# Managing disturbance in the longleaf pine ecosystem: effects of managed fire regime characteristics on fire hazard and community ecology at multiple spatial scales

James B. Cronan

A dissertation
submitted in partial fulfillment of the
requirements for the degree of

Doctor of Philosophy

University of Washington
2026

Reading Committee:
Ernesto Alvarado-Celestino, Chair
Clinton S. Wright
J. Morgan Varner

Program Authorized to Offer Degree:
School of Environmental and Forest Sciences

University of Washington

# Abstract

## Managing disturbance in the longleaf pine ecosystem: effects of managed fire regime characteristics on fire hazard and community ecology at multiple spatial scales

James B. Cronan

Chair of the Supervisory Committee:
Ernesto Alvarado-Celestino
School of Environmental and Forest Sciences

Conservation lands within the range of longleaf pine (*Pinus palustris*) are valuable because they protect remnants of an ecosystem with globally high measures of biological diversity. The longleaf pine ecosystem is adapted to frequent, low-intensity fire, however, naturally occurring fire no longer burns with sufficient frequency to maintain the ecological structure and function necessary to sustain high levels of biological diversity. To compensate, aggressive prescribed fire programs are necessary. The fragmented nature of this ecosystem combined with the difficulty, complexity, and expense of applying regular prescribed fire in a densely populated landscape raises numerous management challenges. The research presented in this dissertation addresses many of the knowledge gaps confronting land managers using prescribed fire in longleaf pine ecosystems. The focus here is to provide information that

describes how changes in the fire regime affect understory vegetation from the perspective of both fire hazard and community ecology: the two main management objectives for prescribed burning in longleaf pine forests. Research addressing these objectives is presented in three chapters. First, in Chapter 3 I examined the effects of season-of-burn on shrub and herbaceous fuel layers and predicted fire behavior on frequently burned mesic pine flatwoods in northern Florida. Compared to single dormant season burns, single growing season burns caused no changes to live understory fuels and had no detectable effect on fire behavior. Shrub coverage and predicted fire behavior were, however, significantly different between two geographic regions sampled. Additionally, shrub height was significantly affected by fire temperature. Predicted fire behavior was strongly correlated with measures of the litter and herb strata. Results from this study suggest that land managers should not initially expect large changes in understory fuel properties or potential fire behavior related to a shift from dormant to growing season prescribed burning, and that geographic location and fire intensity can have significant effects on live fuels and potential fire behavior. Second, in Chapter 4 I evaluated the effects of frequent prescribed fire and forest structure on understory composition in mesic longleaf pine flatwoods. To do this, understory biomass and forest structure were measured in 22 stands of longleaf pine that were burned regularly for at least 20 years. Constrained multivariate ordination and boundary line regression were used to test whether explanatory variables (i.e., fire history and forest structure) affected understory biomass, grouped by genera and plant functional groups. Fire frequency, as measured by the mean fire interval (MFI) and coarse woody debris biomass had marginally significant effects on understory composition. These variables, though uncorrelated, weakly aligned with the first Principal Components axis where sites were arranged along a compositional gradient from typical understory shrubs and wiregrass (*Aristida* *beyrichiana*) to sites characterized by vines and understory hardwoods. Boundary line regression showed a significant negative relationship between forb abundance and MFI; however, this relationship did not extend to graminoids. Boundary line regression did not show any significant effects of MFI on measures of woody plant biomass. Season-of-burn had no significant effects on understory plants in the constrained ordination or boundary line regression. These results suggest that other environmental factors and fire regime characteristics that are more favorable to fire sensitive species would be necessary to significantly influence understory vegetation dynamics. Third, in Chapter 5 I used the Fuelbed Dynamics Model (FDM), a landscape-succession model I developed that incorporates fire and other disturbances, to simulate changes in fuels at Eglin Air Force Base (Eglin) in northwestern Florida for 50-year time periods under four scenarios of prescribed burning. The simulation outputs quantified the effect of different levels of prescribed burning on fire hazard across the longleaf pine-dominated landscape at Eglin where prescribed fire is the primary method used to manage vegetation and mitigate fire hazard. If the rate of prescribed burning is insufficient to maintain a low fire hazard landscape, Eglin's forests could pose substantial wildfire risk to the base's infrastructure, surrounding wildland urban interface communities, and longleaf pine communities. Simulations indicated that fire hazard for surface and canopy fuels would rise under reduced prescribed fire scenarios (20k and 30k ha yr$^{-1}$), would remain relatively unchanged at the baseline level of burning (40k ha yr$^{-1}$), and decline if prescribed burning was increased to 50k ha yr$^{-1}$. The MFI and overstory cover data suggest that fire hazard would ultimately decrease towards the end of the simulation for reduced burn scenarios over a substantial portion of Eglin relative to baseline and increased burn scenarios as forest mesophication favored fire impeding species in management units were fire was excluded and longleaf pine was replaced by broadleaf species and sand pine (*Pinus clausa*).

# TABLE OF CONTENTS

5. Simulated changes in fuels and fire hazard in a longleaf pine (*Pinus palustris*) ecosystem under multiple prescribed fire scenarios………….…………………………......188

# LIST OF FIGURES

# LIST OF TABLES

# ACKNOWLEDGEMENTS

To my committee, thank you for your support and patience over the years. To my chair, Ernesto Alvarado, thank you for your advice and support throughout my degree program. Your assistance throughout this process has been invaluable.

Clint Wright, thank you for providing the ideas and resources that started this work. Seems a distant memory, but this research is either an offshoot of your own dissertation or relicts of your research at the PNW Research Station. Your encouragement and thoughtful feedback from sampling logistics to final edits has contributed enormously to the quality of this work.

Morgan Varner, as the only committee member who works in the longleaf pine forests that are the focus of this work, thank you for providing context and knowledge to position this research within the existing body of scientific work and ensuring it is relevant to management needs. And for pointing out the value of concise writing.

Monika Moskal and Jennifer Ruesink, thank you for agreeing to join this committee during the tail end of my degree program. Your guidance and thoughtful feedback have helped me complete this dissertation.

John Skalski and Mark Kot, thank you for serving on my committee prior to your retirement. Your encouragement and advice are greatly appreciated.

I acknowledge funding from the Joint Fire Science Program under Project Numbers 09-1-02-2 and 13-3-01-26

I am grateful for the support and cooperation of numerous agencies and individuals who worked with us to incorporate research plots into existing prescribed fires, specifically K. Hiers and B. Williams at Eglin Air Force Base, E. Watkins at Apalachicola National Forest, and G. Titus and J. Hinckley at St. Marks National Wildlife Refuge.

I wish to thank staff from the University of Washington, School of Environmental and Forest Sciences and the USDA Forest Service, Pacific Northwest Research Station, who put in long hours in the field to help collect and process data over several years.

Those who assisted with field work included C. Balog, C. Burke, B. Cassell, J. Crowder, J. Dvorak, T. Freed, L. Grand, S. Griscom, K. Jacobson, R. Jones, I. Kostick, J. Landburg, A. Lundquist, J. McDuffey, K. Moffit, J. Restaino, S. Savage, A. Sengsirirak, D. Shoemaker, M. Simmons, and J. Smith.

For analysis and data management. P. Eagle developed the database structure and data entry application. A. Andreu helped develop FCCS fuelbeds. M. Kennedy and A. Steele provided statistical advice. B. Vihnanek coordinated field logistics. M. Petrova and B. Cassell assisted with data analysis for Chapters 3 & 4. I would like to thank those who were instrumental in the development of the landscape-fire-succession model used in Chapter 5. Especially B. Herman and the eScience Institute at the University of Washington, Brian Drye, and the AirFire Team at the Pacific Wildland Fire Sciences Lab. I would like to extend heartfelt thanks to P. Tekkar at the University of Washington, Disability Resources for Students office for her work as a scribe when I was temporarily unable to type due to an injury.

I am grateful for the support and my family and friends over these years. Especially my wife, L. Feng, and son, C. Cronan, whose love and encouragement kept me motivated.

# DEDICATION

I dedicate this dissertation to my wife Li-yun and son Caleb, who have provided unflinching support along the way.

# Chapter 1. Introduction – effects of prescribed fire on fuels and ecology in the longleaf pine (*Pinus palustris*) ecosystem

## 1.1 **Introduction**

The work presented here focuses on two important components of land management in the longleaf pine (*Pinus palustris* Mill.) ecosystem in the southeastern United States. These results clarify our understanding of how prescribed fire can be used to: 1) maintain high levels of biological diversity, and 2) mitigate hazardous fuels. Successful management of natural areas contributes to biologically diverse ecosystems, which enhance societal well-being (CBD, 1992; WHO, 2005). Because it is widely recognized to have societal value (Benton et al., 2021; Díaz et al., 2018; Marselle et al., 2021), and because there is evidence it strengthens both ecosystem function (Bowker et al., 2010; Costanza et al., 2007; Maestre et al., 2012) and resilience (Petchey and Gaston, 2009; Peterson et al., 1998), biodiversity has emerged as a primary management goal (e.g., Dorrough et al., 2002; Molina & White, 2007; Westman, 1990) that is threatened globally by rapid human population expansion (Karlin, 1995; Vitousek et al., 1997).

Disturbance is an ecosystem process (Pickett and White, 1985) that affects ecosystem biodiversity (Connell, 1978), function (Cardinale and Palmer, 2002), and resilience (Konstantinov, 2011; Nystrom et al., 2000; Reice et al., 1990). Natural disturbances in the southeastern US include hurricanes (Batista and Platt, 2003; Busing et al., 2009; Stanturf et al., 2007; Zhao et al., 2006), pests, pathogens (Coulson and Klepzig, 2011), and fire (Frost, 1995; Mitchell and Duncan, 2009; Stanturf et al., 2002). Fire, the primary disturbance agent in the longleaf pine ecosystem, is primarily applied through prescribed fire programs to enhance or ecological values (Heyward, 1939; Van Lear et al., 2005; Waldrop and Goodrick, 2012), mitigate hazardous fuels (O'Brien et al., 2010; Wade and Lunsford, 1989), and is the only natural disturbance regime in this ecosystem that can be reliably managed (Figure 1-1).

**Figure 1-1.** Typical low-intensity surface fire in a fire-maintained stand of longleaf pine on the Apalachicola National Forest in Florida. Photo: James Cronan.

Prior to widespread European settlement the fire regime of the longleaf pine ecosystem was defined by frequent, low-intensity fires (Earley, 2004; Frost, 2006) ignited by both lightning and humans (Lafon, 2010). The knowledgeable and skillful application of prescribed fire in contemporary longleaf pine forests has proven to be an effective tool to manage for biological diversity. This dissertation includes: a review of the fire history literature (Chapter 2), results from field experiments evaluating the effects of fire regime characteristics on fuel hazard (Chapter 3) and community ecology (Chapter 4), and results from simulation modeling evaluating how variable rates of prescribed fire application affect fuels and associated fire hazard (Chapter 5). The collective information provided by these studies contributes to a more fulsome understanding of disturbance-ecosystem interactions that can be integrated into management strategies to enhance biological diversity and mitigate hazardous fuels in longleaf pine forest ecosystems in the southeastern US.

## 1.2 **Chapter 2**

Chapter 2 presents an overview of the longleaf pine ecosystem and a review of fire history literature for the southeastern US. These provide context for the experimental results presented in this dissertation. A review of geography, soils, climate, vegetation, wildlife, and disturbance ecology contextualizes the dissertation research with respect to ecological properties and the broader array of management objectives that may compete with or complement those associated with the use of prescribed fire. In addition, the fire history literature review describes interactions among vegetation, the fire regime, climate, and anthropogenic activities. This is important for understanding the broader implications of results presented in this dissertation.

## 1.3 **Chapter 3**

Prescribed fire is widely used to manage fuel and wildfire risk in the southeastern US (Emery and Hart, 2020). Both frequency and season of burning affect understory composition. Most research on this subject focuses on the ecological effects (e.g., Carrington & Mullahey, 2006; Haywood, 1978; Platt et al., 1988; Shepherd et al., 2012; Streng et al., 1993). Less effort, however, has been dedicated to identifying how differences in burning treatments influence fuels and wildfire risk (e.g., Sparks et al., 2002). Chapter 3 addresses research gaps in post-fire fuel development and implications for fire behavior. Specifically, whether burning in different seasons (i.e., the growing and dormant seasons) influences the composition of surface fuels and if so, how changes in composition impact potential fire behavior.

Assessing the impact on fuels from prescribed burning in different seasons is important because growing-season burns can be used to shift understory vegetation from shrub- to herb-dominance, which can lead to differences in fire behavior (Anderson, 1982). High loading of fine-dead and volatile-live fuels in shrub-dominated fuelbeds can support high-intensity fires that are difficult to control (Andreu et al., 2012; Hough and Albini, 1978; Saglam et al., 2008). In contrast, herb-dominated fuel types do not promulgate high-intensity fires because herb biomass does not accumulate to same extent as shrubs and fuel height remains relatively low (Yospin et al., 2012). Herb-dominated fuel types can increase other measures of wildfire risk, however, as higher surface area-to-volume (SAV) ratio and near-optimal packing of continuous herbaceous fuelbeds can support high rates of fire spread. In addition, as herbaceous fuels cure and their moisture content decreases, they have a higher probability of ignition. Identifying the potential for growing season burns to change fuelbed characteristics and potential fire behavior provides valuable information for managers to consider as growing-season burns are more widely used to promote herbaceous understory vegetation.

This chapter presents results from a field experiment that evaluates how season-of-burn influences surface fuel characteristics and potential fire behavior in longleaf pine flatwoods by: (1) quantifying the effects of prescribed burning in the dormant and growing seasons on post-burn live understory fuel metrics including loading, cover, and height, and (2) determining the extent to which these differences influence potential fire behavior. I measured understory fuels prior to, and for three years following dormant and growing season prescribed burns and tested for effect of season-of-burn on surface fuel and modeled fire behavior characteristics by using repeated measures ANOVA.

## 1.4 **Chapter 4**

Chapter 4 seeks to address knowledge gaps surrounding the impacts of managed fire regimes on understory vegetation composition. Prescribed fire is often used to manage understory vegetation structure and composition. This vegetation layer includes many of the herbaceous species (Hardin and White, 1989) that contribute to the globally high levels of biological diversity in the longleaf pine ecosystem (Myers et al., 2000; Noss et al., 2015). It also provides critical habitat for threatened and endangered wildlife (Van Balen and Doerr, 1978) and game species (Schroeder, 1985). Herbaceous vegetation was historically the dominant understory cover type (Earley, 2004), but decreased dramatically in response to fire exclusion during the early- and mid-1900s (Frost, 2006). One objective of more widespread and more frequent application of prescribed fire in forests of the southeastern US is to increase the coverage and richness of grasses and forbs (Waldrop & Goodrick, 2012). Numerous long-term studies provided convincing evidence that, in some cases, the combination of short (1–3 year) fire return intervals and growing-season burns could shift understory vegetation from woody to herb dominance (Glitzenstein et al., 2003; Waldrop et al., 1987). This strategy could ostensibly provide habitat for the increasingly rare plant and wildlife species of the longleaf pine ecosystem. To date there have been relatively few studies to assess how understory vegetation reacts to variation across landscape scales in managed fire regimes (e.g., Addington et al., 2015; Hannon et al., 2020).

This chapter evaluates the relationship between the prescribed fire regime and measures of understory plant abundance in longleaf pine stands that have been regularly burned for at least 20 years across three conservation areas in northern Florida. I evaluated the degree to which understory vegetation composition in managed stands of longleaf pine is a function of fire regime variables. Specifically, I tested: (1) the effect of prescribed fire parameters on community composition, and (2) the effects of the same prescribed fire parameters on total biomass for the 10 most abundant understory species by using constrained ordination and boundary line regression.

## 1.5 **Chapter 5**

The impact of treatments, such as prescribed fire, on management criteria used to evaluate effectiveness may not manifest for years or decades (Kangas and Kangas, 2005). Identifying the potential outcomes of various natural resource management actions can be aided with simulation models (Korjus, 2014). These models simulate the effects and feedback of land management activities, disturbance, environmental factors, and biotic communities in a comprehensive manner in order to quantify the impacts over time and across the geographic extent of management areas (Keane et al., 2004). When used conservatively simulation models can provide valuable insight into outcomes of management options. Their use has been limited when modeling the impacts of prescribed fire in southeastern US ecosystems owing to the deficiencies in model inputs and logic with respect to longleaf pine forest types. Chapter 5 introduces the Fuelbed Dynamics Model (FDM), a new landscape fire succession model (LFSM) that simulates the effects of managed fire regimes on forest composition and wildfire risk and can be used to forecast potential future conditions in longleaf pine ecosystems. FDM is a probabilistic LFSM developed to simulate the impacts of prescribed fire and other common disturbances in southeastern US ecosystems.

In this chapter, I evaluated the effect of four levels of prescribed fire application on forest composition at the landscape scale at Eglin Air Force Base (hereafter referred to as Eglin) in northwestern Florida with FDM simulations. This simulation experiment evaluated the long-term effect of rates of prescribed burning on: (1) forest and fuelbed composition and (2) wildfire risk. Multiple FDM simulations were conducted for 50 years on each of four annual area-burned prescribed fire scenarios representing baseline conditions (40,000 ha burned $yr^{-1}$), a 25 percent increase (50,000 ha burned $yr^{-1}$), a 25 percent decrease (30,000 ha burned $yr^{-1}$), and a 50 percent decrease (20,000 ha burned $yr^{-1}$) in prescribed burning. Model outputs were averaged for each prescribed fire scenario to produce spatial statistics describing distribution and area for categorical measures of potential fire behavior and forest and fuelbed composition.

Using LFSMs to gain insight into the effects of burning fewer hectares could provide valuable cost-benefit information to help gauge thresholds where reductions in prescribed fire would yield unacceptable declines in habitat value and/or increases in wildfire risk. Even in the absence of pressure to reduce burning, model outputs can be used to help identify area burned targets necessary to meet land management goals for habitat and hazardous fuels management.

## 1.6 **References**

Addington, R.N., Knapp, B.O., Sorrell, G.G., Elmore, M.L., Wang, G.G., Walker, J.L., 2015. Factors affecting broadleaf woody vegetation in upland pine forests managed for longleaf pine restoration. For. Ecol. Manage. 354, 130–138. https://doi.org/10.1016/j.foreco.2015.06.028

Anderson, H.E., 1982. Aids to determining fuel models for estimating fire behavior. USDA Forest Service, Gen. Tech. Rep. INT-122, Ogden, Utah. https://doi.org/https://doi.org/10.2737/INT-GTR-122

Andreu, A.G., Shea, D., Parresol, B.R., Ottmar, R.D., 2012. Evaluating fuel complexes for fire hazard mitigation planning in the southeastern United States. For. Ecol. Manage. 273, 4–16. https://doi.org/DOI 10.1016/j.foreco.2011.06.040

Batista, W.B., Platt, W.J., 2003. Tree population responses to hurricane disturbance: syndromes in a south-eastern USA old-growth forest. J. Ecol. 91, 197–212.

Benton, T., Bieg, C., Harwatt, H., Pudassaini, R., Wellesley, L., 2021. Food system impacts on biodiversity loss. Chatham House, Energy, Environment and Resources Programme, London.

Bowker, M.A., Maestre, F.T., Escolar, C., 2010. Biological crusts as a model system for examining the biodiversity-ecosystem function relationship in soils. Soil Biol. Biochem. 42, 405–417. https://doi.org/https://doi.org/10.1016/j.soilbio.2009.10.025

Busing, R.T., White, R.D., Harmon, M.E., White, P.S., 2009. Hurricane disturbance in a temperate deciduous forest: patch dynamics, tree mortality, and coarse woody detritus. Plant Ecol. 201, 351–363. https://doi.org/201: 351-363

Cardinale, B.J., Palmer, M.A., 2002. Disturbance moderates biodiversity-ecosystem function relationships: experimental evidence from caddisflies in stream mesocosms. Ecology 83, 1915–1927. https://doi.org/https://doi.org/10.1890/0012-9658(2002)083[1915:DMBEFR]2.0.CO;2

Carrington, M.E., Mullahey, J.J., 2006. Effects of burning season and frequency on saw palmetto (*Serenoa repens*) flowering and fruiting. For. Ecol. Manage. 230, 69–78.

https://doi.org/10.1016/j.foreco.2006.04.020

Connell, J.H., 1978. Diversity in tropical rain forests and coral reefs. Science 199, 1302–1310. https://doi.org/10.1126/science.199.4335.1302

Costanza, R., Fisher, B., Mulder, K., Liu, S., Christopher, T., 2007. Biodiversity and ecosystem services: a multi-scale empirical study of the relationship between species richness and net primary production. Ecol. Econ. 61, 478–491. https://doi.org/https://doi.org/10.1016/j.ecolecon.2006.03.021

Coulson, R.N., Klepzig, K.D., 2011. Southern pine beetle II. USDA Forest Service, Gen. Tech. Rep. SRS-140, Asheville, North Carolina.

Díaz, S., Pascual, U., Stenseke, M., Martín-López, B., Watson, R.T., Molnár, Z., Hill, R., Chan, K.M.A., Baste, I.A., Brauman, K.A., Polasky, S., Church, A., Lonsdale, M., Larigauderie, A., Leadley, P.W., van Oudenhoven, A.P.E., van der Plaat, F., Schröter, M., Lavorel, S., Aumeeruddy-Thomas, Y., Bukvareva, E., Davies, K., Demissew, S., Erpul, G., Failler, P., Guerra, C.A., Hewitt, C.L., Keune, H., Lindley, S., Shirayama, Y., 2018. Assessing nature's contributions to people. Science 359, 270–272. https://doi.org/10.1126/science.aap8826

Dorrough, J., Turner, V., Yen, A., Clark, S., Crosthwaite, J., Hirth, J., 2002. Managing for biodiversity conservation in native grasslands on farms. Wool Technol. Sheep Breed. 50, 760–765.

Earley, L.S., 2004. Looking for Longleaf: The Fall and Rise of an American Forest. The University of North Carolina Press, Chapel Hill, North Carolina.

Emery, R.K., Hart, J.L., 2020. Flammability characteristics of surface fuels in a longleaf pine (*Pinus palustris* Mill.) woodland. Fire 3, 1–18. https://doi.org/10.3390/fire3030039

Frost, C.C., 2006. History and future of the longleaf pine ecosystem, in: Jose, S., Jokela, E.J., Miller, D.L. (Eds.), The Longleaf Pine Ecosystem. Springer, New York, pp. 9–48. https://doi.org/10.1007/978-0-387-30687-2_2

Frost, C.C., 1995. Presettlement fire regimes in southeastern marshes, peatlands, and swamps, in: Cerulean, S.I., Engstrom, R.T. (Eds.), Tall Timbers Fire Ecology Conference Proceedings No. 19. Tall Timbers Research Station, Tallahassee, Florida, pp. 39–60.

Glitzenstein, J.S., Streng, D.R., Wade, D.D., 2003. Fire frequency effects on longleaf pine (*Pinus palustris*, P. Miller) vegetation in South Carolina and northeast Florida, USA. Nat. Areas J. 23, 22–37.

Hannon, D.R., Moorman, C.E., Schultz, A.D., Gray, J.M., DePerno, C.S., 2020. Predictors of fire-tolerant oak and fire-sensitive hardwood distribution in a fire-maintained longleaf pine ecosystem. For. Ecol. Manage. 477, 118468. https://doi.org/10.1016/j.foreco.2020.118468

Hardin, E.D., White, D.L., 1989. Rare vascular plant taxa associated with wiregrass (*Aristida stricta*) in the southeastern United States. Nat. Areas J. 9, 234–245.

Haywood, J.D., 2012. Frequency and season of prescribed fire affect understory plant communities in longleaf pine stands, in: Butnor, J.R. (Ed.), Proceedings of the 16th Biennial Southern Silvicultural Research Conference. USDA, Forest Service, e-Gen. Tech. Rep. SRS-156, Asheville, North Carolina, pp. 137–143.

Heyward, F., 1939. The relation of fire to stand composition of longleaf pine forests. Ecology 20, 287–304. https://doi.org/https://doi.org/10.2307/1930747

Hough, W.A., Albini, F.A., 1978. Predicting fire behavior in palmetto-gallberry fuel complexes. USDA Forest Service, Res. Pap. SE-174, Asheville, North Carolina.

Kangas, J., Kangas, A., 2005. Multiple criteria decision support in forest management — the approach, methods applied, and experiences gained. For. Ecol. Manage. 207, 133–143.

https://doi.org/10.1016/j.foreco.2004.10.023

Karlin, E.F., 1995. Population growth and the global environment: an ecological perspective, in: Makaofske, W.J., Karlin, E.F. (Eds.), Technology and Global Environmental Issues. Harper Collins College Division, pp. 19–37.

Keane, R.E., Cary, G.J., Davies, I.D., Flannigan, M.D., Gardner, R.H., Lavorel, S., Lenihan, J.M., Li, C., Rupp, T.S., 2004. A classification of landscape fire succession models: spatial simulations of fire and vegetation dynamics. Ecol. Modell. 179, 3–27. https://doi.org/https://doi.org/10.1016/j.ecolmodel.2004.03.015

Konstantinov, A.V., 2011. Changes in resilience to fire disturbance in lowland pine forest ecosystems. Biol. Bull. 38, 974–979. https://doi.org/https://doi.org/10.1134/S1062359011100062

Korjus, H., 2014. Forest research challenges in forest management planning. For. Res. 3, 1000. https://doi.org/10.4172/2168-9776.1000e110

Lafon, C.W., 2010. Fire in the American South: vegetation impacts, history, and climatic relations. Geogr. Compass 4, 919–944. https://doi.org/https://doi.org/10.1111/j.1749-8198.2010.00363.x

Maestre, F.T., Quero, J.L., Gotelli, N.J., Escudero, A., Ochoa, V., Delgado-Baquerizo, M., García-Gómez, M., Bowker, M.A., Soliveres, S., Escolar, C., García-Palacios, P., Berdugo, M., Valencia, E., Gozalo, B., Gallardo, A., Aguilera, L., Arredondo, T., Blones, J., Boeken, B., Bran, D., Conceição, A.A., Cabrera, O., Chaieb, M., Derak, M., Eldridge, D.J., Espinosa, C.I., Florentino, A., Gaitán, J., Gatica, M.G., Ghiloufi, W., Gómez-González, S., Gutiérrez, J.R., Hernández, R.M., Huang, X., Huber-Sannwald, E., Jankju, M., Miriti, M., Monerris, J., Mau, R.L., Morici, E., Naseri, K., Ospina, A., Polo, V., Prina, A., Pucheta, E., Ramírez-Collantes, D.A., Romão, R., Tighe, M., Torres-Díaz, C., Val, J., Veiga, J.P., Wang, D., Zaady, E., 2012. Plant species richness and ecosystem multifunctionality in global drylands. Science 335, 214–218. https://doi.org/10.1126/science.1215442

Marselle, M.R., Hartig, T., Cox, D.T.C., de Bell, S., Knapp, S., Lindley, S., Triguero-Mas, M., Böhning-Gaese, K., Braubach, M., Cook, P.A., de Vries, S., Heintz-Buschart, A., Hofmann, M., Irvine, K.N., Kabisch, N., Kolek, F., Kraemer, R., Markevych, I., Martens, D., Müller, R., Nieuwenhuijsen, M., Potts, J.M., Stadler, J., Walton, S., Warber, S.L., Bonn, A., 2021. Pathways linking biodiversity to human health: a conceptual framework. Environ. Int. 150. https://doi.org/10.1016/j.envint.2021.106420

Millenium Ecosystem Assessment, 2005. Ecosystems and Human Well-being: Synthesis. Island Press, Washington, DC.

Mitchell, R.J., Duncan, S.L., 2009. Range of variability in southern coastal plain forests: its historical, contemporary, and future role in sustaining biodiversity. Ecol. Soc. 14.

Molina, R., White, R., 2007. Managing biodiversity in Pacific Northwest forests. For. Ecol. Manage. 246, 1–3. https://doi.org/10.1016/j.foreco.2007.03.045

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature 403, 853–858. https://doi.org/10.1080/21564574.1998.9650003

Noss, R.F., Platt, W.J., Sorrie, B.A., Weakley, A.S., Means, D.B., Costanza, J., Peet, R.K., 2015. How global biodiversity hotspots may go unrecognized: lessons from the North American Coastal Plain. Divers. Distrib. 21, 236–244. https://doi.org/10.1111/ddi.12278

Nystrom, M., Folke, C., Moberg, F., 2000. Coral reef disturbance and resilience in a human-dominated environment. Trends Ecol. Evol. 15, 413–417.

https://doi.org/https://doi.org/10.1016/S0169-5347(00)01948-0

O'Brien, J.J., Mordecai, K.A., Wolcott, L., Snyder, J., Outcalt, K.W., 2010. Fuel managers field guide: hazardous fuels management in subtropical pine flatwoods and tropical pine rocklands. USDA Forest Service, Gen. Tech. Rep. SRS-123, Asheville, North Carolina. https://doi.org/https://doi.org/10.2737/SRS-GTR-123

Petchey, O.L., Gaston, K.J., 2009. Effects on ecosystem resilience of biodiversity, extinctions, and the structure of regional species pools. Theor. Ecol. 2, 177–187. https://doi.org/https://doi.org/10.1007/s12080-009-0041-9

Peterson, G., Allen, C.R., Holling, C.S., 1998. Ecological resilience, biodiversity, and scale. Ecosystems 1, 6–18. https://doi.org/https://doi.org/10.1007/s100219900002

Pickett, S.T.A., White, P.S., 1985. The ecology of natural disturbance and patch dynamics. Academic Press, New York. https://doi.org/10.1016/C2009-0-02952-3

Platt, W.J., Evans, G.W., Davis, M.M., 1988. Effects of fire season on flowering of forbs and shrubs in longleaf pine forests. Oecologia 76, 353–363. https://doi.org/https://doi.org/10.1007/BF00377029

Reice, S.R., Wissmar, R.C., Naiman, R.J., 1990. Disturbance regimes, resilience, and recovery of animal communities and habitats in lotic ecosystems. Environ. Manage. 14, 647–659. https://doi.org/https://doi.org/10.1007/BF02394715

Saglam, B., Bilgili, E., Kucuk, O., Durmaz, B.D., 2008. Fire behavior in Mediterranean shrub species (Maquis). African J. Biotechnol. 7, 4122–4129. https://doi.org/https://doi.org/10.4314/ajb.v7i22.59536

Schroeder, R.L., 1985. Habitat suitability index models: northern bobwhite. USDI Fish and Wildlife Service, Bio. Rep. 82 (10.104), Washington, DC.

Shepherd, B.J., Miller, D.L., Thetford, M., 2012. Fire season effects on flowering characteristics and germination of longleaf pine (*Pinus palustris*) savanna grasses. Restor. Ecol. 20, 268–276. https://doi.org/10.1111/j.1526-100X.2010.00759.x

Sparks, J.C., Masters, R.E., Engle, D.M., Bukenhofer, G.A., 2002. Season of burn influences fire behavior and fuel consumption in restored shortleaf pine-grassland communities. Restor. Ecol. 10, 714–722. https://doi.org/https://ui.adsabs.harvard.edu/link_gateway/2002ResEc..10..714S/doi:10.1046/j.1526-100X.2002.01052.x

Stanturf, J.A., Goodrick, S.L., Outcalt, K.W., 2007. Disturbance and coastal forests: a strategic approach to forest management in hurricane impact zones. For. Ecol. Manage. 250, 119–135. https://doi.org/https://doi.org/10.1016/j.foreco.2007.03.015

Stanturf, J.A., Wade, D.D., Waldrop, T.A., Kennard, D.K., Achtemeier, G.L., 2002. Background paper: fire in southern forest landscapes, in: Wear, D.N., Greis, J.G. (Eds.), Southern Forest Resource Assessment. USDA Forest Service, Gen. Tech. Rep. SRS-53, Asheville, North Carolina, pp. 607–630. https://doi.org/https://doi.org/10.2737/SRS-GTR-53

Streng, D.R., Glitzenstein, J.S., Platt, W.J., 1993. Evaluating effects of season of burn in longleaf pine forests: a critical literature review and some results from ongoing long-term study, in: Hermann, S. (Ed.), Tall Timbers Fire Ecology Conference Proceedings No. 18. Tall Timbers Research Station, Tallahassee, Florida, pp. 227–263.

United Nations, 1992. Convention on Biological Diversity. New York.

Van Balen, J.B., Doerr, P.D., 1978. The relationship of understory vegetation to red-cockaded woodpecker activity, in: Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies. pp. 82–92.

Van Lear, D.H., Carroll, W.D., Kapeluck, P.R., Johnson, R., 2005. History and restoration.of the longleaf pine-grassland ecosystem: implications for species at risk. For. Ecol. Manage. 211, 150–165. https://doi.org/DOI 10.1016/j.foreco.2005.02.014

Vitousek, P.M., Mooney, H.A., Lubchenco, J., Melillo, J.M., 1997. Human domination of Earth's ecosystems. Science 277, 494–499. https://doi.org/https://doi.org/10.1126/science.277.5325.494

Wade, D.D., Lunsford, J.D., 1989. A guide for prescribed fire in southern forests. USDA Forest Service, Tech. Pub. R8-TP 11, Atlanta, Georgia.

Waldrop, T.A., Goodrick, S.L., 2012. Introduction to prescribed fire in southern ecosystems. USDA Forest Service, Science Update SRS-054, Asheville, North Carolina.

Waldrop, T.A., Van Lear, D.H., Lloyd, F.T., Harms, W.R., 1987. Long-term studies of prescribed burning in loblolly pine forests of the Southeastern Coastal Plain. USDA Forest Service, Gen. Tech. Rep. SE-45, Asheville, North Carolina. https://doi.org/https://doi.org/10.2737/SE-GTR-45

Westman, W.E., 1990. Managing for biodiversity. Bioscience 40, 26–33. https://doi.org/https://doi.org/10.2307/1311236

Yospin, G.I., Bridgham, S.D., Kertis, J., Johnson, B.R., 2012. Ecological correlates of fuel dynamics and potential fire behavior in former upland prairie and oak savanna. For. Ecol. Manage. 266, 54–65. https://doi.org/DOI 10.1016/j.foreco.2011.10.046

Zhao, D.H., Allen, B., Sharitz, R.R., 2006. Twelve year response of old-growth southeastern bottomland hardwood forests to disturbance from Hurricane Hugo. Can. J. For. Res. 36, 3136–3147. https://doi.org/https://doi.org/10.1139/x06-204

# Chapter 2. Ecology and fire history of the longleaf pine (*Pinus palustris*) ecosystem

## 2.1 Abstract

Frequent application of prescribed fire is essential to maintaining high levels of biological diversity and mitigating hazardous fuels: the primary management goals for longleaf pine forests. This dissertation evaluates prescribed fire strategies relative to these goals. This chapter presents an overview of the longleaf pine ecosystem and a literature review of fire history to provide context for research presented in this dissertation. The ecosystem overview is important for understanding how this research can be applied given the ecological dynamics and broader array of management objectives that may compete with or complement those associated with the use of prescribed fire.

The fire history literature review presents a comprehensive assessment of fire history studies conducted within the longleaf pine ecosystem. It describes interactions among vegetation, the fire regime, climate, and anthropogenic activities and is divided into three sections defined by major shifts in the longleaf pine ecosystem. First, the late Pleistocene to the early Holocene (40,000-4000 years BP). This encompasses the last glacial maximum when longleaf pine forests were constrained to refugia to the establishment of the contemporary longleaf pine ecosystem. Second, the late Holocene (4000 - 200 years BP). This period includes the substantial influence of Native Americans. The third section covers the period of European colonization (200 years BP - present). A period that includes extensive impacts of European settlement. This information is important for understanding how the research presented in this dissertation fits into the broader model of fire-environment interactions within the longleaf pine ecosystem.

## 2.2 **Introduction**

Indicators of ecosystem persistence such as fossil assemblages and species endemism have led some to suggest that pine savannas of the southeastern US have been present for millions of years (Noss et al., 2015; Platt, 1999). Paleoecological data suggests that the southeastern US has supported vegetation communities similar to present day southern pine forests for the past 40,000 years and direct evidence of fire occurring in this region dates back 30,000 years (Watts et al., 1992). In response to the long-range persistence of fire, species in this ecosystem have evolved traits adapted to some degree of regular fire (Stout and Marion, 1993). The suite of adaptations for each species is unique so relatively minor changes in the fire regime can shift plant composition. For example, plants with resprouting capabilities are adapted to fires every 3-5 years while annual herbs are best adapted to fires that occur every 1-2 years (Waldrop et al., 1987). These shifts have implications for wildlife habitat (Engstrom, 1993; Rosche et al., 2017; Van Balen and Doerr, 1978), wildfire risk (Brose and Wade, 2002; Sparks et al., 2002), carbon sequestration (Puhlick et al., 2022), and tree growth (Ford et al., 2010).

Today, longleaf pine forests with frequently occurring fires have high conservation value. They host high biodiversity (Estill and Cruzan, 2001; Stein et al., 2000) and provide habitat to rare, threatened, and endangered plant and animal species (Engstrom, 1993; Guyer & Bailey, 1993; Sheehan & Klepzig, 2022). Longleaf pine-dominated ecosystems were once widespread across the southeastern United States (US) from eastern Texas to the Atlantic coast and from southern Virginia south to Florida. Since European settlement, intensive development and land use has reduced their extent by 97-98 percent from 24-36 million ha to 1.3 million ha at present (Frost, 1993; Oswalt et al., 2012). While there was a period of afforestation during the late 1800s and early 1900s, these forests were ecologically degraded in response to fire exclusion caused by aggressive fire suppression policies implemented during the early 1920s and 1930s (Fowler and Konopik, 2007). Since the mid-1900s, there has been increasing recognition of the importance of frequent fire for managing longleaf pine forests (Komarek, 1968). The use of prescribed fire has increased steadily during this time and currently 2.2-2.7 million ha are burned in the southeastern US annually (Melvin, 2020). In an ecosystem with high ecological sensitivity to fire regime characteristics, such as longleaf pine, a comprehensive understanding of ecosystem characteristics and the historical relationship between fire and vegetation is critical to successfully applying prescribed fire to meet ecological and fuels management goals. This chapter reviews these topics to provide context for applying research presented in this dissertation to prescribed fire management strategies and is organized into two sections. The first provides an overview of the longleaf pine ecosystem and the second is a literature review of relevant fire history studies.

## 2.3 **Background – longleaf pine ecosystem**

### 2.3.1 *Introduction to the ecosystem*

The longleaf pine ecosystem is characterized by open forest dominated by longleaf pine with an understory of low growing woody and herbaceous species (Peet, 2006). Understory species richness is high with over 50 species recorded per square meter (Walker & Peet, 1984) and up to 140 species per hectare (Peet & Allard, 1993). Overall, this region ranks among the highest areas of biodiversity globally (Noss et al., 2015).

### 2.3.2 *Geography and soils*

The longleaf pine ecosystem spans a 2000-km long arc along the Atlantic and Gulf coast of North America from 95° 17’W in eastern Texas to 76° 18’W in southern Virginia (Figure 2-1). It reaches 150-250 km inland except in northeastern Alabama and northwestern Georgia where longleaf pine extends inland 400 km to 34° 26’N. Longleaf pine occurs in Florida north of 26° 22’N. The longleaf pine ecosystem occupies several physiographic provinces including a substantial portion of the Coastal Plain Physiographic Province (Fenneman and Johnson, 1946). A small portion of the ecosystem extends into the southern terminus of some Appalachian Mountain provinces and the southeastern edge of the Piedmont Physiographic Province.

There are four soil orders common in longleaf pine forests of the Coastal Plain: Alfisols, Utisols, Spodosols, and Entisols (Platt, 1999). All have thin A-horizons with little organic material. Alfisols are most common in western sections of the Coastal Plain and are characterized by high base saturation (greater than 35 percent) and occasionally, fragipan layers. Ultisols occur mostly in inland sections and are highly leached with low base saturation (less than 35 percent). Spodosols, found throughout Florida, are sandy and have spodic horizon – a subsurface layer of where organic matter has accumulated along with iron and/or aluminum – which may lie above an argillic horizon of clay (Brown et al., 1990). Entisols – recent soils with minimal weathering – are found along the coastline because they were formed by fluctuating sea levels over the past several million years. Entisols are characterized by a thin A-horizon over unconsolidated sands or bedrock (Mylavarapu et al., 2014).

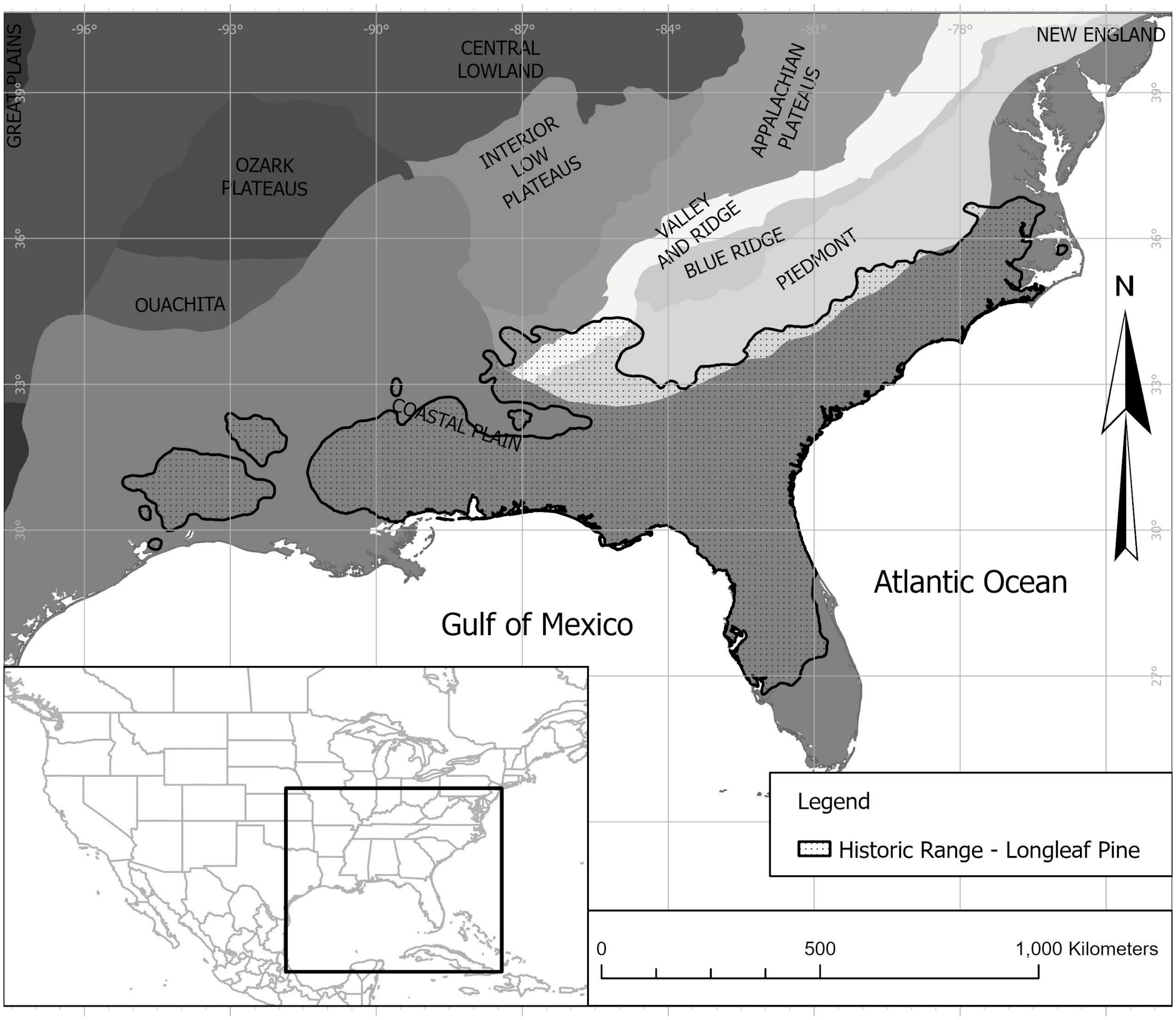


**Figure 2-1.** Historic range of longleaf pine and physiographic provinces of the United States (Fenneman & Johnson, 1946).

### 2.3.3 *Climate*

Climate is characterized by long growing seasons with hot temperatures, high humidity, and frequent lighting storms. The climate of the Coastal Plain has maritime influences from the Gulf of Mexico and Atlantic Ocean. Growing seasons are 240 – 330 days, increasing from north to south (Greller, 1989). Annual precipitation across the range of longleaf pine is fairly consistent at around 1270 mm (National Oceanic and Atmospheric Administration, 2022). Precipitation is highest during the summer and winter months with drier conditions in the spring and autumn (Chen & Gerber, 1990).

The summer months are characterized by hot temperatures and high humidity with frequent convective thunderstorms. Rainfall is primarily from thunderstorms generated by warm moist, maritime air pushed inland by afternoon sea breezes (Chen & Gerber, 1990). The hottest months of the year occur in July and August where average temperatures are 27.3 – 28.7°C from north (Norfolk, VA) to south (Tampa, FL) (National Oceanic and Atmospheric Administration, 2022).

In autumn temperatures cool, precipitation declines, and there is a transition from convective to synoptic-scale weather systems. These include tropical cyclones (i.e., hurricanes) and mid-latitude low pressure systems. Hurricanes can cause widespread damage from flooding and wind (Ho et al., 1987; Kruk et al., 2010). Hurricane frequency for a given location along the coast of the southeastern US is approximately 5-15 years (Simpson and Lawrence, 1971) with a range of 4-52 years (Keim et al., 2007).

Winter weather tends to fluctuate from dry cool air following cold fronts to warmer and more humid conditions as high-pressure systems progress from west to east. Precipitation including rain and occasionally snow, especially at higher latitudes, primarily occurs during the passage of low-pressure systems and their associated cold fronts (Chen & Gerber, 1990). The coldest months are January and February and average temperatures are 5.7 – 16.1°C from north (Norfolk, VA) to south (Tampa, FL) (National Oceanic and Atmospheric Administration, 2022).

Spring is defined by warmer and drier conditions with a shift from synoptic scale weather systems to convection-driven storms. The strength of low-pressure systems and associated cold fronts begins to wane, although early-spring storms can generate tornadoes. Tornadoes are most prevalent in Texas through inland sections of Louisiana, Mississippi, Alabama, and Georgia (Grazulis, 1982).

Lightning is an ecologically important weather feature throughout the range of longleaf pine because it is a major source of wildfire ignition (Komarek, 1964). The southeastern US has more lighting strikes per year than anywhere else in the United States (Christian et al., 2003). Lightning density is concentrated in central Florida where there are more than 90 thunderstorm days per year (Chen & Gerber, 1990). Thunderstorms can occur any time of year but the mechanisms that generate them vary from tropical cyclones in late summer and fall, cold fronts in the winter and early spring, and convective sea-breeze driven storms in the summer (Chen and Gerber, 1990). The latter mechanism is responsible for most thunderstorm activity in the southeast US and lighting strike density peaks during the summer months (Hodanish et al., 1997).

Climate change has impacted the southeastern United States but relative to the rest of the country this region has experienced the lowest degree of warming (Portmann et al., 2009). An analysis of 60 years of climate data shows the following trends in the southeastern region (Powell and Keim, 2015). Nighttime temperatures are warmer but mean and daily high temperatures are unchanged. Total annual precipitation has increased across western portions of this region and decreased in the east. The number of days with heavy precipitation (>20 mm) has increased. Spring months have become drier while precipitation in autumn has increased nearly 50 percent from 1895 to 2015 (Williams et al., 2017), a trend mostly attributed to the increase in intensity of non-tropical storms (Bishop et al., 2019). Hurricane intensity has increased (Bishop et al., 2019; Gilliam, 2021). Despite the relatively muted impacts of climate change to date, the southeastern US is forecast to experience warming of 2-4˚ F (Kunkel et al., 2013) and substantial increases in aridity overt the next five decades (Dai, 2011).

### 2.3.4 *Vegetation*

The longleaf pine ecosystem is notable for its homogeneous overstory of longleaf pine and open understory with high species richness of low stature plants, with forbs and grasses accounting for the largest number of species (Platt, 1999) when there is frequent (< 3 years), low intensity (< 350 kW $m^{-1}$) fire (Figure 2-2) and increasing cover and biomass of woody species as fire frequency decreases (Figure 2-3). Southeastern ecosystems have 482 endemic plant species; many of these are concentrated in longleaf pine forests of central Florida and the Apalachicola region on the Florida panhandle (Estill and Cruzan, 2001). There are 191 rare plant taxa in the southeastern US and 122 are considered threatened or endangered throughout their range (Hardin and White, 1989). The understory of longleaf pine forests includes a wide gradient of species composition and vegetation structure that is a function of geography, soil moisture, and fire frequency.

Numerous classification schemes have been developed for southeastern pine community types, but perhaps the most relevant and comprehensive was developed exclusively for longleaf pine forests by Peet (2006). He compiled previously published longleaf pine vegetation types into six ecological groups and then divided each type further across each ecoregion with which it overlapped resulting in 135 longleaf vegetation associations. The six ecological groups represent gradients of soil moisture and percent silt in the A horizon and are listed in order from lowest to

**Figure 2-2.** View of mesic longleaf pine flatwoods depicting open overstory and understory dominated by forbs and grasses on Fort Stewart in Georgia. Photo: James Cronan.

highest soil moisture; they include: 1) xeric sand barrens, 2) sub-xeric sandy uplands, 3) silty uplands, 4) clayey and rocky uplands, 5) flatwoods, and 6) savannas, seeps, and prairies.

Xeric sand barrens are scattered across the Coastal Plain. Deep, coarse, well-drained sands create water-limited environments. As such, productivity is low and forests are characterized by low stem density and short tree heights. The understory is occupied by drought-tolerant oaks including turkey oak (*Quercus laevis* Michx.). The groundcover is sparse and includes low stature woody shrubs such as dwarf huckleberry (*Gaylussacia dumosa* (Andrews) Torr. &A. Gray) and fruticose lichens including species in the genus *Cladonia* (Hill ex P. Browne). Because of low productivity, fine fuels accumulate slowly, and fire-free intervals are longer relative to more productive ecological groups.

**Figure 2-3.** View of mesic longleaf pine flatwoods depicting open overstory and understory dominated by shrubs on the Apalachicola National Forest in Florida. Photo: James Cronan.

Sub-xeric sandy uplands resemble xeric sand barrens in that well-drained sandy soils cause droughty conditions, but these types have a more continuous groundcover of grass including pineland threeawn, Beyrich threeawn (*Aristida beyrichiana* Trin. & Rupr.), and little bluestem (*Schizachyrium scoparium* (Michx.) Nash). In the eastern ecoregions longleaf pine is the dominant overstory species while in the Western Gulf Coastal Plain additional species are present in the overstory including shortleaf pine (*Pinus echinata* Mill.), loblolly pine (*Pinus taeda* L.), black hickory (*Carya texana* Buckley), and southern red oak (*Quercus falcata* Michx.). Numerous oak species occupy the understory including turkey oak, bluejack oak, Darlington's oak (*Quercus hemisphaerica* Bartram ex Willd.), runner oak (*Quercus pumila* Walter), and blackjack oak (*Quercus marilandica* Münchh.).

Silty uplands are uncommon. Unlike drier groups, subcanopy oaks are not common. Several species of oak are found in the shrub layer and other species present include southern blueberry (*Vaccinium tenellum* Aiton), poison oak (*Toxicodendron pubescens* Mill.), and eastern persimmon (*Diospyros virginiana* L.). This group has the highest species richness of herbs for upland habitats in the United States with up to 170 species occurring in a single hectare.

Clayey and rocky uplands include longleaf pine forests on rock substrates of the inner Coastal Plain, Piedmont, and Southern Appalachian Mountain provinces. Understory shrub species occur that are not associated with other longleaf pine ecological groups including mountain laurel (*Kalmia latifolia* L.) and farkleberry (*Vaccinium arboretum* Marsh). Other tree species may be codominant including black gum (*Nyssa sylvatica* Marshall), shortleaf pine, chokecherry (*Prunus virginiana* L.), scarlet oak (*Quercus coccinea* Münchh.), and Georgia oak (*Quercus georgiana* M.A. Curtis).

Flatwoods occur in areas with low, flat topography and poorly drained sandy spodosols. Types in this group are widespread throughout the Southern Coastal Plain east of the Mississippi River. Slash pine (*Pinus elliottii* Engelm.) replaces longleaf pine in flatwoods below its southern limit and where soil moisture is high. The understory of flatwoods is open with groundcover characterized by fire-maintained shrubs and herbs including saw palmetto (*Serenoa repens* (W. Bartram) Small), shiny blueberry (*Vaccinium myrsinites* Lam.), Beyrich threeawn, dwarf live oak (*Quercus minima* (Sarg.) Small), and hairy wicky (*Kalmia hirsuta* Walter).

Savannas, seeps, and prairies occur in areas with wet fine-textured soils. The high soil moisture results in the lowest tree density among all the longleaf groups. These types are mostly found along the outer Coastal Plain to the northeast and west of peninsular Florida. Overstory composition can be dominated by longleaf pine, pitch pine (*Pinus rigida* Mill.), slash pine, or combinations of all three. The groundcover is dominated by herbaceous species and notable for showy flowering plants.

### 2.3.5 *Wildlife*

Vertebrate diversity is notable. This ecosystem has the highest species richness of reptiles and amphibians in the United States (Guyer and Bailey, 1993; Kiester, 1971) and provides habitat for 212 vertebrates, of which, 38 occur exclusively in longleaf pine forests (Means, 2006). Numerous vertebrae species are rare (Trani-Griep, 2002). Federally protected species that rely on fire-maintained longleaf pine forests, include the eastern indigo snake (*Drymarchon couperi* Holbrook, 1842), flatwoods salamander (*Ambystoma cingulatum* Cope, 1868), and the red-cockaded woodpecker (*Picoides borealis* Vieillot, 1809; Krusac et al., 1995; Means, 2006). Several notable inhabitants of the longleaf ecosystem are rare or extinct owing to dramatic reductions in habitat following European colonization. Extinct species include the Carolina parakeet (*Conuropsis carolinensis* Linnaeus, 1758), passenger pigeon (*Ectopistes migratorius* Linnaeus, 1766), and the ivory-billed woodpecker (*Campephilus principalis* Linnaeus, 1758; Engstrom, 1993). Species are divided into those whose range is limited primarily to longleaf pine forests (specialists) and those whose range overlaps with the range of longleaf pine but also includes other ecosystems (residents).

Amphibians have the highest number of longleaf specialists, followed by reptiles (Means, 2006). Means (2006) identified 17 species of specialists and 35 species of residents among amphibians and 13 specialists and 56 residents among reptiles. Longleaf pine specialists include the gopher tortoise (*Gopherus polyphemus* Daudin, 1801), eastern indigo snake, diamond-backed rattlesnake (*Crotalus adamanteus* Palisot de Beauvois 1799), pine woods snake (*Rhadinaea* *flavilata* Cope, 1871), and Florida pinesnake (*Pituophis melanoleucus mugitus* Barbour, 1921), while amphibians include the flatwoods salamander (Engstrom, 1993; Stout and Marion, 1993). The gopher tortoise is often labelled a keystone species of this ecosystem because so many other species depend on its burrows for shelter (Folkerts et al., 1993; Jackson & Milstrey, 1989).

Avian longleaf specialists include the red-cockaded woodpecker, white-breasted nuthatch (*Sitta carolinensis* Latham, 1790), brown-headed nuthatch (*Sitta pusilla* Latham, 1790), northern bobwhite quail (*Colinus virginianus* Linnaeus, 1758), and Bachman's sparrow (*Peucaea aestivalis* M. H. K. Lichtenstein, 1823; Engstrom, 1993). Northern bobwhite is an important game species, and the red-cockaded woodpecker is federally endangered. Both depend on open, fire-maintained stands of longleaf pine. The red-cockaded woodpecker requires live trees at least 90 years old for nesting cavities (Rudolph and Conner, 1991). As with the gopher tortoise, the red-cockaded woodpecker is also considered a keystone species for the longleaf pine ecosystem because abandoned nest cavities remain for decades (Conner and Rudolph, 1995) – well after the individual trees die and become snags (Platt and Rathburn, 1993) – providing shelter for a number of animal species (US Fish and Wildlife Service, 2003).

Of the 36 species of mammals that inhabit longleaf pine forests only three are specialists (Means, 2006). These include the fox squirrel (*Sciurus niger*), Florida mouse (*Podomys floridanus*), and southeastern pocket gopher (*Geomys pinetis*; Means, 2006). The fox squirrel forages on the ground and prefers the low-stature herbaceous groundcover of fire-maintained longleaf pine (Brown, 1997). The southeastern pocket gopher is frequently burned longleaf pine forest with an open grassy understory, but they have also been documented in developed grassy environments such as golf courses, roadsides, and pastures (Humphrey, 1992). The Florida mouse is dependent on gopher tortoise burrows, often digging side burrows (Layne & Jackson, 1994).

Most of the extinct species of the Coastal Plain were likely longleaf residents and their disappearance is, in many cases, attributed to human causes. Recent extirpations occurred in the early 1900s when land clearing fragmented habitat and extant areas of longleaf could no longer support their populations. Platt (1999) notes that American bison (*Bison bison*) and the red wolf (*Canis rufus*) disappeared from the longleaf pine forest in the early 1900s, the Carolina parakeet went extinct in 1900, the passenger pigeon in 1914, and the ivory-billed woodpecker in 1969. These dates coincide with widespread logging and agricultural conversion of longleaf pine forests. An earlier wave of extinctions at the end of the Pleistocene included 46 genera of mammals and 19 genera of birds (Holman, 1991). This round of extinction, which lasted from 13,000 to 11,000 years BP, coincided with the arrival of the first Paleo-Indians in North America and was possibly caused by overhunting as people colonized the North American continent for the first time (Martin, 1967). Wildlife habitat for several species dependent on fire-maintained longleaf pine continued to decline during the first half of the 1900s as fire suppression policies led to a period of fire exclusion throughout the longleaf pine ecosystem (Komarek, 1963).

### 2.3.6 *Disturbance regimes*

The longleaf pine ecosystem is shaped by disturbance including fire, wind, and pathogens. Each varies in their effects, frequency, spatial extent, and geographical range. They often interact with each other in ways that compound or negate their ecological effects. Anthropogenic disturbance is intertwined with fire and changes substantially over time, so it is discussed in the fire history section.

Fire is the most frequent and influential disturbance (Komarek, 1974). The longleaf pine ecosystem is highly adapted to low-intensity, high-frequency fires which have influenced the evolutionary development of vegetation (Platt et al., 2016) to the point where species richness begins to decline within 10 years after fire exclusion (Toribio-Diaz et al., 2019). Fires are generally low-intensity, mostly top-kill understory vegetation, and cause little or no overstory damage or mortality (Brockway and Lewis, 1997). Multiple lines of evidence, including dendrochronology (e.g., Huffman et al., 2004; Stambaugh et al., 2011; White & Harley, 2016), paleoecology (e.g., Watts et al., 1992; Albritton, 2009; Jones & Jackson, 2012; Tanner et al., 2018), historical accounts (e.g., Earley, 2004; Frost, 2006), witness tree records (e.g., Cowell, 1995), long-term fire treatment studies (e.g., Glitzenstein et al., 2003; Haywood et al., 2001; White et al., 1991), and model simulations (e.g., Guyette et al., 2012) conclude that fire is a common and integral part of the longleaf pine ecosystem disturbance regime. There is evidence indicating that this relationship with fire has been ongoing for 2.5 million years (Graham, 1999; He et al., 2012) within the pine (*Pinus* L.) genus. Others posit that many species in the longleaf pine ecosystem have evolved with fire to such an extent that they are dependent on it (Mutch, 1970). Reviews of historical data show that both frequent fire and longleaf pine forests were widespread at the time of European settlement (Foster et al., 2004). Today, fire is mostly limited to prescribed burns in natural areas. Wildfires are not widely managed for ecological benefits because natural areas are too small, fragmented, and close to populated areas for large-scale application. Approximately 50 percent of protected longleaf pine forests are not managed with prescribed fire (Outcalt, 2000) and are ecologically degraded due to fire exclusion.

After fire, windthrow, primarily from hurricanes, is the most frequent disturbance. High winds can cause extensive overstory mortality;  spatial extent of damage varies from landscape-scale effects from hurricanes (Kenney et al., 2021) to stand-level effects from straight-line winds and tornadoes (Glitzenstein and Harcombe, 1988). Hurricane strike data from 1901 to 2005 analyzed by Keim et al. (2007) indicate that hurricanes make landfall in the same coastal section every 5–10 years along the west- and south-facing coastlines of the Gulf of Mexico and the southern half of peninsular Florida and every 10–30 years on the northwest Gulf Coast of Florida (from Tallahassee to Tampa) and the Atlantic Coastline from Cape Canaveral, Florida to North Carolina. Farther north, hurricane frequency decreases to once every 50–100 years (Keim et al., 2007), but the frequency of post-tropical storms with high winds increases (Kruk et al., 2010). Wind strength decreases rapidly after hurricanes make landfall (Emanuel, 2005). High-intensity hurricanes (i.e., category 5 storms) can impact wide areas and cause extensive mortality. For example, in 2018 Hurricane Michael impacted 28 percent of longleaf pine habitat in Florida and overstory mortality ranged from 88 percent at the center to less than 10 percent 50–100 km away (Zampieri et al., 2020). Similar mortality (80 percent) was observed for slash pine near the center of Hurricane Andrew, another category 5 hurricane that struck southern Florida in 1992 (Armentano et al., 1995). It is important to note that high intensity hurricanes are relatively rare with return intervals of 20–100 years for category 3 or greater storms (Keim et al., 2007) and up to 600 years for category 5 storms (Liu et al., 2008). Effects of hurricanes on structure and composition are greater in pine forests relative to deciduous forests (Gang et al., 2020) where percentage crown damage is lower (Batista and Platt, 1997). Wind events may have indirectly played a role in pine savanna establishment by generating large amounts of dead woody fuels that, in subsequent fires, contributed to high burn severity, that in turn inhibited woody plant regrowth (Myers & van Lear, 1998). Projected increases in hurricane intensity and frequency associated with climate change are expected to increase overstory mortality directly through increased incidence of damaging winds and from higher severity fires caused by elevated fuel loading from downed trees (Gilliam, 2021). The spatial extent of impacts from other types of wind events is small relative to hurricanes. For instance, tornadoes have been known to cause extensive overstory damage to southern pine forests but their impacts are localized and frequency is lower with return intervals estimated to be in the thousands of years (Glitzenstein & Harcombe, 1988).

A wide array of pathogens affect trees across the southeastern US and though some can cause extensive mortality, longleaf pine is generally not affected due to high resistance (Martinson et al., 2007; Ward and Mistretta, 2006). Of the bark beetle species known to attack southern pines, the most damaging is the southern pine beetle (SPB; *Dendroctonus frontalis* Zimmermann, 1868). Annual losses in timber revenue owing to SPB infestations are estimated at $43 million (Coulson and Klepzig, 2011). SPB causes mortality by excavating galleries in the phloem and inner bark of pine species in the southeastern US and mid-Atlantic region. Endemic beetle populations are relatively low and primarily affect individual or small groups of damaged (e.g., lightning, wind, mechanical harvesting, fire, or disease) trees that cannot mount a strong defense (Bryant et al., 2006). Epidemic population surges occur nearly every year at the landscape scale (1000s of ha) across the SPB's range causing extensive tree mortality. Reasons for individual outbreaks are not entirely clear, but hypotheses are focused around predator-prey interactions, interannual and geographic changes in weather, host interactions, and interspecific competition  (Coulson and Klepzig, 2011). Long-term trends in outbreak frequency have largely been tied to changes in land use patterns, forest composition, and land management policy (Clarke et al., 2016). Longleaf pine is more resistant to SPB attack relative to other pine species (Hodges et al., 1979) because trees produce larger quantities of resin for longer periods of time to ward off attacks (Hodges et al., 1977). There are four other species of bark beetles known to attack southern pines. They include the black turpentine beetle (*Dendrochtonus terebrans* (Oliver, 1795)), and three species of engraver beetles (*Ips avulsus* (Eichhoff, 1868), *I. calligraphus* (Germar, 1824), and *I. grandicollis* (Eichhoff, 1868)). All four are known to follow behind SPB during outbreaks (Bryant et al., 2006). Several fungal species are associated with longleaf pine including brown-spot needle blight (*Lecanosticta acicola* (Thüm.) Syd.; Derr & Melder, 1969) and Ophiostomatoid fungi, but neither cause widespread mortality. Brown-spot needle blight primarily affects longleaf pine seedlings in the grass stage in stands that are not exposed to frequent fire (Derr and Melder, 1969). Ophiostomatoid fungi are localized and limited to situations where trees are under stress due to reintroduction of fire after long fire-free periods (Matusick et al., 2010), mechanical damage from silvicultural operations (Otrosina et al., 1999), or high-severity fire (Hanula et al., 2002).

## 2.4 **Fire history**

This section reviews literature pertaining to fire history in the longleaf pine ecosystem during the last 40,000 years and is divided into three time periods, each with increasingly detailed information as the quantity and quality of records improves. These time periods are: 1) the late Pleistocene and early Holocene (40,000–4,000 years BP), 2) the late Holocene (4,000–200 years BP), and 3) European settlement (200 years BP–present).

### 2.4.1 *Late Pleistocene and early Holocene (40,000–4,000 years BP)*

The late Pleistocene and first half of the Holocene Epochs were defined by the advancement and melting of continental ice sheets (Clark et al., 2009). The longleaf pine ecosystem retreated to localized refugia to the south of its current range as continental ice sheets advanced and then retreated as the climate warmed. There were four major climatic divisions that drove vegetation patterns during this period:

1) Late-Pleistocene Epoch interstadial (73,000-30,000 years BP)
2) Last glacial maximum (LGM) (29,000–16,000 years BP)
3) Glacial retreat (15,000–11,500 years BP)
4) Early to mid-Holocene Epoch interstadial (11,500–4,000 years BP)

The late Pleistocene interstadial was a period of relatively stable climate that lasted 40,000 years (CLIMAP Project Members, 1976). Fire regime characterizations during this period are based on similarities between vegetation composition and inferred climate derived from sediment cores with contemporary analogues. A sample from Camel Lake in northwest Florida suggests that vegetation resembled contemporary forests with abundant pine (*Pinus* L.) and both wetland and dry-site hardwoods, including oak (*Quercus* L.), hickory (*Carya* Nutt.), ash (*Fraxinus* L.), ironwood (*Ostrya* Scop.), gum (*Nyssa* L.), and titi (*Cyrilla* Garden ex L.; Watts et al., 1992). The inferred climate was similar to, but slightly drier than the modern climate, but there is no paleoecological evidence indicating the occurrence of longleaf pine.

The LGM began around 30,000 years BP with the onset of long-term gradual cooling and by 21,000 years BP the Laurentide ice sheet had reached its maximum extent stretching from southern New York to Southern Indiana (Dyke and Prest, 1987). North America was on average 10-20°C cooler and precipitation was 40 mm less than present (Bartlein et al., 1998; Jackson et al., 2000). Only a few paleoecological samples can be used to characterize the fire regime during the LGM (Patterson et al., 1987). A peat core dated to 30,000–25,000 years BP from Sandy Creek Run in central Georgia provides the earliest direct evidence of fire in the southeast (LaMoreaux et al., 2009). Pollen and charcoal analysis indicated the presence of open grasslands interspersed with stands of pine and spruce (*Picea* A. Dietr.) and infrequent occurrence of fire. Similar open coniferous forests interspersed with grasslands during the LGM were indicated by sediment core data collected further north in South Carolina (Watts, 1980). Northwest Florida was likely more favorable for vegetation growth relative to the central Georgia location, but still dry and 3–4°C cooler than today (Willard et al., 2007). Paleoecological data show that the northern and central parts of Florida supported a more heavily forested landscape with pine, oak, and hickory taxa (Watts et al., 1992; Willard et al., 2007). In this region both climate and vegetation were more conducive to fire and would have supported a more active fire regime relative to central Georgia. Genetic analysis suggests that longleaf pine was constrained to a single refugia in southern Texas and northern Mexico during the LGM (Schmidtling and Hipkins, 1998).

The glacial retreat that followed the LGM was characterized by millennia of climatic upheaval, long-term warming, and substantial melting of the North America’s Cordilleran and Laurentide ice caps. The end of this period was marked by climate stabilization and the transition to the Holocene Epoch interstadial. During this time longleaf pine was migrating northward into Texas and eastward along the Coastal Plain (Schmidtling and Hipkins, 1998). Latitudinal ecosystem gradients were tightly compressed across what is now the longleaf pine ecosystem with boreal forest extending to South Carolina, a mixture of boreal and temperate species in Georgia and northern Florida, and warm temperate species in peninsular Florida (Delcourt and Delcourt, 1984; Watts, 1970; Whitehead, 1973). A peat core representing part of this period (13,000–11,000 years BP) contained charcoal concentrations that were substantially lower than the LGM. This decrease in fire frequency was attributed to a cooler and wetter climate (LaMoreaux et al., 2009). Vegetation was characterized as open oak woodlands with alder growing on riparian areas. Pine abundance, which was common during the LGM, declined substantially. A decline that was also recorded in northern Florida where pine abundance dropped abruptly 14,000 years BP (Watts et al., 1992). Pine was replaced by hickory, other deciduous species, and spruce. Further south near Tampa, Florida macrofossil and pollen data also indicated a cooling trend beginning 14,700 years BP and hickory abundance decreased while pine increased (Willard et al., 2007). Unlike sites farther north, this cooling trend was associated with drier conditions. While the authors make no comments on fire, drier conditions coupled with the flammable litter of pine-dominated forests in a dry, temperate climate would conceivably support a more active fire regime at these locations.

The early to mid-Holocene Epoch (11,500–4,000 years BP) was marked by continued climate amelioration, disappearance of the continental ice sheets (Bartlein et al., 1998; Margold et al., 2018), and northward expansion of southern pines (Webb et al., 1987). Across the current range of longleaf pine, boreal taxa continued to migrate north and were replaced by temperate species. These forests were initially oak-dominated, but by 9,000–7,000 years BP, oak abundance declined while pine increased (Williams et al., 2004). Sediment cores from the southeastern US indicate a shift to vegetation adapted to warmer environments. For example, in Florida wetter conditions 7,760 years BP accompanied a shift from forest dominated by broad-leaf species including oak, ironwood, beech, and hickory to pine and the appearance of contemporary shrub taxa including Ericaceous shrubs (*Ericaceae* Juss.), sweetgale (*Myrica* L.), and titi (Watts et al., 1992). This shift is present in pollen profiles collected at other sites throughout the southern tier of longleaf pine's current range (Watts, 1980, 1971, 1969). It is unclear if longleaf pine was part of this expansion as there is no definitive evidence of its presence at any of these locations. These expanding pine forests were most likely comprised of other southern pine species which had LGM refugia more proximate to these sampling locations (Schmidtling, 2003; Wells et al., 1991). The mid-Holocene expansion of southern pines was limited to the southern half of the longleaf pine ecosystem. In central Georgia, oak-dominated forests persisted through the mid-Holocene (LaMoreaux et al., 2009). Corresponding charcoal analysis indicates fire activity was increasing, though infrequent relative to contemporary levels. Similar levels of fire activity were also detected from radio-carbon dated soil charcoal samples collected in North Carolina (Fesenmyer and Christensen, 2010).

Human settlement across North America (Meltzer, 2003) had an increasingly important bearing on the fire regimes in the southeastern US (Nowacki and Abrams, 2008). Humans migrated from Asia into parts of unglaciated Alaska as early as 15,000 years BP (Slobodin, 2001; Vasil'ev, 2001). The earliest presence of humans was noted from the southwestern US through the Great Plains by 11,500–11,000 years BP (Meltzer, 2003) and with settlement of the remainder of the North American continent over the next 1000 years (Fagan, 1991). In the southeastern US, the early to mid-Holocene is anthropologically referred to as the Paleo-Indian (10,500–9,500 years BP) and Archaic (8,000–3000 years BP) periods. Human populations were organized into hunter-gather societies and primarily used fire to manage and hunt game (Fowler and Konopik, 2007). Both climate and human settlement potentially caused increased fire activity, but ascribing this change to either is problematic because there is insufficient palaeoecological sample breadth to establish a reliable correlation.

### 2.4.2 *Late Holocene (4,000–200 years BP)*

By 4,000 years BP, contemporary plant communities and fire regimes had become established across much of longleaf pine's current range (LaMoreaux et al., 2009; Watts et al., 1992). This is reflected in pollen and macroscopic fossil records showing pine-dominated forest with sub-dominant oaks and an ericaceous shrub layer analogous to contemporary southern pine forests (Albert, 2007; LaMoreaux et al., 2009; Watts, 1971; Willard et al., 2010). Based on its historical distribution longleaf pine was presumed to be the dominant pine at many of these locations (Watts, 1971). Widespread increases in fire activity accompanied this vegetation shift (Delcourt & Delcourt, 1997; Fesenmyer & Christensen, 2010; LaMoreaux et al., 2009; White, 2007) which persisted throughout the late Holocene (Kocis, 2012; Tanner et al., 2018; West, 2007). Climatic and anthropogenic factors were drivers of contemporary longleaf pine ecosystem development and its associated high-frequency fire regime.

Climatic factors included a shift at the onset of the late Holocene to cooler temperatures (Bartlein et al., 1998). It is counterintuitive that cooler conditions corresponded with an increase in fire activity and the northward expansion of the longleaf pine ecosystem (Webb et al., 1987), but this can be explained by other factors. First, the northward migration of longleaf pine and other plant species adapted to warmer climates (Albert, 2007; LaMoreaux et al., 2009) were attributed to a warming trend during the winter months across the southeastern United States that occurred despite overall cooler conditions (Webb et al., 1987). Second, increased fire activity was likely a product of fuel-mediated vegetation change, where the influence of vegetation characteristics on the fire regime is self-reinforcing to an extent that can override opposing climate drivers. In this instance, fuels characteristics in current analogues would suggest that the pine litter and understory associates of late Holocene forests were more flammable (Behm et al., 2004; Emery and Hart, 2020) than the oak-dominated forests they replaced (Kane et al., 2008). Fires could then have burned under more marginal conditions and catalyzed the expansion of the longleaf pine ecosystem northward so long as there were sufficient ignition sources.

Anthropogenic factors that influenced the fire regime were largely associated with population density and land use. Initially there was a slow increase in population density and increasingly agricultural-based land use as Native American culture progressed from nomadic hunter-gatherers of the Archaic period to more sedentary communities of the Woodland (3000–1000 years BP), and then Mississippian periods (1000–500 years BP). This was followed by an abrupt population decline during the protohistoric period (1521–1700 AD). The Protohistoric period spans from first contact with Europeans to intensive land occupation by Spanish and other Euro-American settlers (Tebeau, 1980). Despite the initial relative lack of contact between Native Americans and Europeans, exposure to novel diseases caused declines in Native American populations that were later exacerbated by forced migration, war, genocide, and other impacts of European colonialism (Thornton, 2002).

Native American populations were important drivers of landscape-scale vegetation patterns across eastern North America through their use of fire as a land management tool (Abrams, 1992; Abrams & Nowacki, 2008; Black et al., 2006; Delcourt & Delcourt, 1985; Delcourt & Delcourt, 1998; Fowler & Konopik, 2007; Lorimer, 2001; Scharf, 2010; Springer et al., 2010). Across the southern range of the longleaf pine ecosystem, however, high lightning density (Christian et al., 2003; Mitchener and Parker, 2005; Orville, 1991) likely provided enough ignitions such that contributions from anthropogenic activity were negligible (Abrams and Nowacki, 2008). Furthermore, anthropogenic ignition sources were less common in this region because agriculture, a major contributor to anthropogenic ignitions, was not widely practiced owing to nutrient-poor, sandy soils and reliance on coastal waters for food sources. Other environmental conditions would have further diminished the importance of anthropogenic ignition sources by expanding potential fire size. These include a longer fire season, and flat terrain with fewer fuel breaks. As with lightning frequency, both features decreased with increasing latitude. As a consequence, anthropogenic ignition sources became an increasingly important determinant of fire frequency. This, coupled with a lack of ignitions until the widespread development of agricultural activities during the Mississippian period would explain the later arrival of pine-dominated forests at sites along the northern half of the longleaf pine ecosystem (Albert, 2007; Whitehead & Sheehan, 1985). There is some evidence tying increased fire activity and pine expansion during the Mississippian period to the development of agricultural-based human settlements along the northern half of the longleaf pine ecosystem. In northern Mississippi, maize, a central American food crop (Delcourt, 1987), in the pollen record was positively correlated with a spike in pine pollen and charcoal concentrations 2400 years BP (Whitehead & Sheehan, 1985).

Paleoecological data show the impacts of Native American population declines on the fire regime during the protohistoric period. This includes paleoecological evidence of a decline in fire activity across the northern half of the longleaf pine ecosystem where anthropogenic use of fire was a primary source of ignitions and no change across the southern half where higher lightning frequency provided sufficient ignitions to maintain a frequent fire regime. Pollen data from northwestern Mississippi at the northern boundary of the longleaf pine ecosystem indicates a reduction in herb taxa along with declining pine and increasing oak presence during this period, bracketed by opposite trends in the Mississippian and historic periods when human population density was higher (Scharf, 2010). While there is no direct measure of fire, the decline in herbs and pine with corresponding increases in oak are strong indicators that fire frequency declined (Spencer et al., 2017). Albert (2007) also noted a decrease in pine and increase in oak at the northeastern periphery of longleaf pine's range in Texas during the protohistoric period, although this was attributed to climactic trends. At sites across eastern North America to the north of the longleaf pine ecosystem, Native American population decline was associated with a decrease in fire frequency (Springer et al., 2010) and increases in fire-sensitive arboreal taxa (Abrams, 2005; Black et al., 2006; Buckner, 2000; Delcourt, Delcourt, Ison, Sharp, & Henderson, 1998; Hicks, 2000; Kay, 2000; Mann, 2000). Farther to the south, across Florida, charcoal concentrations increased during the protohistoric period (Albritton, 2009; Kocis, 2012; Tanner et al., 2018) indicating that fire frequency was not as affected by declines in the Native American population relative to sites farther north.

Dendrochronological data collected from the northern half of the longleaf pine ecosystem show that fire frequency remained stable during the protohistoric-historic transition and that anthropogenic activity was the primary ignition source throughout the protohistoric period. The former conclusion is unexpected given that paleoecological research showed that fire activity decreased with population density during the Mississippian-protohistoric transition. Given this trend, there should have been a corresponding increase in fire activity as population density rebounded during the protohistoric-historic transition. This is especially so since dendrochronological records show that most fires in this region were human caused. The arrival of European settlers would not have greatly changed the use of fire as a land management tool because historical accounts often remark that fire was used by settlers as much, or more than Native Americans (Earley, 2004; Heyward, 1939). Fire scar data from the Kisatchie National Forest in west-central Louisiana record a mean fire interval (MFI) of 3.2 years during the late protohistoric period (1650–1713) and 3.3 years during the historic period (1714–1970; Stambaugh et al., 2011). Fires primarily occurred during the late growing season during the late protohistoric (40 percent) and early historic (67 percent) periods. The Native American population in Stambaugh et al.'s (2011) study area declined precipitously from 250,000 to 15,000 by the late 1600s (Burton and Smith, 2008) and European settlement was sparse suggesting the relatively high fire frequency persisted despite lower human population density. On the Talladega National Forest in northeastern Alabama the late protohistoric period fire regime (1660–1831) in longleaf pine forest was also characterized by frequent fire (MFI: 3 years; Bale, 2009). Greater than 90 percent of these fires occurred during the dormant season, a result that strongly suggests that human ignitions were driving fire frequency since lightning is rare during this time of year in northern Alabama (Christian et al., 2003). A similar MFI (2.6 years) was recorded prior to widespread settlement (< 1840) in montane longleaf pine stands in northwestern Georgia, although fires occurred throughout the year (Klaus, 2019). Primarily dormant season fires were also recorded in protohistoric fire scar records collected from longleaf pine at other locations across the northern half of the longleaf pine ecosystem including Big Thicket National Preserve in Texas and Sandy Island off the coast of South Carolina (Henderson, 2006). The prevalence of late-growing season and dormant season fires across this area suggests that the fire regime was maintained by human ignitions because the lightning season falls within the early to mid-growing season (Bentley and Stallins, 2005; Hodanish et al., 1997). The MFI at locations sampled by Henderson (2006) was not partitioned into time periods that correspond with settlement patterns but were generally longer than the previously mentioned studies owing to smaller geographic features that constrained potential fire size.

Across the southern half of the longleaf pine ecosystem dendrochronological records show that, relative to the northern half, the protohistoric fire regime had a slightly shorter MFI, but with the same stability during changes in population density and primarily growing season fires. These trends suggest that lightning plays a larger role in maintaining the fire regime across the southern half of the longleaf pine ecosystem. Fires were evenly distributed throughout the year during the protohistoric period at a loblolly-longleaf pine forest adjacent to Lake Louise in southern Georgia and longleaf pine forests on Eglin Air Force Base in northwestern Florida (Henderson, 2006). The MFI was 6.7 years at Lake Louise during the protohistoric period (1463–1664), but this site was riparian, and the surrounding upland likely had a shorter MFI. The MFI at Eglin could not be partitioned due to poor data quality and was approximately three years from 1626 through the implementation of fire suppression policies in the early-1900s. At a slash-longleaf pine savanna at St. Joseph Bay State Buffer Preserve, also in northwestern Florida, dendrochronological records revealed that 88 percent of the fires during the protohistoric period (1592–1830) occurred during the growing season (April – August) and MFI was 2–3 years (Huffman, 2006). Growing season fires and short MFI values (1–2 years) were also recorded during the protohistoric period (1784–1823) in longleaf-slash pine forests at Avon Park Air Force Range in central Florida (Huffman & Platt, 2014). Fire seasonality at these sites coincides with peak lightning frequency (Komarek, 1964; Rother et al., 2018), suggesting that lightning is the primary ignition source. The percentage of dormant season fires at Avon Park decreased to almost zero during a 20-year period of land abandonment caused by the Seminole Wars. In contrast, 20–30 percent of fires occurred during the dormant season prior to this period when the land was occupied by Native Americans and afterwards when the land was settled by Europeans. The MFI, however, remained unchanged. This indicates that both groups were using fire as a land management tool. That fire frequency remained unchanged suggested human activities modified fire seasonality, but not frequency (Huffman & Platt, 2014). Primarily growing-season fires that maintained high-frequency fire regimes were also noted in slash pine forests on islands in the Florida Keys (Harley et al., 2013) and along the Gulf Coast (Huffman, 2006) further suggesting that lightning ignitions in Florida were high enough to maintain the frequent fire intervals necessary to sustain longleaf pine forests. The MFI values at these locations were longer than expected for southern pine forests, 6–9 years in the Florida Keys and 4 years on the Gulf Coast. As with sites at Big Thicket and Sandy Island (see above), this can be attributed to the small burnable area patch size (Frost, 2000; Harcombe et al., 1993).

High fire frequency documented by paleoecological and dendrochronological records are supported by historical accounts. Early travelers were often struck by the ubiquitous nature of fire, its low intensity, the seeming indifference of trees to regular disturbance, and the open park-like pine forests (Figure 2-4). Frost (2006) provides an extensive review of historical accounts of the disturbance regime during the protohistoric period including a quote from a British traveler in the early 1800s who, upon transiting a recently burned stand of longleaf pine in South Carolina commented:

> *There was no underwood properly so-called, while the shrubs had all been destroyed a week or two before by a great fire. The pine-trees, the bark of which was scorched to a height of about 20 feet, stood on ground as dark as if it had rained Matchless Blacking for the last month. Our companions assured us that although these fires were frequent in the forest, the large trees did not suffer. This may be true, but certainly they did look very wretched, though their tops were green as if nothing had happened.*

Accounts from renowned American naturalist William Bartram who traveled extensively though the southeast noted that fire was commonplace across the landscape (Harper, 1958). These accounts were repeated by others who documented their travels through the pre-settlement pine forests of the southeast (Day, 1953; Lawson, 1709; Smith, 1910).

The protohistoric period largely overlaps with the Little Ice Age, a period of colder climate across North America and this confounds attempts to link changes in the fire regime to Native American population declines. The climate in Florida likely became drier during the Little Ice Age (Willard et al., 2006) and these dry periods are thought to have contributed to measures of increased fire frequency (Kocis, 2012). This may have offset any effects of reduced anthropogenic ignitions across the northern half of the longleaf pine ecosystem.

**Figure 2-4.** Open park-like condition of historic fire-maintained southern pine forest. *In the pine woods, Florida,* ca. 1900–1906, photograph, accessed October 28, 2025, https://lccn.loc.gov/2016803946

### 2.4.3 *European settlement*

European settlement, or the historic period represents the most recent 200 years, a period when spatial extent of the longleaf pine ecosystem shrunk by 97 percent owing to intensive land use concurrent with European settlement. The historic period is sub-divided into three periods following Fowler and Konopik (2007):

1) Industrialization (1825–1920)
2) Fire exclusion (1920–1980)
3) Fire management (1980–present)

### 2.4.4 *Industrialization (1825–1920)*

Intensive land use during the industrialization period spread west and south throughout the region. Large-scale deforestation associated with industrialization was preceded by a brief period of European settlement where the primary land use was cattle grazing (Prunty, 1965). Early use of fire by settlers was widespread (Lafon, 2010), but the ecological effect of cultural burning practices imported from their home countries (Johnson and Hale, 2002), or adopted from Native American practices was thought to be limited. More intensive land clearing first occurred in Virginia during the early 1600s but was geographically limited to small areas for over 100 years (Frost, 1993). Several events during the first half of the 1800s rapidly accelerated the scale and pace of deforestation across the southeast and included: the ceding of Florida by the Spanish in 1821, which opened vast tracts of Florida and the Gulf Coast to settlement; the invention of the copper still in 1834, which increased the efficiency of the naval stores industry; and adoption of steam power, which greatly increased the efficiency of logging operations and transportation networks (Frost, 2006). The naval stores industry, logging, and agricultural conversion rapidly replaced cattle grazing as the primary land use by European settlers. By 1907 timber harvesting of longleaf pine peaked at 1.3 billion board feet (Wahlenberg, 1946).

Fire frequency generally increased with the onset of industrialization across eastern North America (Spencer et al., 2017) and this is supported by dendrochronological records across the northern half of the longleaf pine ecosystem where lower lightning density magnifies the sensitivity of fire frequency to changes in anthropogenic ignitions. Dendrochronological samples recorded biannual fires during the industrialization period in longleaf pine on the De Soto National Forest in Mississippi (White & Harley, 2016) and in west-central Louisiana (Stambaugh et al., 2011). At both locations biannual fires occurred when populations of European settlers were high. Stambaugh et al. (2011) found that MFI was shorter (1.3 years) during this period (1791–1880) than at any other point in the dendrochronological record (1650–1905). A similar trend of shorter MFI (1.2–2.6 years) during industrialization (1832-1940) relative to the protohistoric period (2.6–3.2 years) was recorded in fire scar records from longleaf pine on the Talladega National Forest (Bale, 2009) and in northwestern Georgia (Klaus, 2019). Fires during this period occurred primarily during the dormant season when lightning strike density was low and human ignitions would have been higher, thus high fire frequency was attributed to fire use by European settlers. To the south and east, at Eglin and Sandy Island, high fire frequency corresponded with periods of industrialized land use by settlers (Henderson, 2006). The Eglin site is the only location in the southern half of the longleaf pine ecosystem where higher fire frequency was noted during industrialization. Dendrochronological samples collected from a longleaf-slash pine savanna on the St. Joseph Bay State Buffer Preserve had consistent MFI (3.2 years) during the industrialization (1830–1883) and protohistoric (1592–1830) periods (Huffman et al., 2004). However, there was a shift from a low percentage of dormant season fires prior to

1830 to greater than 50 percent dormant season fires after 1830 and this was attributed to ignitions by settlers. A similar trend was observed at Avon Park where 1–2 year MFI remained stable despite changes in land use, although there was a shift from growing season to dormant season fire seasonality during industrialized land use from 1919 to 1930 (Huffman & Platt, 2014).

Paleoecological research also indicates increased fire activity following European settlement. Sediment cores form the Yazoo Basin in Mississippi show an abrupt increase in disturbance related genera (e.g. *Ambrosia* spp.) following European settlement in the 1800s (Scharf, 2010) and increased fire activity in samples collected from Fort Benning, Georgia was attributed to intensified deer hunting by the Creek Indian tribe as a means to provide products for trade with European settlers (Foster & Cohen, 2007).

### 2.4.5 *Fire exclusion (1920–1980)*

The transition from industrialization to fire exclusion was accompanied by marked changes in land use. Once cleared, longleaf pine forests no longer represented a large source of timber or naval stores, an industry that was already becoming obsolete with the development of fossil fuels. Agriculture continued, but arable lands had already been converted. By 1900, 27 percent of longleaf pine uplands had been converted to agriculture (Frost, 1993) and by 1930 only a few virgin stands remained (Crocker, 1987; Oswalt et al., 2012). With the decline of these industries, forest cover rebounded. This period of afforestation coincided with the implementation of fire suppression policies. On abandoned lands, the combination of feral hogs (Wakeley, 1954), burning logging slash (Wade and Lunsford, 1989), limited seed sources (Oswalt et al., 2012), and annual burning (Otto & Anderson, 1982; Van Lear et al., 2005) caused widespread failure of longleaf pine regeneration (Frost, 1993; Mohr, 1896). Poor regeneration was correctly diagnosed by foresters at the time as herbivory from hogs and the negative effects of annual pasture burning and high-severity logging slash burns. However, they incorrectly believed that any fire – rather than the detrimental forms associated with industrialization – would cause high mortality among longleaf pine seedlings (Pinchot and Ashe, 1897). Their assessment gained widespread acceptance and culminated in several campaigns to end cultural burning practices during the early and mid-1900s (Johnson and Hale, 2002), a period that coincided with the adoption of national fire suppression policies (Pyne, 1982). Fire suppression policies and the reduction in potential fire size due to forest fragmentation (Frost, 2000; Harcombe et al., 1993) severely reduced fire occurrence across the range of the longleaf pine ecosystem. It is estimated that longleaf pine was able to regenerate on about of a third of afforested lands during the late 1800s and early 1900s (Wahlenberg, 1946) but the lack of fire degraded their ecological value. This included loss of the herb layer (Toribio-Diaz et al., 2019), wildlife habitat destruction (Means, 2006), and a successional shift from fire-adapted pine to fire sensitive hardwoods (Outcalt & Brockway, 2010; Ware et al., 1993). The push to eliminate fire from southeastern forests occurred despite opposition from local scientists and land managers who had already documented the ecological importance of fire (Andrews, 1917; Garren, 1943; Greene, 1931; Heyward, 1939; Stoddard, 1931).

The impact of fire exclusion was widely recorded in dendrochronological fire scar records. The MFI in montane longleaf pine forests of northwestern Georgia lengthened from 1.2 years during the historic period (1840–1915) to 11.4 years during fire exclusion (1915–present; (Klaus, 2019). In longleaf pine forests of southern Mississippi, the MFI lengthened from 4.9 years during the protohistoric period (1760–1879) to 8.0 years during fire exclusion (1936–1979;

White & Harley, 2016). On Little St. George Island in northwestern Florida where the fire regime was maintained by lightning ignitions, the MFI lengthened from four years during a period preceding active fire suppression (1924–1945) to nine years when the State of Florida managed the island under a full fire suppression policy (1963–2001; Huffman et al., 2004). In central Florida the MFI increased from primarily one to two years to three years or greater after 1931 (Huffman & Platt, 2014). On Big Pine Key, an island in the Florida Keys the MFI increased from 4.6 years prior to the implementation of fire suppression in 1956 to 7.25 years in subsequent years (Harley et al., 2013). The only locations where fire frequency did not decline were large private landholdings where frequent burning was continually practiced during the fire exclusion period to maintain habitat for game species (Rother et al., 2020). While these changes of just a few years in MFI may seem marginal, long-term research on the effects of fire frequency on vegetation dynamics shows that these relatively small changes impact forest structure (Waldrop et al., 1992). Given that most of the biological plant diversity in longleaf pine savannas is represented by forbs (Hardin and White, 1989), fire exclusion caused a substantial loss of biodiversity in remaining pine savannas (Abrahamson & Abrahamson, 1996a, 1996b; Glitzenstein et al., 2003; Maliakal et al., 2000).

The shift from fire-tolerant pines to fire-sensitive hardwoods caused by fire exclusion has been documented by other historical records as well. This trend is seen in historical forest composition data derived from Georgia Land Lottery Survey maps (Waters, 2020). Historical aerial photographs in Florida also document the invasion of sand pine, a fire-sensitive species in fire-excluded longleaf pine forest (McCay, 2000).

Despite the initial increase in forest cover, the decrease of the longleaf pine ecosystem resumed later in this period due to industrial land use practices. In the early 1900s longleaf pine forest, albeit mostly second growth, is estimated to have occupied 50 percent of its historical range (Frost, 1993). By the 1990s that amount had shrunk to five percent (Outcalt and Sheffield, 1996). Reasons included conversion of natural longleaf stands to pine plantations, agricultural clearings, and land development. Loblolly and slash pine were preferred by timber companies, and longleaf pine forests were often converted to loblolly or slash pine plantations (Schultz, 1997). In 1900 pine plantations were essentially non-existent in the southeastern US and by 1997 they covered 12 million ha (South and Buckner, 2004). Gradually, over the course of the fire exclusion period, foresters became increasingly aware of the importance of fire across the southeastern US. By 1950 prescribed fires were commonly used to manage forage for cattle, control hardwoods in pine plantations, and improve the quality of browse for game species (Wade et al., 2000). Despite its increasing use, reluctance to implement prescribed burns remained widespread due to the inertia associated with careers spent suppressing fire and the legal liability associated with potential loss of control (Riebold, 1971).

### 2.4.6 *Fire management (1980–present)*

The fire management period began in the late 1970s during a broadening of public land management goals, from primarily timber and game, to include ecosystem properties and nongame species. This shift was, in part, influenced by passage of environmental laws such as the Endangered Species Act. The growing number of conferences dedicated to this topic was evidence of the emerging importance of this new management focus (Johnson and Hale, 2002). These gatherings promoted an increased awareness that prescribed fire was a necessary component of the longleaf pine ecosystem (Matthews et al., 2020). Consequently, the use of prescribed fire increased. Estimates indicate that by the late 1980s prescribed fire was implemented on about 1.6 million ha of forests annually (Wade and Lunsford, 1989) and by 2011 annual area burned in prescribed fires was 2.6 million ha (Melvin, 2012). Applications of prescribed fire increased to include: hazardous fuels reduction, post-silvicultural site preparation, hardwoods control, habitat restoration, and game habitat management (Stanturf et al., 2002). Aside from increased area burned, the type of prescribed fire changed as well. Throughout the 1980s and 1990s land managers increased the area treated with surface burns and reduced the area treated with post-logging slash control burns, especially on federal lands (Haines et al., 2001). This trend reflected the emphasis on restoring historic fire regimes and the declining importance of timber harvesting. Land managers also began to incorporate growing season-burns based on evidence that, when applied frequently, they more effectively maintained herbaceous understories species (e.g., Waldrop et al., 1987). The US Forest Service in Florida began experimenting with growing-season burns in the mid-1980s and they accounted for 44 percent of the annual area burned on the Apalachicola National Forest by 1995 (Ferguson, 1998) and 60–75 percent of the annual area burned on the Ocala National Forest by 2010 (Custer, 2011). On the Apalachicola National Forest, the shift to growing season burning was accompanied by shorter fire intervals and a change in management strategy aimed at mimicking the historic fire regime. This resulted in an increase in the annual area burned from 10,000 ha $yr^{-1}$in 1959 to 18,000 ha $yr^{-1}$ in 1996 (Ferguson, 1998). After 2010, annual area burned by prescribed fire in southeastern US forests remained relatively flat with two million ha burned in 2019 (Melvin, 2020). Forest inventory data suggest approximately 400,000 ha of longleaf pine forest have a significant component of hardwoods that could benefit from additional prescribed fire (Oswalt et al., 2012). Fire exclusion in these areas is among the largest contributors to longleaf pine habitat degradation (Brudvig et al., 2014). Even with better management plans (Clark et al., 2018; Foster et al., 2019) and continued public support for prescribed fire programs (Gordon et al., 2020; Loomis et al., 2001) the rate of prescribed burning has not increased despite a clear need. Management surveys indicate numerous obstacles including smoke management regulations, residential development, public hesitancy, and lack of resources (Haines et al., 2001).

Some dendrochronological research shows that MFI shortened during the management period while others do not detect a difference. For example, in southern Mississippi the MFI decreased from 8.0 years during the fire exclusion period (1936–1979) to 3.4 years during the management period (1980–2013) with a high percentage (69 percent) of dormant season burns (White & Harley, 2016). In longleaf-slash pine savannas at Avon Park prescribed fire has been used regularly since 1940 and along with ordinance ignitions has maintained a fire regime with mostly 3-year intervals but that is longer than the historical average of 1–2 years when ignitions by non-military sources maintained the fire regime (Huffman & Platt, 2014). The fire regime on Little St. George Island did not show an increase in fire frequency during the management period. The MFI was 9 years, but this was because the agency managing the island maintained a strict fire suppression policy until 2000 and no prescribed burns were implemented (Huffman et al., 2004). Fire scar analyses in Florida, South Carolina (Henderson, 2006) and Georgia (Waters, 2020) contain chronologies that extend into the management period but did not compare MFI between periods of fire suppression and management. Fire scar analysis on private lands in northern Florida and southern Georgia that were managed as game reserves show a continuous history of frequent fire that extended through the suppression period and into the management period (Rother et al., 2020). More recent fire history studies have used prescribed fire records and satellite imagery to assess fire regimes during the management period. Analysis of prescribed fire records at Fort Bragg, North Carolina showed the MFI for longleaf pine uplands was three years for the period 1991–2019 while a more detailed review using satellite imagery showed that wetter longleaf pine savannas burned less frequently and had a MFI of five years (Wall et al., 2021). This analysis showed that management staff were achieving fire frequency objectives in forested uplands, but prescribed fires were frequently burning out when they reached wetter areas. A similar analysis of prescribed fire records for the Talladega National Forest found an MFI of 5.7 years for areas under fire management and concluded that the prescribed fire program was lagging behind objectives for hazardous fuel management and ecosystem restoration (Stober et al., 2020).

Longleaf pine forest cover continued to decline during the fire management period despite increasing awareness of the biological value and species richness of the ecosystem and the severity of historic degradation. From 1987 to 1995 an estimated 4300 ha of longleaf pine forest were cleared annually in Florida (Outcalt, 1998) and an analysis of longleaf pine cover showed continuous decline from 1970 to 2010 (Oswalt et al., 2012). To reverse this decline Congress authorized America's Longleaf Restoration Initiative (ALRI) in 2009 with the goal of initiating or completing restoration of longleaf pine on 3.2 million ha of state and private lands by 2025. The initiative provided funding and support from federal agencies to assist collaborative partnerships with private, local, and state land management organizations to coordinate and implement restoration programs (America's Longleaf, 2018). Subsequent analysis of Forest Inventory Analysis (FIA) data across the southeastern US found that despite adding considerable area of restored longleaf pine habitat during the first half of ALRI, there was still a net loss of longleaf cover (McIntyre et al., 2018). This led to the addition of federal lands to the ALRI goals through the US Forest Service's Million-Acre Challenge launched in 2017. Recent analysis of FIA data does show that, by some measures, the number and size of longleaf pine trees are increasing, but more slowly than other more fire-sensitive competitors, including hardwoods and loblolly pine (Ojha et al., 2021). This suggests that prescribed fire programs are unable to apply fire frequently enough over a large enough area to maintain or increase longleaf pine coverage and characteristics. It should be noted that the FIA data are a somewhat problematic source for evaluating ALRI because results may be biased towards capturing degradation relative to restoration. Other assessments show better progress towards ALRI (America's Longleaf, 2018) and Million-Acre Challenge goals (Matthews et al., 2020), but still indicate that the pace of restoration is insufficient to meet the 2025 ALRI goal of restoring longleaf pine on 3.2 million ha.

## 2.5 **Conclusions**

This review describes the long history of interdependence between the longleaf pine ecosystem and fire. Extensive evidence chronicles thousands of years of frequent fire in this ecosystem. The strength and consistency of this evidence provides a strong case for the use of prescribed fire to manage natural areas with longleaf pine forests. The research presented in subsequent chapters contains important insights on how prescribed fire can be used in the longleaf pine ecosystem to achieve two of the most oft-cited management goals: maintaining high levels of biological diversity and mitigating hazardous fuels. The following chapters should be considered in the context of the broader properties of this ecosystem reviewed in this chapter. For example, longleaf pine grows on a wide range of soils which can affect forest composition and productivity. The former may have a strong influence on how prescribed fire can be used to meet management objectives while the latter may limit how quickly fuel accumulates to a level that can support prescribed burning. Even among longleaf forests with similar composition subtle differences in soil texture can lead to different outcomes under similar fire regimes. Taking the time to understand the broader characteristics of this ecosystem will improve the chances of successfully implementing prescribed fire strategies detailed in this dissertation. Likewise, fire history studies described in this chapter document a several-millennia-long relationship between people and fire across the longleaf pine ecosystem. This relationship has likely extended the range of the longleaf pine ecosystem, and its attendant frequent fire regime, further north than would have been possible otherwise. This has led to a gradient of fire regime characteristics. Therefore, fire managers wishing to replicate historical fire regime characteristics should understand that the frequency and seasonality of fire changed with latitude. A fuller understanding of fire history in the longleaf pine ecosystem can improve the probability of successfully implementing prescribed fire strategies.

While this review focuses on historical trends it is also important to consider projected changes. Climate change poses a major challenge to natural resource management and the projected increase in temperatures, drought, and hurricanes threaten the longleaf pine ecosystem. Fortunately, longleaf pine is well-adapted to drought (Samuelson et al., 2019), but there remains a large amount of uncertainty regarding how a changing climate will affect its growth and reproduction (Bowman and Chen, 2022), and the growth and reproduction of other species in this ecosystem. Forecast impacts of climate change based on outputs from landscape simulation models suggest that climate change will not have a direct impact on the quality of red-cockaded woodpecker habitat which is considered an overall indicator of longleaf pine ecosystem health, but hotter and drier weather may constrain prescribed fire programs to a degree that degrades habitat (Lucash et al., 2022). These simulations suggest that hurricanes, even under historic frequency and intensity levels, pose a greater threat to red-cockaded woodpecker habitat than impacts from climate change because category 4 and 5 hurricanes can substantially impact habitat (Armentano et al., 1995; Kenney et al., 2021; Zampieri et al., 2020). Recent increases in hurricane intensity have been linked to climate change and forecasts suggest that the incidence of high-intensity hurricanes will continue to increase (Sobel et al., 2016; Walsh et al., 2016). Because hurricanes increase fire danger through accumulation of dead woody debris (Myers & van Lear, 1998) land managers may be forced to divert resources used to maintain fire frequency to mitigating fuel hazard – a potential scenario in a climate that is hotter, more prone to drought, and with a higher incidence of high-intensity hurricanes. If this trend continues hurricanes will pose a greater threat to the longleaf pine ecosystem, especially if programs like ALRI and the Million-Acre Challenge are unable to meaningfully reverse long-running declines in longleaf pine forest cover.

## 2.6 **References**

Abrahamson, W.G., Abrahamson, C.R., 1996a. Effects of fire on long-unburned Florida uplands. J. Veg. Sci. 7, 565–574. https://doi.org/10.2307/3236306

Abrahamson, W.G., Abrahamson, J.R., 1996b. Effects of a low-intensity winter fire on long-unburned Florida sand pine scrub. Nat. Areas J. 16, 171–183.

Abrams, M.D., 2005. Prescribing fire in eastern oak forests: Is time running out? North. J. Appl. For. 22, 190–196. https://doi.org/https://doi.org/10.1093/njaf/22.3.190

Abrams, M.D., 1992. Fire and the development of oak forests. Bioscience 42, 346–353. https://doi.org/10.2307/1311781

Abrams, M.D., Nowacki, G.J., 2008. Native Americans as active and passive promoters of mast and fruit trees in the eastern USA. Holocene 18, 1123–1137. https://doi.org/Doi

10.1177/0959683608095581

Albert, B.M., 2007. Climate, fire, and land-use history in the oak-pine-hickory forests of northeast Texas during the past 3500 years. Castanea 72, 82–91. https://doi.org/https://doi.org/10.2179/0008-7475(2007)72[82:CFALHI]2.0.CO;2

Albritton, J.W., 2009. A 1700-year history of fire and vegetation in pine rocklands of National Key Deer Refuge, Big Pine Key, Florida: charcoal and pollen evidence from Key Deer Pond. Masters Thesis. University of Tennessee, Knoxville, