University of North Carolina Asheville
Journal of Undergraduate Research
Asheville, North Carolina
May 2019

Effects Of Wildfire And Interguild Competition On Fungal Decomposition In A Temperate Mixed-Hardwood Forest

Tallis Donnelly
Biology
The University of North Carolina Asheville
One University Heights Asheville
North Carolina 28804 USA

Faculty Advisor: Dr. Jonathan Horton

Abstract

Decompositional dynamics between soil-dwelling fungi control the degree to which carbon from organic matter is either stored or released, potentially as atmospheric CO_2. Two groups (guilds) of fungi — plant root-associated ectomycorrhizae (ECM) and free-living saprotrophs — have been observed to significantly influence net decomposition rates. A decrease in decomposition is typically observed as a result of interguild competition, due in part to differences between guilds in carbon sourcing. As post-fire remediators and pioneer species, fungi are particularly relevant to the study of ecosystem effects of forest fire. The outbreak of forest fires in Western North Carolina in 2016 provided a rich opportunity for research, especially significant considering the projected increase in wildfire with the progression of global climate change. I established plots in an area affected by the Party Rock Fire, with three sets of paired burned/unburned plots containing subplots which were either trenched to disrupt ECM systems or left untrenched. By measuring soil respiration and decomposition of organic matter by mass in these plots over a year, I sought to elucidate the effects of fire upon ecosystem-level decomposition processes, and thus upon interguild fungal interactions. Higher rates of decomposition were predicted in trenched plots than in untrenched, and lower rates in burned plots than in unburned due to shifts in carbon-to-nitrogen ratio. C:N was not significantly altered by the fire, but soil respiration rates were greater in unburned than burned when compared by trenching treatment, and greater with leaf litter than with bare soil, suggesting the competitive suppression of fungal decomposition is limited to the litter layer in this system.

1. Introduction

Earth's soils store approximately half of all its carbon (C)[1], and it has been proposed that fungal species interactions directly control these soil C sinks in most ecosystems by competing for resources and either depleting soil organic matter of more scarce nutrients, thereby leaving the remaining recalcitrant C immobile in soil, or uptaking less nutrient-rich organic matter and subsequently mobilizing C into either biomass or atmospheric CO_2 via respiration[2]. Because increases in temperature and CO_2 due to climate change could exacerbate the C-releasing pathways of this system[3], understanding the mechanisms and variability of this fungal-mediated process is crucial.

Soil-dwelling fungal species can be broadly described in guilds based on nutritional niche, including free-living saprotrophic fungi or plant-associated ectomycorrhizal fungi (ECMs). ECM fungi are less C-limited because they gain sugars from their host plants which helps them decompose more recalcitrant litter (higher carbon-to-nitrogen ratio (C:N)) to acquire nutrients (e.g. N)[4]. The Gadgil Effect describes the phenomenon of reduced decomposition in soil due to competitive suppression of saprotrophic fungi by ECMs, originally observed by Gadgil and Gadgil[5,6]. This phenomenon can be a valuable way of discussing soil C sink or release processes--under the Gadgil Effect dynamics, presence of ECMs promotes C storage, while their exclusion results in increased C release[7].

The magnitude and direction of the Gadgil Effect have varied in studies across climates and bioregions, suggesting that multiple factors influence the system, such as distribution and abundance of fungal community[8], depth of labile C in soil[9], and host specificity of ECMs[10]. One popular proposed mechanism of the Gadgil Effect is that the nutrient mining of recalcitrant litter by ECMs creates a positive feedback loop further increasing C:N ratios of remaining litter and slowing decomposition by both guilds[11,12].

Soil-dwelling fungi can be post-fire remediators due to their roles in biogeochemical cycling, their mutualistic exchanges with plants, and mycelial reduction of erosion and nutrient leaching[13,14]. The removal of C and N from bulk soil due to incineration of soil organic matter[15] is likely to reduce overall fungal decomposition and possibly alter fungal community structure. Chen and Cairney[16] found a sharp reduction in prevalence of basidiomycetes in the burned soils. Similarly, Smith *et al.*[17] saw ECM species richness reduced significantly by burn, although fungal species richness has been found unchanged in other fire studies[18,19], suggesting that traits of the ecosystem and the burn may influence such effects.

