SPECIES DOMINANCE AFFECTS SOIL FERTILITY IN FREQUENTLY BURNED COASTAL PLAIN *PINUS* SPP. FORESTS, VIRGINIA, USA

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Abstract

Prescribed fire is a common management practice for Eastern forests, especially in Coastal Plain forests dominated by Southern yellow pine (*Pinus* spp.) species such as longleaf pine (*P. palustris* Mill.) and shortleaf pine (*P. echinata* Mill.). We present a summary of findings from the Blackwater Ecological Preserve in the Zuni Pine Barrens located in southeastern Virginia, USA. In support of previous findings from this region, we found reduced soil fertility (in terms of Ca, Mg, P, and K concentrations) associated with frequently burned pine stands, in comparison to an infrequently burned mixed pine-hardwood stand. Notably, we also found elevated C:N associated with *P. palustris* dominance after approximately 30 years of dormant season prescribed fire.

*This is a partial, condensed report for this study, which can be accessed in full online at: https://doi.org/10`.1080/00103624.2025.2475972.

1. Introduction

Climatic shifts associated with anthropogenic climate change are also associated with increased wildfire risk (Mitchell et al., 2014; Rocca et al., 2014). In forests of the eastern United States (US), climate change is also one of the drivers of an ecological transition known as mesophication, which is defined by major shifts in forest composition and structure in the eastern US (Alexander et al., 2021; Nowacki and Abrams, 2008). This process is characterized by the expansion of mesophytes, which historically dominate mesic or wet sites, into xeric or dry regions. Mesophytes, such as red maple (*Acer rubrum* L.) are often highly shade tolerant, which provides a competitive advantage over less shade tolerant xerophytes, like oak (*Quercus* spp.) and shortleaf pine (*Pinus echinata* Mill.). Mesophication has also been attributed to exploitative high-yield timber harvesting practices (Ryan et al., 2024), increased deer herbivory (Hanberry and Faison, 2023), and wildland fire suppression and exclusion (Nowacki and Abrams, 2008). While xerophytes often possess adaptations to fire, such as thick bark or resprouting potential, mesophytes are more commonly

fire-intolerant (Abrams, 1992; Keeley and Pausas, 2022). As a result, the restoration of historic fire regimes through prescribed burning has long been proposed as a management priority in the southeastern US with the dual purpose of reducing wildfire risk by consuming hazardous fuel and reversing mesophication by promoting fire-adapted pyrophytes.

In particular, prescribed fire has been popularized in the Southeast for the restoration of fire-adapted or pyrophytic pine communities on the Coastal Plain (Guldin, 2019). Two species of interest are *P. echinata* and longleaf pine (*Pinus palustris* Mill.). In the eastern US, the dominance of *P. echinata* species east of the Mississippi River has decreased by more than 50% since 1980 (Guldin and Black, 2018). Restoration of *P. palustris* and *P. echinata* forests via the combination of planting and burning has become a management priority, especially on National Forests (Guldin, 2019), but the effects of this management on stand dynamics, ecological diversity, and nutrient cycling have not been fully described throughout the region.

The original objective of this research project was to evaluate the influence of fire regime on the storage and utilization of non-structural carbohydrates (NSCs) in *P. echinata* saplings. NSCs are primarily composed of non-soluble sugars and starches (Hartmann and Trumbore, 2016). Soluble sugars typically support functions associated with plant growth, but starch reserves are more commonly associated with post-disturbance regrowth and recovery (Chapin III et al., 1990; Mooney and Hays, 1973; Paula and Ojeda, 2009). We aimed to evaluate how variation in NSC storage and utilization corresponded to post-fire functional trait expression. Because that study is still ongoing, this report comprises findings from a similar study from southeastern Virginia (DeFeo et al., 2025).

We aimed to characterize the effect of species dominance for mineral soil and O Horizon fertility under a high frequency, low severity fire regime. We hypothesized that:

1) Fertility of the organic horizon and upper mineral soil would differ with historic management and species composition;
2) Fertility of the organic horizon and upper mineral soil would also differ with pine species dominance.

