

Fire effects on soil biota alter the strength and direction of plant-soil feedbacks

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Abstract

Background and aims

Plant soil feedbacks (PSF) are reciprocal mechanisms through which plants modify 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.

Methods

In this work we evaluated how fire effects on *Schizachyrium scoparium* and *Rudbeckia hirta* trained soil biota influenced feedbacks on plant growth. We tested this by experimentally manipulating fires and evaluating plant growth responses to burned and unburned inter- and intraspecific soil biota treatments.

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 potentially modify plant growth, 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 contribute to plant community assembly and fire-fuel dynamics in fire recurrent grassland and savanna ecosystems. Further, this study shows that fire effects on PSFs vary between plant species, and may contribute to the dominance of C4 grasses in pyrophilic ecosystems.

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). Since plant growth responds to fire effects on soil biota, this implies that fire may modify plant-soil feedbacks through changes to soil biota.

Plant-soil feedbacks (PSF) are pathways through which plants modify their soil environment and influence future plant growth (van der Putten et al. 2013). Interactions between plants and soil microbiota are known to be particularly important components of PSFs due their effects on plant growth, health, and fitness (Bever 1994, 2002; Ke et al. 2015). Negative feedbacks arise when plants grow larger in soil trained by other plant species, while positive feedbacks occur when plants grow larger in conspecific trained soil. When scaled up to the community level, PSFs are also important determinants of plant community composition, diversity, and long-term successional trajectories (Kardol et al. 2013; Bauer et al. 2015, 2020; Maron et al. 2016). Despite over three decades of ecological PSF research however, our understanding of how environmental effects (e.g., fire disturbance) influence PSFs is quite poor (Hewitt et al. 2022; Beals et al. 2022; Kardol et al. 2022).

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 structure (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). 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 and their soil communities in a greenhouse setting. 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, experimental fires were ignited in half of the pots, and the resulting soil treatments were used to inoculate a second generation of the two plant species. 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 1) direction (positive/negative) and 2) strength of PSFs? We hypothesized that fire's effect on PSFs would vary based on plant species. We predicted that fire would reduce negative PSFs, and neutralize positive PSFs.

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*, *Ratibida pinnata*, *Andropogon gerardii*, *Schizachyrium scoparium*, *Echinacea purpurea*, *Solidago juncea*, and *Chamaecrista fasciculata*. 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 widely distributed across US grasslands (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), meaning they can 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 hours, 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. Sieved background soil (2 cm) was collected in Columbus, OH and combined 1:1 with sand, then autoclaved twice for 2 hours at 120°C. In October 2022, 500 mL of sterilized sand:soil mix was added to 15 cm clay pots, followed by 100 mL of prairie soil inoculum, then inoculum was covered with 200 mL of sterilized sand:soil mix. 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. 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 2014 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 to edge of the pot rim. Each fire burned for an average of 6 min with pot fires falling within +/- 15 sec of this time, and following fire, ash was removed from to top of each pot. 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. Soils from all pots were collected in separate sterile bags, then soil in each bag was homogenized and stored 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 2 species x phase 1 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 within species and fire treatments (as in (Pernilla Brinkman et al. 2010)), and 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., better growth in soil trained by own species), and values less than 0 denote negative feedbacks (i.e., better 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 were used to reduce type I error that arises with multiple testing (e.g., multiple ANOVA tests). 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 ($r < |0.8|$). The MANOVA model also controlled for starting plant heights, greenhouse row, 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 ($r < |0.8|$), 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 ($F_{1,40}=21.5$, $p < 0.0001$; Tables 1, 2; Fig. 1) 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. 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 ($p = 0.03$). In summary, fire effects on inocula modified the strength and direction of feedbacks on plant growth.

Table 1
MANOVA results for fire and soil biota treatments on plant height and leaf length during months 1 and 3

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

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 ($F_{1,59}=13.4$, $p = 0.0005$; Tables 3,4) and heavier with any type of burned inocula ($F_{1,59}=7.03$, $p < 0.01$; Fig. 2a-b). Fire also modified the strength and direction of feedback effects on *S. scoparium* plants ($F_{3,59}=21.5$, $p = 0.001$; Fig. 2). 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. 2a-c). Root:shoot ratios were not 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.

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

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 effects 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

Level	Contrast	Estimate	S.E.	d.f.	t-test	p-value
Root:Shoot ratio	<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
	<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
.: $p \leq 0.1$, *: $p \leq 0.05$, **: $p \leq 0.01$, ***: $p \leq 0.0001$						

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. 3a), 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. 3b).

Table 5
ANOVA results for total and aboveground plant-soil feedbacks

Model term	d.f.1	d.f.2	F-test	p-value	F-test	p-value
			Total biomass		Aboveground biomass	
<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
.: $p \leq 0.1$, *: $p \leq 0.05$, **: $p \leq 0.01$, ***: $p \leq 0.0001$						

Discussion

Fire effects on soil biota altered plant growth and plant-soil feedbacks. 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. 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. 2023) relative to non-graminoid taxa (Beckage 2011, Howe 1994, 1995) (Howe 1994, 1995; Beckage et al. 2011), and suggest that PSF responses to fire are plant functional group specific. 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 fires which 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 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. 2023), 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). 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. 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, and supports early evidence (Beals et al. 2020, 2022) and hypotheses (De Long et al. 2019; Kardol et al. 2022) 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 Douppnik, Jr. 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. 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. While ash was removed immediately following fire to prevent this effect in our study, fire-associated increases in nutrient availability (particularly P and N) could weaken positive PSFs if plants have increased access limiting nutrients that are usually accessed through microbial mutualist partners (e.g., mycorrhizae). 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 influence plant growth and potentially drive long-term changes in plant and microbial communities. Future work should 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.

Declarations

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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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Competing Interests

The authors have no relevant financial or non-financial interests to disclose.

Data availability

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

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Figures

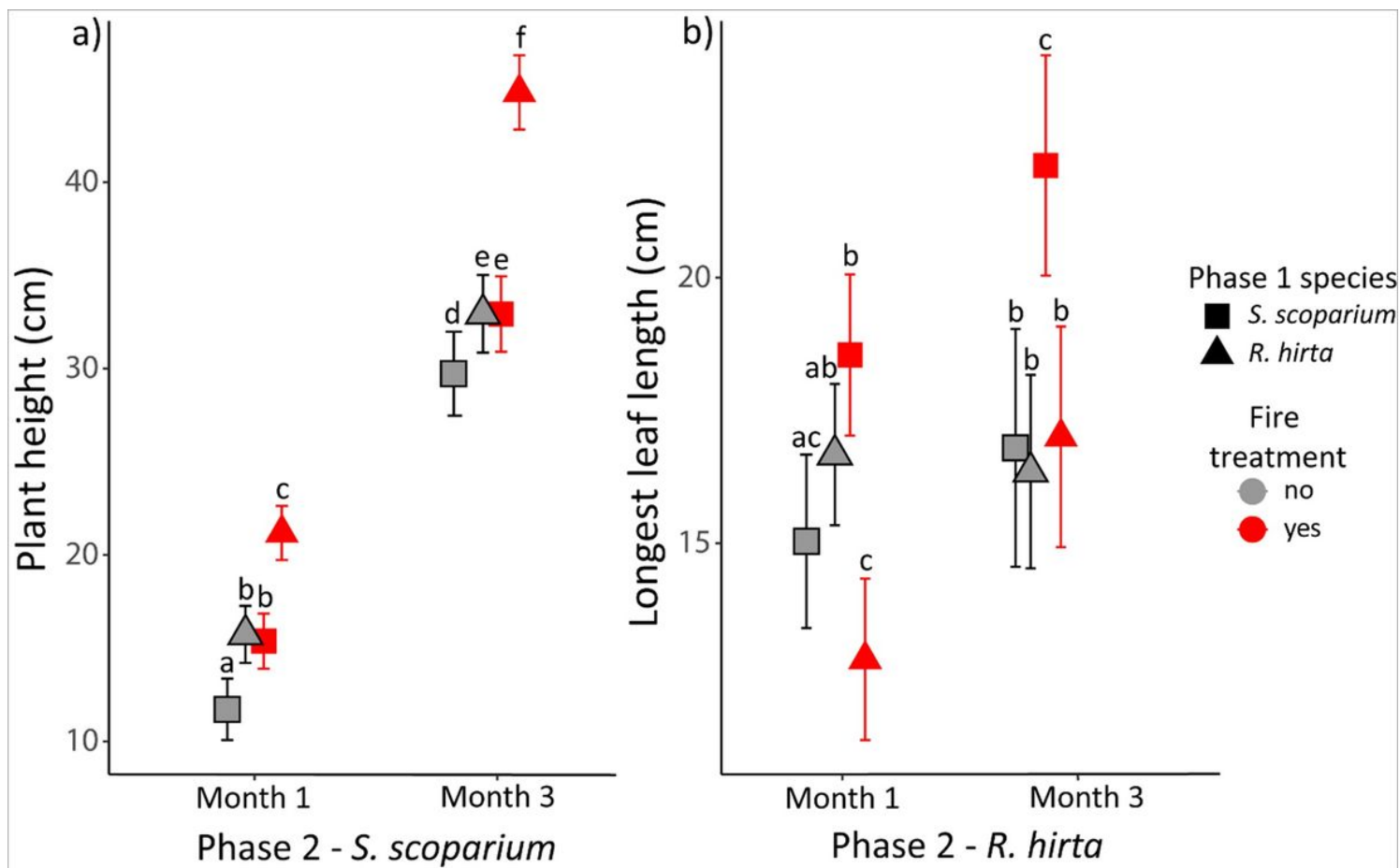


Figure 1

Plant height and leaf length responses to fire and soil biota treatments. a) *S. scoparium* displayed negative PSFs that were neutralized by burned inocula. *S. scoparium* the largest in burned soil trained by *R. hirta*. b) *R. hirta* leaf lengths were shorter when grown with burned *R. hirta* soil biota, and longer when grown with burned *S. scoparium* soil biota

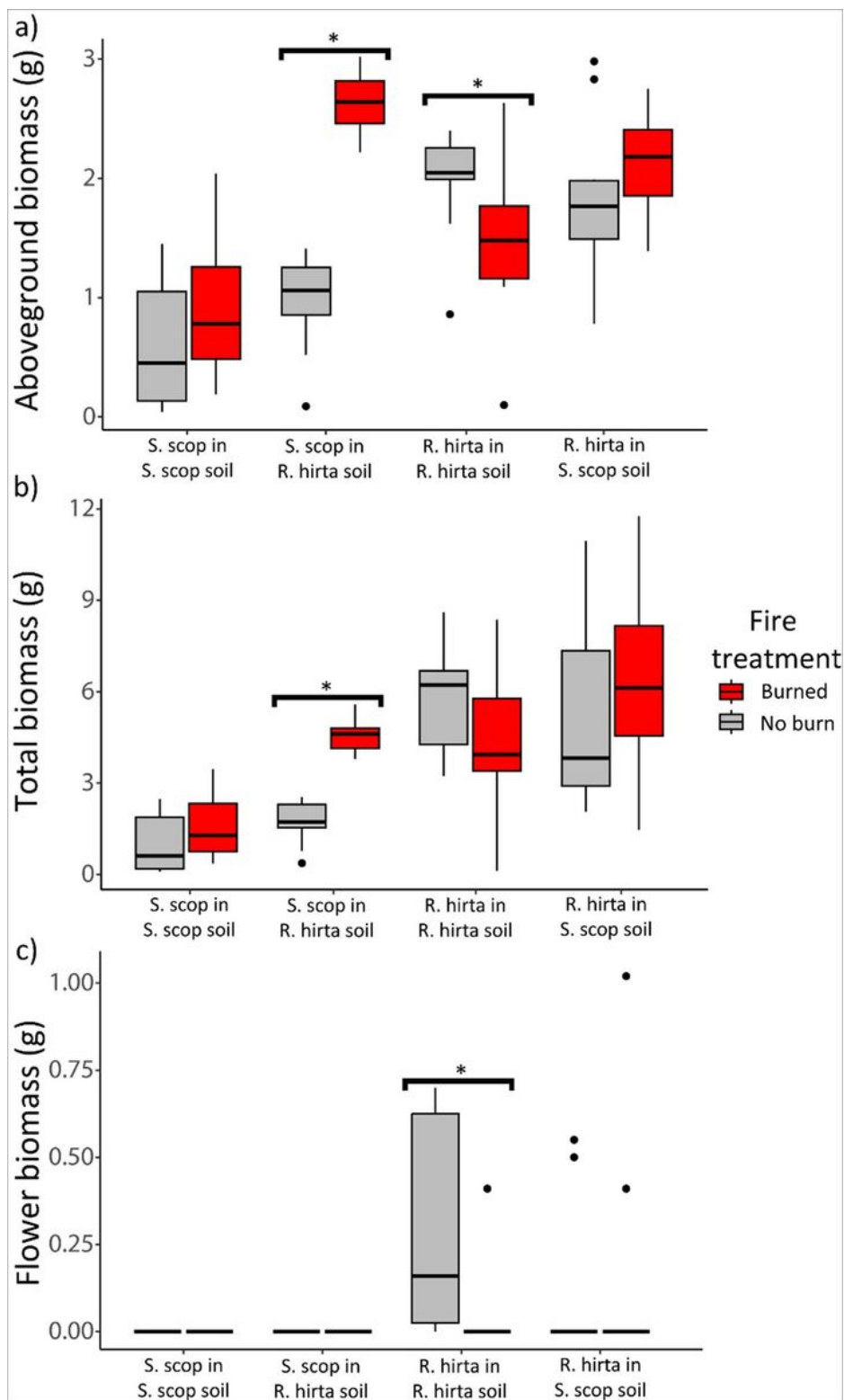


Figure 2

Plant biomass and root:shoot ratio responses to fire and soil biota treatments. S. scop is short for *S. scoparium*. 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

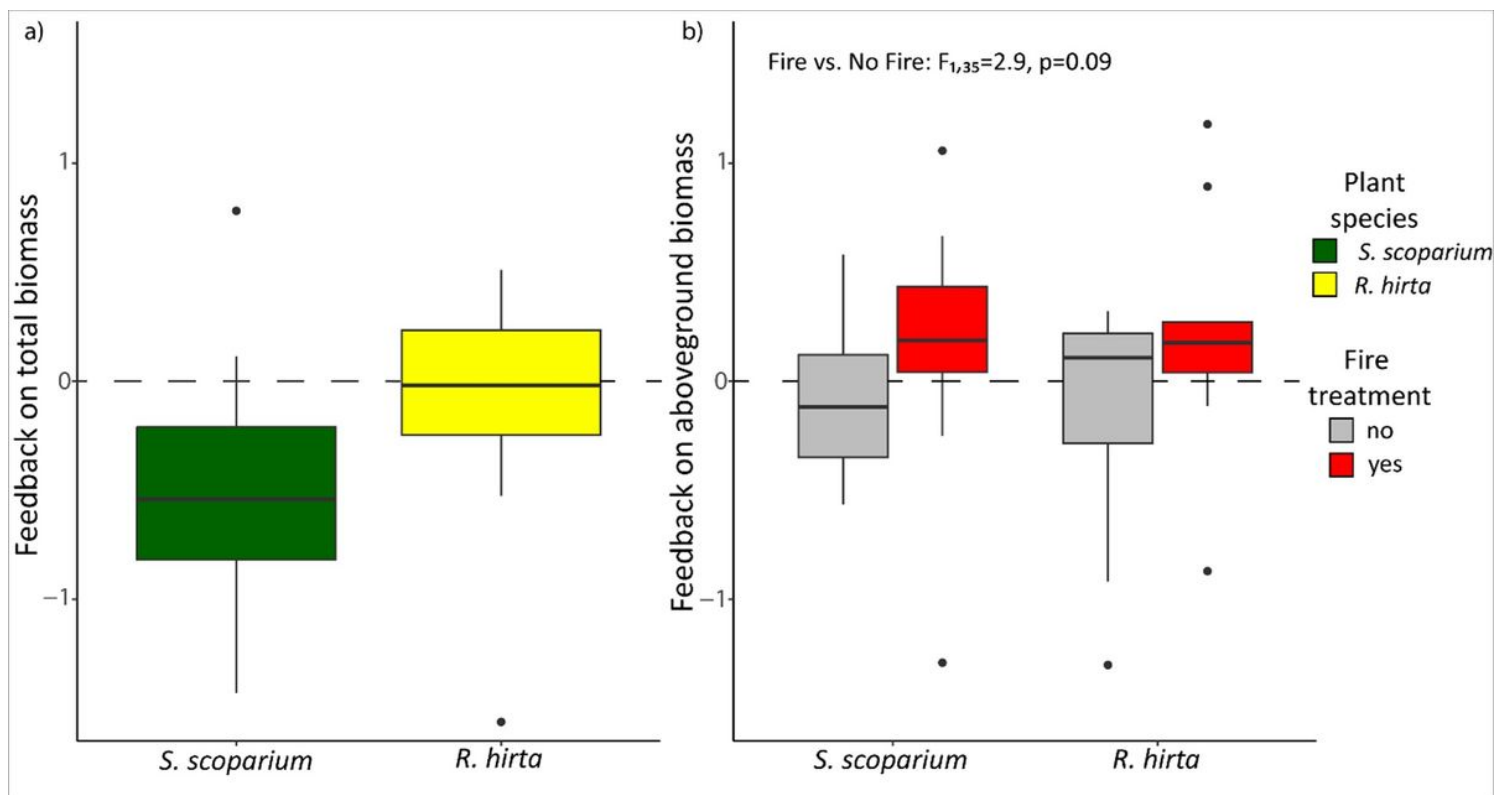


Figure 3

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.