The outbreak of forest fires in Western North Carolina in fall 2016 provided a rich opportunity for research, and is of particular relevance considering the projected increase in wildfire with the progression of global climate change[20]. With this one-year study, I sought to elucidate the effects of fire upon ecosystem-level decomposition processes, and upon the interguild fungal interactions that drive them. I predicted higher rates of decomposition in plots where ECM connections with host plants were severed by trenching than in untrenched plots, due to the Gadgil Effect. Lower decomposition rates were expected in burned plots than in unburned, because of the removal of labile carbon sources by fire as well as anticipated fire effects on soil C:N ratios.

2. Methods

2.1 Study Plots

In July 2017, I established six 0.04 ha paired circular plots (three in burned and three in unburned areas) in a mixed hardwood forest on Shumont Mountain in Western North Carolina's Chimney Rock State Park. This site was part of the 2016 Party Rock Fire, which burned for a month and covered a total of 7154 acres[21]. In each plot, I randomly established 24 1m^2 subplots. Half of these subplots were trenched to a depth of 50 cm (and retrenched monthly) to sever ECM fungal connections.

All trees were tagged, identified, and their diameter at breast height was measured to characterize tree community in each plot. I calculated relative density, relative dominance, relative frequency, and determined from resultant importance values that *Acer rubrum, Kalmia latifolia, Quercus montana,* and *Quercus rubra* were most important in both burned and unburned plots (Figure 1).

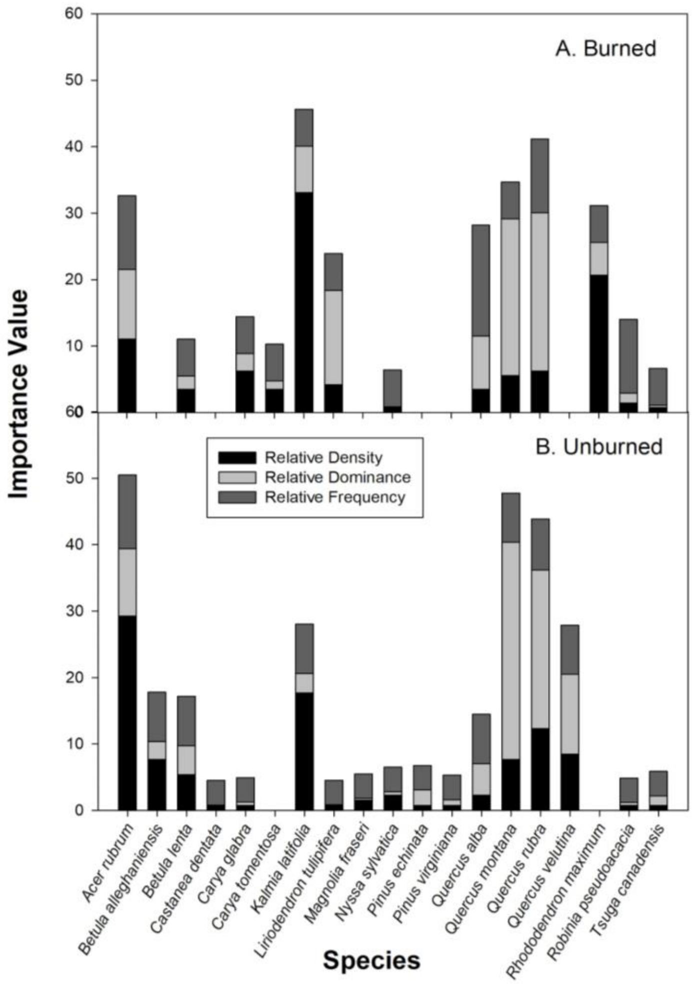

Figure 1. Measures of species abundance and resultant importance values in burned (A) and unburned (B) plots for all trees within plots.

2.2 Litter Bags

I collected leaf litter from areas adjacent to the study plots, allowed them to air dry in the lab for one week, then assembled 144 (one for each subplot) 20 x 20 cm mesh bags constructed of fiberglass 1mm^2 insect screening and containing 10 g of leaf litter. The week of June 8, 2017, a litter bag was fastened to the ground in the center of each subplot with two 8.5 cm galvanized steel nails through opposite corners. In unburned plots, litter bags were placed under the litter layer on top on the soil.

A set of litterbags, one from each treatment combination in each plot, was retrieved 3, 6, 9 and 12 months after placement, and weighed to determine the amount of mass lost. I estimated decomposition rates using the equation (1) where x_t is mass at time (t), x_0 is initial mass, and k is the decomposition rate[22].

$$x_t/x_o = e^{-kt} \qquad (1)$$

2.3 Soil Sampling

I took a soil core, two cm in diameter and 10 cm deep or to rock, from the center of each 12-month subplot then bulked to a single sample each burned (n=3) and unburned (n=3) plot. Bulk samples were sent to North Carolina Department of Agriculture and Consumer Services for analysis of a suite of nutrients and to the NC State Environmental and Agricultural Testing Service lab for determination of carbon and nitrogen content.

2.4 Soil Respiration Measurements

In one trenched and one untrenched subplot in each study plot, pvc collars (10 cm diameter, 4.5 cm height) were installed to a depth of 3 cm for soil respiration measurements conducted monthly using the LI-6400 portable photosynthesis system, fitted with the LI-6400-09 soil respiration chamber (LI-COR; Lincoln, Nebraska). In unburned plots, respiration was measured from cores containing bare soil (litter removed) and also soil with intact litter.

2.5 Statistical Analysis

I used several one-way analyses of variance to test the effect of each treatment level for all collected metrics: soil nutrients, litter decomposition, and soil respiration. First I tested the effect of burn on soil characteristics. Then for each month litter bags were collected, I tested the effect of burn on trenched and untrenched subplots, and the effect of trench on burned and unburned plots, using proportion of mass remaining. I ran three tests for soil respiration rates: one assessing burn treatment in trenched and untrenched subplots, one assessing trench treatment in burned and unburned plots, and one assessing litter presence/absence in unburned trenched and untrenched subplots. Because of the small sample size within each treatment combination, I regarded $p \leq 0.10$ as significant. All analyses were done in SAS v 9.4 (SAS Institute; Cary, NC).

3. Results

Litter bags lost mass at a significantly higher rate in unburned than burned plots across the entire time of the study (Figure 2). For the first harvest (month 3), trenched bags lost significantly more mass than untrenched (Table 1). However, the pattern reversed by the end of the study, with marginally significant higher mass loss in untrenched versus trenched plots. Trenching did not have any statistically significant effects on litter bag decomposition in months 6 and 9.

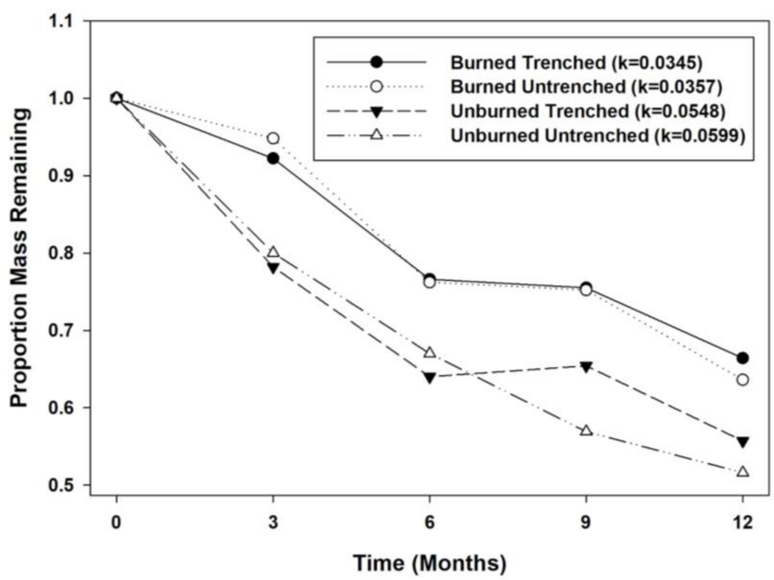

Figure 2. Proportion of mass remaining in litter bags over time, with steeper slopes (k values) indicating greater rate of decomposition. Burned plots showed significantly slower rates of mass loss than unburned.

Table 1. *F* and *p* values for litter decomposition analyses.

	Burned vs Unburned		**Trenched vs Untrenched**	
Time (months)	***f***	***p***	***f***	***p***
3	195.08	<0.0001	5.21	0.0292
6	37.99	<0.0001	0.42	0.5216
9	24.22	<0.0001	1.38	0.2492
12	34.56	<0.0001	3.18	0.0847

I found no significant burn effects on bulk C%, N%, C:N or any other soil nutrients, but soil pH and base saturation were significantly higher in burned plots than in unburned (Table 2).

Table 2. Soil sample means for all tested parameters. pH and base saturation show significant differences by burn, while all others are not significantly different.

Soil Nutrient	**Burned**	**Unburned**	***p***
C (wt. %)	5.56 ± 1.73	4.13 ± 0.27	0.4762
N (wt. %)	0.28 ± 0.09	0.24 ± 0.02	0.6649
C:N	19.7 ± 0.19	17.9 ± 2.29	0.4203
pH	**4.83 ± 0.10**	**4.15 ± 0.10**	**0.0005**
HM (%)	1.62 ± 0.21	1.30 ± 0.14	0.2421
W/V (g/cm^3)	0.86 ± 0.02	0.70 ± 0.10	0.1793
BS (%)	**34.8 ± 4.34**	**17.5 ± 2.32**	**0.0055**
CEC ($meq/100cm^3$)	5.63 ± 0.14	7.27 ± 1.06	0.1561
P (mg/dm^3)	31.3 ± 9.96	20.0 ± 2.59	0.2964
K (mg/dm^3)	66.8 ± 5.33	83.7 ± 14.0	0.2872
Ca (mg/dm^3)	288 ± 46.5	173 ± 68.0	0.1931
Mg (mg/dm^3)	43.3 ± 1.58	37.5 ± 7.27	0.4509
S (mg/dm^3)	32.8 ± 1.11	33.8 ± 3.48	0.7897
Mn (mg/dm^3)	54.7 ± 16.9	22.1 ± 7.93	0.1119
Zn (mg/dm^3)	2.22 ± 0.16	3.1 ± 0.50	0.1214
Cu (mg/dm^3)	0.55 ± 0.09	0.52 ± 0.03	0.7387
Na (mg/dm^3)	0.10 ± 0	0.10 ± 0	-

No differences in soil respiration were statistically significant across the full year. When analyzing the effect of burn, unburned plots showed higher mean rates of CO_2 efflux than burned in all instances of significant difference for both trenched and untrenched subplots(Figure 3). Similarly, mean respiration was greater in untrenched than trenched plots in all instances of significant difference for both burned and unburned plots (Figure 4). Unburned trenched plots showed greater respiration with intact litter layer than with bare soil in both July and August (Figure 5). Table 3 lists statistical values for all respiration analyses.

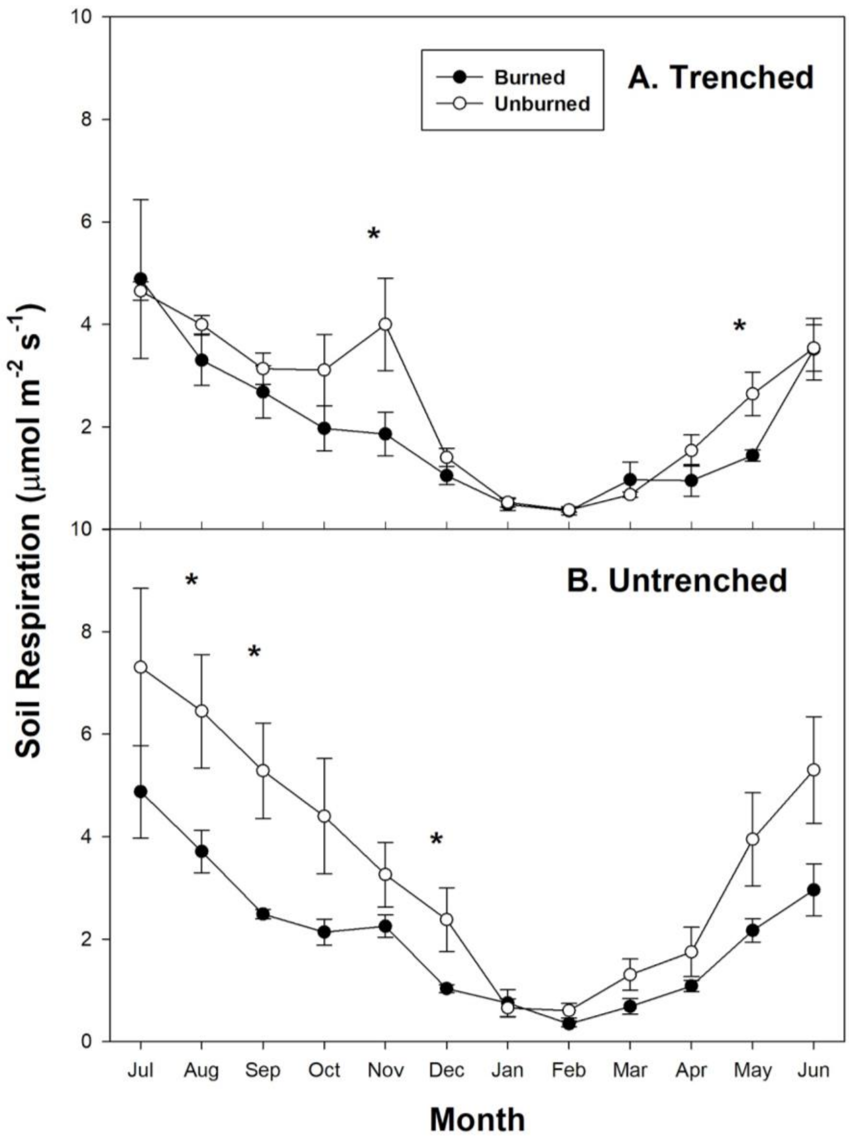

Figure 3. Burned versus unburned mean soil respiration, with asterisks denoting significant differences by burn.

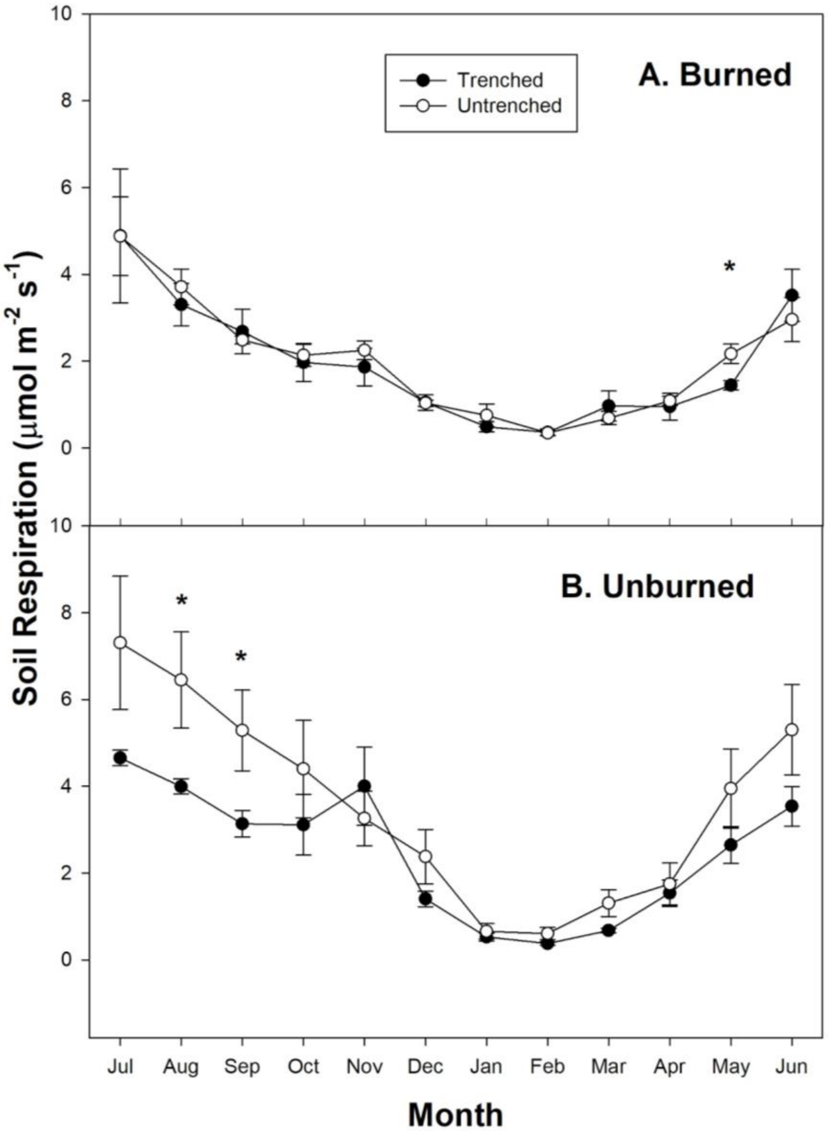

Figure 4. Trenched versus untrenched mean soil respiration, with asterisks denoting significant differences by trench.

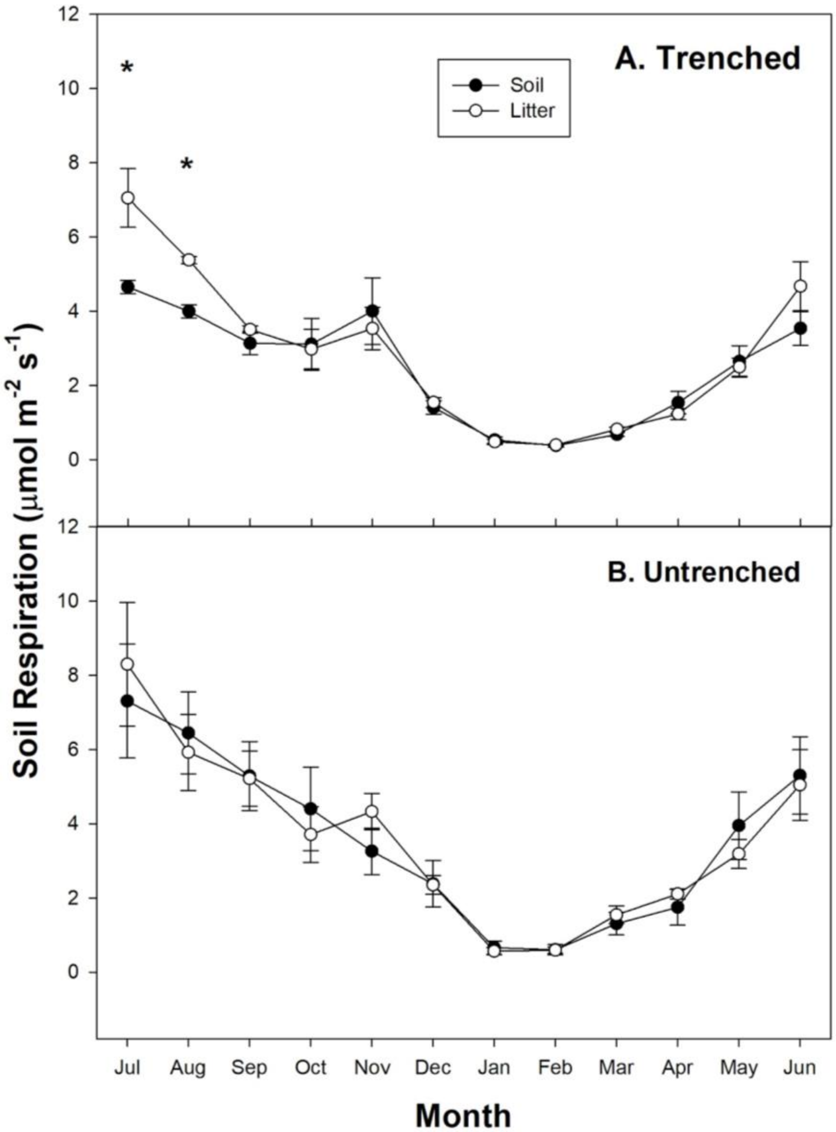

Figure 5. Mean soil respiration with bare soil and with intact litter layer in unburned plots, with asterisks denoting significant differences between litter treatments.

Table 3. *F* and *p* values for all soil respiration analyses.

	Burn Treatment				Trench Treatment				Litter Treatment			
	Trenched		Untrenched		Burned		Unburned		Trenched		Untrenched	
	f	***p***	***f***	***p***	***f***	***p***	***f***	***p***	***f***	***p***	***f***	***p***
Jul	0.02	0.8875	1.86	0.2447	0.00	0.9961	2.94	0.1615	**8.76**	**0.0416**	0.19	0.6836
Aug	1.76	0.2556	**5.35**	**0.0817**	0.40	0.5614	**4.77**	**0.0942**	**47.46**	**0.0023**	0.12	0.7451
Sep	0.57	0.4908	**8.97**	**0.0402**	0.14	0.7272	**4.82**	**0.0930**	1.32	0.3143	0.00	0.9542
Oct	1.91	0.2388	3.85	0.1211	0.11	0.7603	0.95	0.3855	0.02	0.8870	0.26	0.6363
Nov	**4.60**	**0.0986**	2.29	0.2046	0.65	0.4646	0.46	0.5356	0.19	0.6841	1.79	0.2517
Dec	1.99	0.2314	**4.56**	**0.0995**	0.01	0.9360	2.24	0.2091	0.37	0.5756	0.00	0.9709
Jan	0.07	0.8001	0.09	0.7795	0.85	0.4079	0.42	0.5506	0.17	0.7051	0.22	0.6668
Feb	0.03	0.8609	2.93	0.1619	0.03	0.8765	2.36	0.1995	0.12	0.7437	0.01	0.9386
Mar	0.69	0.4517	3.32	0.1426	0.56	0.4941	4.12	0.1123	3.16	0.1501	0.38	0.5731
Apr	1.83	0.2472	1.81	0.2499	0.16	0.7072	0.14	0.7317	0.82	0.4171	0.32	0.6094
May	**7.47**	**0.0522**	3.61	0.3010	**8.37**	**0.0444**	1.68	0.2642	0.09	0.7763	0.59	0.4838
Jun	0.00	0.9776	4.07	0.1137	0.50	0.5178	2.40	0.1961	2.01	0.2290	0.03	0.8652

4. Discussion

The differences in litter bag decomposition illustrate distinct effects of burning on decompositional rates. Soil and tree community characterizations support that these differences are attributable to burn and not due to fundamental site differences. However, because I did not find a soil C:N ratio shift linked to burn, the mechanism for this difference is not well elucidated.

Contrary to my hypothesis, trenching reduced respiration in some subplots. This suggests that ECM may contribute more significantly to net respiration in this system, rather than hindering potentially higher respiration activity of saprobes. Burning reduced soil respiration in both trenched and untrenched plots, but this effect was not consistent. Because burning consumed much of the litter, this may have resulted in the loss of some saprotrophic fungi from the local system. However, the fact that underlying mineral soil nutrient levels were unchanged suggests that the fire was not very intense and likely did not heat the soil very much, thereby reducing negative effects on fungi deeper in the soil. This is consistent with the findings of Cowan *et al.*[23] who, in a study on effects of burn intensity on soil chemistry and mycorrhizal community at different soil depths, observed no differences in soil chemistry or fungal species abundance between unburned and low burn treatment (which incinerated litter but did not heat soil more than 5 cm deep).

Trenching also resulted in higher respiration with intact litter layer when compared to bare soil in unburned plots. Barring disturbance effects, this suggests that there may be competition between saprotrophic and ECM fungi in the litter layer and that when ECM are restricted, respiration from saprotrophic fungi increases, showing the expected Gadgil Effect. In a longer-term (four-year) trenching study, Sterkenburg *et al.*[9] saw Gadgil interactions similarly limited to the litter layer, with yeasts and molds increasing most in abundance when ECMs were excluded. They reasoned that the deeper strata of soil were not metabolically accessible to litter most saprotrophs, leaving these more recalcitrant depths open for opportunistic taxa to exploit. This explanation, however, relies on the proposition that these more recalcitrant soils lie outside the fundamental niche of the saprotrophic guild, which is directly contrary to the findings of Bödeker *et al.*[24], whose soil-depth partitioning study supported the theory of overlapping fundamental niches, with saprobic exclusion in deeper horizons due to competition-driven niche partitioning. It is probable that the extent of fundamental niche overlap between ECM and saprotrophic guilds is variable by such ecosystem characteristics as litter quality, soil development, and fungal species distribution.

The complexity of fungal decomposition processes on an ecosystem level is still little-understood, particularly regarding the variable effects of interguild competition and forest fire. However, the role these processes play in global C cycling dynamics warrants continued investigation. Here, I sought to determine whether wildfire-induced changes in soil C:N affects fungal decomposition in a way that is consistent with the Gadgil Effect. C:N was not significantly altered by the fire, but soil respiration rates were greater in unburned than burned plots when compared by trenching treatment, and greater with leaf litter than with bare soil, and suggest that the competitive suppression of decomposition is limited to the litter layer in this system. Continued study of this ecology is necessary to more fully understand an important component of C cycling and storage, as well as a potential tool in efforts to reduce climate change progression.

5. References

1. Tarnocai C, Canadell J.G., Schuur E.A.G., Kuhry P, Mazhitova G, Zimov S. 2009. Soil organic carbon pools in the northern circumpolar permafrost region. Global Biogeochemical Cycles. 23:GB2023. 11 p.
2. Averill C, Hawkes C.V. 2016. Ectomycorrhizal fungi slow soil carbon cycling. Ecology Letters. 19:937-947
3. Pickles B.J., Egger K.N., Massicotte H.B., Green S. 2012. Ectomycorrhizas and climate change. Fungal Ecology. 5:73-84
4. Read D.J., Perez-Moreno J. 2002. Mycorrhizas and nutrient cycling in ecosystems − a journey towards relevance? New Phytologist. 157:475-492
5. Gadgil R.L., Gadgil P.D. 1971. Mycorrhiza and Litter Decomposition. Nature. 233:138
6. Gadgil R.L., Gadgil P.D. 1974. Suppression of litter decomposition by mycorrhizal roots of Pinus radiata. New Zealand Journal of Forestry Science. 5 (1):33-41
7. Averill C, Turner B.L., Finzi A.C. 2014. Mycorrhiza-mediated competition between plants and decomposers drives soil carbon storage. Nature. 505:543-546
8. Brzostek E.R., Dragoni D, Brown Z.A., Phillips R.P. 2015. Mycorrhizal type determines the magnitude and direction of root-induced changes in decomposition in a temperate forest. New Phytologist. 206:1274-1282
9. Sterkenburg E, Clemmenser K.E., Ekblad A, Finlay R.D., Lindahl B.D. 2018. Contrasting effects of ectomycorrhizal fungi on early and late stage decomposition in a boreal forest. The ISME Journal. 12:2187-2197
10. Yguel B, Courty P, Jactel H, Pan X, Butenschoen O, Murray P.J., Prinzing A. 2014. Mycorrhizae support oaks growing in a phylogenetically distant neighborhood. Soil Biology & Biochemistry. 78:204-212
11. Orwin K.H., Kirschbaum M.U., St John M.G., Dickie I.A. 2011. Organic nutrient uptake by mycorrhizal fungi enhances ecosystem carbon storage: a model-based assessment. Ecology Letters. 14:493-502
12. Fernandez C.W., Kennedy P.G. 2016. Revisiting the ‘Gadgil effect’: do interguild fungal interactions control carbon cycling in forest soils? New Phytologist. 209:182-194
13. Claridge A.W., Trappe J.M., Hansen K. 2009. Do fungi have a role as soil stabilizers and remediators after forest fire? Forest Ecology and Management. 257:106-1069
14. Cairney J.W.G., Bastias B.A. 2007. Influences of fire on forest fungal communities. Canadian Journal of Forest Research. 37:207-215
15. Bormann B.T., Homann P.S., Darbyshire R.L., Morrissette B.A. 2008. Intense forest wildfire sharply reduces mineral soil C and N: the first direct evidence. Canadian Journal of Forest Research. 38:2771-2783
16. Chen, D.M., and Cairney, J.W.G. 2002. Investigation of the influence of prescribed burning on ITS profiles of ectomycorrhizal and other soil fungi at three Australian sclerophyll forest sites. Mycological Research. 106: 533–540
17. Smith, J.E., McKay, D., Brenner, G., McIver, J., and Spatafora, J.W. 2005. Early impacts of forest restoration treatments on the ectomycorrhizal fungal community and fine root biomass in a mixed conifer forest. Journal of Applied Ecology 42: 526–535
18. Jonsson, L., Dahlberg, A., Nilsson, M.C., Zackrisson, O., and Karen, O. 1999. Ectomycorrhizal fungal communities in late-successional Swedish boreal forests, and their composition following wildfire. Molecular Ecology 8:205–215
19. De Roman, M., and De Miguel, A.M. 2005. Post-fire, seasonal and annual dynamics of the ectomycorrhizal community in a Quercus ilex L. forest over a 3-year period. Mycorrhiza, 15: 471–482

20. Davis R, Yang Z, Yost A, Belongie C, Cohen W. 2017. The normal fire environment—Modeling environmental suitability for large forest wildfires using past, present, and future climate normal. Forest Ecology and Management. 390:173-186

21. NC State Parks: "Four Seasons Hike: Party Rock. 2017 Oct. About the Division of Parks & Recreation" [accessed 2018 Nov 18]. https://www.ncparks.gov/chimney-rock-state-park/events-and-programs /four-seasons-hike-party-rock

22. Olson JS. 1963. Energy storage and the balance of producers and decomposers in ecological systems. Ecology 44:322–331

23. Cowan AD, Smith JE, Fitzgerald SA. 2016. Recovering lost ground: Effects of soil burn intensity on nutrients and ectomycorrhiza communities of ponderosa pine seedlings. Forest Ecology and Management 378: 160–172

24. Bödeker I.T.M., Björn D.L., Olson A, Clemmensen K.E. 2016. Mycorrhizal and saprotrophic fungal guilds compete for the same organic substrates but affect decomposition differently. Functional Ecology. 30:1967-1978