hirta</i> : fire (+ vs. -)	0.02	1.61	59	0.02	0.99
	<i>S. scoparium</i> in <i>S. scoparium</i> soil: fire (+ vs. -)	1.19	1.16	59	1.02	0.31
	<i>S. scoparium</i> in <i>R. hirta</i> soil: fire (+ vs. -)	4.77	1.13	59	4.22	0.0001***
	<i>R. hirta</i> in <i>R. hirta</i> soil: fire (+ vs. -)	-1.38	1.16	59	-1.19	0.24
	<i>R. hirta</i> in <i>S. scoparium</i> soil: fire (+ vs. -)	1.40	1.12	59	1.26	0.21
Aboveground biomass	<i>S. scoparium</i> in <i>S. scoparium</i> soil: fire (+ vs. -)	0.35	0.22	59	1.57	0.12
	<i>S. scoparium</i> in <i>R. hirta</i> soil: fire (+ vs. -)	1.68	0.22	59	7.70	<0.0001***
	<i>R. hirta</i> in <i>R. hirta</i> soil: fire (+ vs. -)	-0.46	0.22	59	-2.04	0.05*
	<i>R. hirta</i> in <i>S. scoparium</i> soil: fire (+ vs. -)	0.31	0.22	59	1.43	0.16
Total biomass	<i>S. scoparium</i> in <i>S. scoparium</i> soil: fire (+ vs. -)	0.72	0.78	59	0.92	0.36
	<i>S. scoparium</i> in <i>R. hirta</i> soil: fire (+ vs. -)	3.20	0.76	59	4.22	0.0001***
	<i>R. hirta</i> in <i>R. hirta</i> soil: fire (+ vs. -)	-0.78	0.78	59	-1.01	0.32
	<i>R. hirta</i> in <i>S. scoparium</i> soil: fire (+ vs. -)	1.02	0.75	59	1.36	0.18
Flower biomass	<i>S. scoparium</i> in <i>S. scoparium</i> soil: fire (+ vs. -)	-0.01	0.09	59	-0.09	0.93
	<i>S. scoparium</i> in <i>R. hirta</i> soil: fire (+ vs. -)	-0.02	0.09	59	-0.24	0.81
	<i>R. hirta</i> in <i>R. hirta</i> soil: fire (+ vs. -)	-0.30	0.09	59	-3.39	0.001**
	<i>R. hirta</i> in <i>S. scoparium</i> soil: fire (+ vs. -)	0.04	0.09	59	0.50	0.62
Root:Shoot ratio	<i>S. scoparium</i> in <i>S. scoparium</i> soil: fire (+ vs. -)	0.13	0.36	59	0.36	0.72
	<i>S. scoparium</i> in <i>R. hirta</i> soil: fire (+ vs. -)	-0.08	0.35	59	-0.23	0.82
	<i>R. hirta</i> in <i>R. hirta</i> soil: fire (+ vs. -)	-0.16	0.36	59	0.45	0.66
	<i>R. hirta</i> in <i>S. scoparium</i> soil: fire (+ vs. -)	0.03	0.35	59	0.10	0.92

.: $p \leq 0.1$, *: $p \leq 0.05$, **: $p \leq 0.01$, ***: $p \leq 0.0001$

growth and physiological responses. Taken together, this suggests that fire interacts with species specific differences in soil biota to influence PSFs and plant growth.

Fire's ability to modify PSFs indicates that interactions between fire, microbes, and plant hosts, influence above- and belowground community dynamics. Fire's generally positive effect on graminoid growth (this study, Hulbert 1969; Bond et al. 2003; Hopkins et al. 2023a, b), often at the expense of forbs (Howe 1994, 1995), suggests that fire associated neutralization of negative, PSFs may contribute to the dominance of grasses in frequently burned grassland and savanna ecosystems. However, even when inoculated with burned soil biota, *S. scoparium* growth was still greater in interspecific soil treatments. This may mean that negative PSFs for grasses can still build-up in the

presence of fire, particularly if fires are not severe enough to remove grass associated pathogens (Roy et al. 2014). Consideration of more C4 grass species is required to test this effect, however. Lower severity fire may also favor forbs (Wragg et al. 2018; Hopkins et al. 2023a), particularly if the growth promoting ability of *R. hirta* associated soil biota observed in this study and Bauer et al. 2017 is not reduced by fire. While consideration of more plant species is necessary, variation in PSFs responses to fire amongst plant and microbial taxa can also help inform land management practices in fire recurrent ecosystems (Kardol et al. 2023; Warneke et al. 2023). For example, reducing the frequency of prescribed fire may allow negative feedbacks to build-up on some dominant plant taxa (e.g., *S. scoparium*), benefitting less dominant taxa and boosting above- and belowground

Fig. 3 Plant biomass and root:shoot ratio responses to fire and soil biota treatments. *S. scop* is short for *S. scoparium*. A “*” indicates statistically significant differences between treatments. a) *S. scoparium* plants produced more aboveground biomass when grown with burned, *R. hirta* trained inocula, while *R. hirta* plants produced less biomass when grown with burned *R. hirta* trained inocula. b) *S. scoparium* plants were larger when grown with burned *R. hirta* inocula, and c) *R. hirta* plants produced fewer flowers with burned *R. hirta* inocula

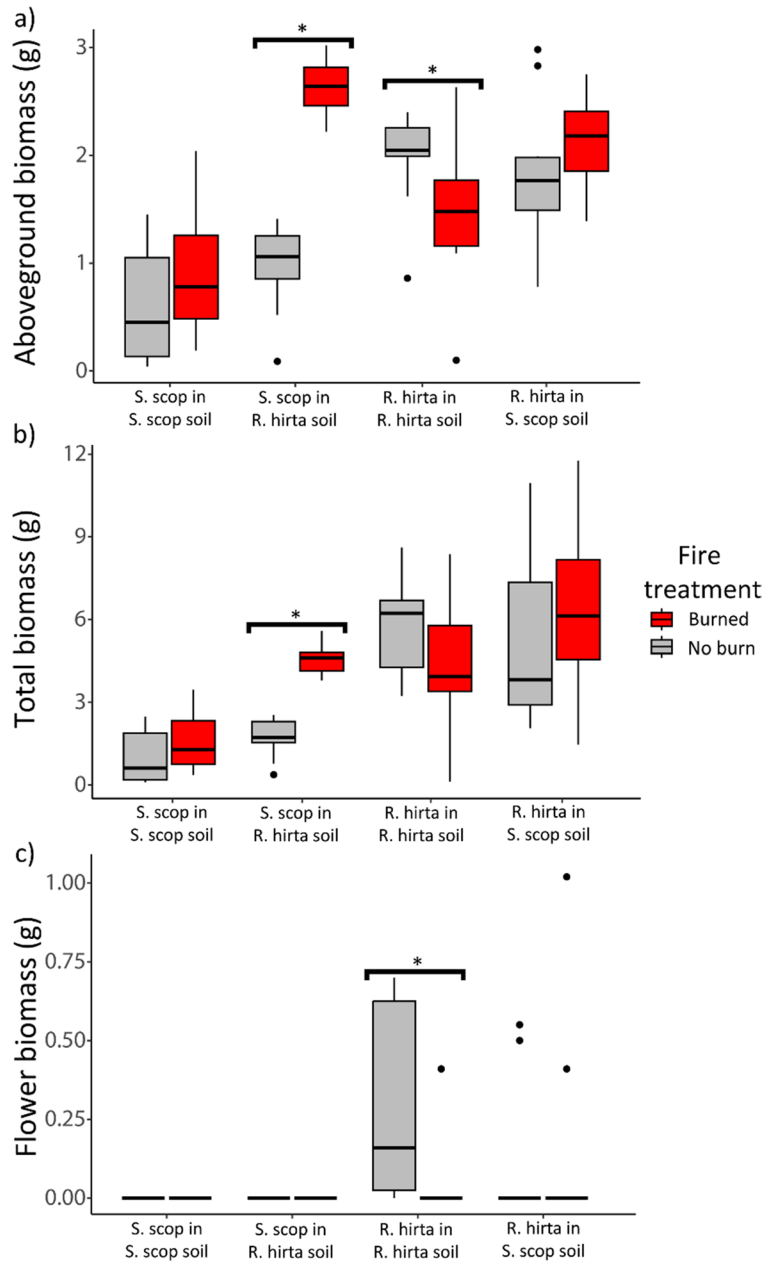


Table 5 ANOVA results for total and aboveground plant-soil feedbacks calculated using the log ratio metric described in Klironomos 2002

∴ $p \leq 0.1$, *: $p \leq 0.05$, **: $p \leq 0.01$, ***: $p \leq 0.0001$

Model term	d.f.1	d.f.2	F-test	p-value	F-test	p-value
			Total biomass		Aboveground bio-mass	
<i>plant species</i>	1	35	7.2	0.01**	0.007	0.9
<i>fire treatment</i>	1	35	2.1	0.2	2.9	0.09
<i>plant species x fire</i>	1	35	0.5	0.5	0.1	0.7

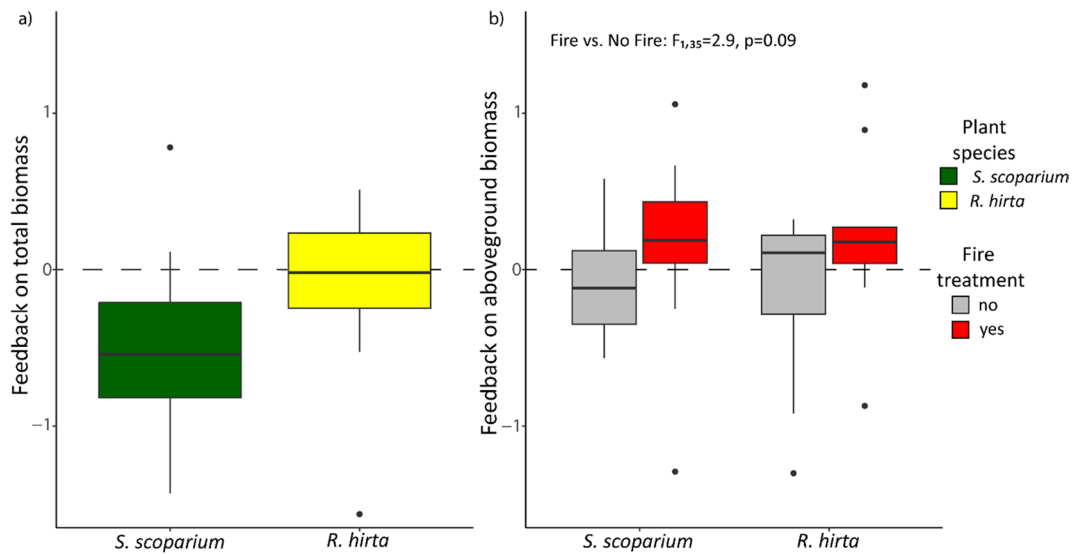


Fig. 4 Fire and plant species ID effects on plant-soil feedback (PSF) metrics. a) Total *S. scoparium* biomass displayed negative PSFs, whereas *R. hirta* total biomass did not respond

to phase 1 effects on soil biota. b) Fire reduced negative PSF effects on aboveground plant biomass; however, this effect was stronger in *S. scoparium* plants

biodiversity (He et al. 2019; Fraterrigo and Rembel-ski 2021). The potential for fire to modify plant communities through PSFs demonstrates the importance of considering environmental effects on interactions between plants and microbes.

PSF research has traditionally focused on testing reciprocal interactions between plant species and their soil biota in controlled environments. Our work shows the importance of considering environmental effects on PSFs (e.g., fire), and supports early evidence (Beals et al. 2020, 2022) and hypotheses (De Long et al. 2019; Kardol et al. 2023) suggesting links between environmental effects (e.g., stress and disturbance) and PSFs. It is also worth noting that disturbance (e.g., tillage) has long been used in agricultural systems to reduce negative effects of soil biota on crop yields (Sumner and Doupnik 1981; Bockus and Shroyer 1998), providing applied examples of environmental effects on PSFs. In natural settings, other environmental effects like grazing and drought could be important as well, since plant-microbe interactions are known to become more positive with higher levels of ecological stress (i.e., Stress Gradient Hypothesis; David et al. 2018; Hawkes et al. 2020; Bastías et al. 2022). This implies that hosts known to culture growth promoting soil biota (e.g., *R. hirta*) could produce strong, positive PSFs if ecological stress drives

the adaptation of mutualistic plant-microbe interactions. While not considered in this study, it is also worth noting that nutrient pulses and changes in soil characteristics (e.g., soil pH) associated with combustion and ash may modify PSFs (Johnson and Curtis 2001; Certini 2005; Butler et al. 2018; Kardol et al. 2023). Fire-associated increases in nutrient availability (particularly P and N) could weaken positive PSFs if plants have increased access to limiting nutrients that are usually accessed through microbial mutualist partners (e.g., mycorrhizae). While this study controlled for fire effects on soil abiotic factors by using the same background soil for all Phase 2 pots, it is highly likely that fire effects on soil abiotic and biotic factors interactively influence PSFs in natural systems. Summarizing, environmental effects can modify PSFs in ways that determine long-term changes in community dynamics and productivity.

In conclusion, fire altered the strength and direction of PSFs between *S. scoparium* and *R. hirta*. This work is the first to demonstrate fire effects on PSFs between two plant species. By experimentally manipulating fire, we were able to identify mechanisms through which fire can modify plant growth and potentially influence plant community dynamics. As this study was limited to two plant-species, future work should fire effects on more species, and test how

other types of environmental effects (e.g., soil acidification and drought) and fire regime components (e.g., severity and frequency) influence PSFs, how disturbance effects on PSFs vary with time, how changes in specific microbial groups mediate fire effects on PSFs, and how PSFs contribute to fuel load dynamics in fire recurrent ecosystems. To conclude, fire not only drives immediate changes to plant and microbial communities, but can also modify PSF mechanisms that determine above- and belowground interactions.

Data availability

The datasets generated during the current study are available in the Dryad repository, <https://doi.org/https://doi.org/10.5061/dryad.zw3r228d6>.

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Author contributions JRH and AEB developed and designed the experiment. JRH set up and managed the greenhouse portion of the experiment. JRH collected and analyzed all data. JRH and AEB wrote the manuscript.

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