2. Methods

2.1 Study Area

This study is located on the Blackwater Ecological Preserve (BEP), within the Zuni Pine Barrens Preserves, in Isle of Wight County, Virginia, USA. The property is owned and managed by Old Dominion University, in cooperation with the Virginia Department of Conservation and Recreation. The BEP hosts four distinct pine-dominated forest stands that we utilized for this study. Three stands have been burned approximately once every two to three years since the mid-1980s. The overstory of each frequently burned stand is dominated by 1) *P. palustris*, 2) loblolly pine (*P. taeda* L.), or 3) pond pine (*P. serotina* Michx.). The fourth stand was burned for the first time on record in 2023 and is dominated by yellow pine (primarily *P. palustris and P. taeda*) with co-dominant turkey oak (*Q. laevis* Walt.) and sourwood (*Oxydendrum arboreum* L.) (hereinafter referred to as the ‘mixed pine-hardwood stand’).

2.2 Field Sampling

In each stand, we collected approximately 30 samples of soil and organic detritus. Plot locations were randomly generated. First, a sample of organic material was removed manually; this was primarily comprised of leaf litter, but duff (Oa +Oe Horizons) was included where it was present. Soils were removed from this same location using an Oakfield Model H soil probe (Oakfield Apparatus, Oakfield, WI, USA; inner diameter 2.06 cm). Soil samples were divided into upper (0-5 cm) and lower (5-10 cm) mineral soil layers. Because we did not have enough duff material to complete chemical analysis in one of the stands, we had to combine two plots in that stand. We then randomly combined two plots in each of the other stands; the final sample size per stand is 29.

2.3 Lab Analyses and Statistical Methods

Soils and organic material were characterized in terms of pH, C:N and concentrations of P, Ca, K, and Mg. After sampling, materials were oven dried at 65°C for three days and hand sieved to 2 mm. Lab analyses were contracted to Brookside Laboratories in New Bremen, OH, USA.

Statistical analyses were conducted in JMP Pro 17.0 (SAS Institute Inc., Cary, NC, USA). We performed a one-way analysis of variance (ANOVA) on rank-transformed soil data, using stand as the explanatory variable. For post-hoc testing, we used the Each-Pair Student's T Test. Finally, a combination of principal component analysis (PCA) and cluster analysis were used to portray trends in fertility amongst the four stands.

3. Results and Discussion

We found that the fertility of the O Horizon and mineral soil did differ between our four stands. In support of our first hypothesis, for the O Horizon, prescribed fire management was associated with elevated pH and reduced C:N, K, Mg, and P (p<0.01 for all responses; see Table 3 in DeFeo et al. (2025)). In the mineral soil, pH was still elevated, and Ca was significantly reduced, as well as C:N, K, Mg and P (p<0.01 for all responses). Prior research has highlighted the relatively short-term influence of dormant season prescribed fire on soil fertility (McKee, 1982). Given the length of time that these stands have been managed with fire, we attribute these results not to the fire itself, but to management which has maintained an open, pine savanna structure with reduced hardwood basal area (Coates et al., 2020).

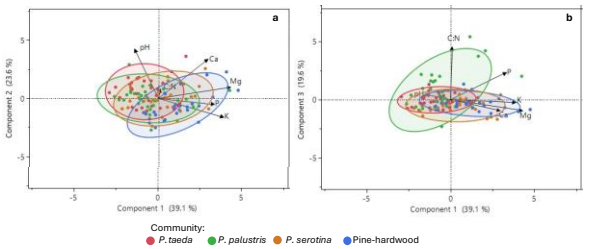

Figure 1. Modified from DeFeo et al. (2025). Principal component analysis and 90% prediction ellipses for soil fertility within the O horizon among frequently burned pine-dominated stands and an infrequently burned mixed pine-hardwood stand at Blackwater Ecological Preserve, Isle of Wight County, Virginia, USA.

In support of our second hypothesis, we also found significant variation in our response variables due to pine species community (Figure 1). From our cluster analysis, we observed distinction in terms of Ca, Mg, P, and K between the frequently burned pine stands and the infrequently burned mixed pine-hardwood stand (Figure 1a). Most notably, in the O Horizon and upper

mineral soil layer, we observed a significantly elevated C:N ratio associated with *P. palustris* (p<0.01 for all comparisons; see Table 2 in DeFeo et al. (2025)). This was most apparent in the O Horizon (Figure 1b).

These results are interesting because of their potential implications for fire behavior in these stands. Longleaf pine is known for adaptations to fire; this species is also known for chemical variation in bark, wood, and needle tissues that may be promoting more intense fire behavior (e.g. greater flame lengths, hotter temperatures) (Eberhardt and Samuelson, 2022; Fonda, 2001; Renner et al., 2023; Ross and Fikis, 1980; Sah et al., 2006). We did not look at origin sources for soil and detrital carbon in this study. However, if fuel conditions in our *P. palustris* stand were conducive to more intense fire behavior, the elevated C:N response observed here could be attributed to additional inputs of black carbon. Residues of black carbon, which form via the incomplete combustion of organic material, can be a relatively inert form of carbon storage (Schmidt and Noack, 2000).

Next, we aim to replicate this study, with the goal of informing prescribed fire management in diverse yellow pine forests across landscape and regional scales. We will incorporate diversity and productivity data for soil microbial communities, in order to better describe influences of management from a nutrient cycling perspective. Because we observed variation in soil carbon in our sites, we will include additional analysis to more closely track carbon stocks.

4. References

Abrams, M.D., 1992. Fire and the Development of Oak Forests. BioScience 42, 346–353. https://doi.org/10.2307/1311781

Alexander, H.D., Siegert, C., Brewer, J.S., Kreye, J., Lashley, M.A., McDaniel, J.K., Paulson, A.K., Renninger, H.J., Varner, J.M., 2021. Mesophication of Oak Landscapes: Evidence, Knowledge Gaps, and Future Research. BioScience 71, 531–542. https://doi.org/10.1093/biosci/biaa169

Chapin III, F.S., Schulze, E.-D., Mooney, H.A., 1990. The Ecology and Economics of Storage in Plants. Annu. Rev. Ecol. Syst. 21, 423–446.

Coates, T.A., Johnson, A., Aust, W.M., Hagan, D.L., Chow, A.T., Trettin, C., 2020. Forest composition, fuel loading, and soil chemistry resulting from 50 years of forest management and natural disturbance in two southeastern Coastal Plain watersheds, USA. For. Ecol. Manag. 473, 118337. https://doi.org/10.1016/j.foreco.2020.118337

DeFeo, J.A., Coates ,T. Adam, Carter ,David R., and Flanders, N.P., 2025. Overstory Species Dominance Impacts Soil Fertility in Frequently Burned Coastal Plain Pine (*Pinus* spp.) Forests: A Case Study from the Zuni Pine Barrens, Virginia, USA. Commun. Soil Sci. Plant Anal. 0, 1–13. https://doi.org/10.1080/00103624.2025.2475972

Eberhardt, T.L., Samuelson, L.J., 2022. Comparison of lignin and polysaccharide sugar contents for slash, longleaf, and loblolly pine growth rings formed during periods of soil moisture extremes. Wood Sci. Technol. 56, 389–408. https://doi.org/10.1007/s00226-022-01359-0

Fonda, R.W., 2001. Burning Characteristics of Needles from Eight Pine Species. For. Sci. 47, 390–396.

https://doi.org/10.1093/forestscience/47.3.390
Guldin, J.M., 2019. Restoration of Native Fire-Adapted Southern Pine-Dominated Forest Ecosystems: Diversifying the Tools in the Silvicultural Toolbox. For. Sci. 65, 508–518. https://doi.org/10.1093/forsci/fxz005
Guldin, J.M., Black, M.W., 2018. Restoration of shortleaf pine in the southern united states—strategies and tactics (General Technical Report No. SRS-234), Proceedings of the 19th biennial southern silvicultural research conference. U.S. Department of Agriculture, Forest Service, Southern Research Station, Asheville, NC.
Hanberry, B.B., Faison, E.K., 2023. Re-framing deer herbivory as a natural disturbance regime with ecological and socioeconomic outcomes in the eastern United States. Sci. Total Environ. 868, 161669. https://doi.org/10.1016/j.scitotenv.2023.161669
Hartmann, H., Trumbore, S., 2016. Understanding the roles of nonstructural carbohydrates in forest trees – from what we can measure to what we want to know. New Phytol. 211, 386–403. https://doi.org/10.1111/nph.13955
Keeley, J.E., Pausas, J.G., 2022. Evolutionary Ecology of Fire. Annu. Rev. Ecol. Evol. Syst. 53, 203–225. https://doi.org/10.1146/annurev-ecolsys-102320-095612
McKee, W.H., 1982. Changes in soil fertility following prescribed burning on Coastal Plain pine sites (No. SE-RP-234). U.S. Department of Agriculture, Forest Service, Southeastern Forest Experiment Station, Asheville, NC. https://doi.org/10.2737/SE-RP-234
Mitchell, R.J., Liu, Y., O'Brien, J.J., Elliott, K.J., Starr, G., Miniat, C.F., Hiers, J.K., 2014. Future climate and fire interactions in the southeastern region of the United States. For. Ecol. Manag. 327, 316–326. https://doi.org/10.1016/j.foreco.2013.12.003
Mooney, H.A., Hays, R.I., 1973. Carbohydrate Storage Cycles in Two Californian Mediterranean-Climate Trees. Flora 162, 295–304. https://doi.org/10.1016/S0367-2530(17)31709-7
Nowacki, G.J., Abrams, M.D., 2008. The Demise of Fire and "Mesophication" of Forests in the Eastern United States. BioScience 58, 123–138. https://doi.org/10.1641/B580207
Paula, S., Ojeda, F., 2009. Belowground starch consumption after recurrent severe disturbance in three resprouter species of the genus *Erica*. Botany 87, 253–259. https://doi.org/10.1139/B08-134
Renner, J.S., Mensah, R.A., Jiang, L., Xu, Q., 2023. A critical assessment of the fire properties of different wood species and bark from small- and bench-scale fire experiments. J. Therm. Anal. Calorim. 148, 1423–1434. https://doi.org/10.1007/s10973-022-11443-z
Rocca, M.E., Brown, P.M., MacDonald, L.H., Carrico, C.M., 2014. Climate change impacts on fire regimes and key ecosystem services in Rocky Mountain forests. For. Ecol. Manag. 327, 290–305. https://doi.org/10.1016/j.foreco.2014.04.005
Ross, R.A., Fikis, D.V., 1980. Gasification reactions of chars and modified chars produced from jack pine bark. Can. J. Chem. Eng. 58, 230–234.

https://doi.org/10.1002/cjce.5450580214
Ryan, S.M., Copenheaver, C.A., Carter, D.R., Lorber, J.H., 2024. Evidence of mesophication following selective cutting and shelterwood in Virginia's eastern deciduous forest, USA. For. Ecol. Manag. 560, 121840. https://doi.org/10.1016/j.foreco.2024.121840
Sah, J.P., Ross, M.S., Snyder, J.R., Koptur, S., Cooley, H.C., 2006. Fuel loads, fire regimes, and post-fire fuel dynamics in Florida Keys pine forests. Int. J. Wildland Fire 15, 463–478. https://doi.org/10.1071/WF05100
Schmidt, M.W.I., Noack, A.G., 2000. Black carbon in soils and sediments: Analysis, distribution, implications, and current challenges. Glob. Biogeochem. Cycles 14, 777–793. https://doi.org/10.1029/1999GB001208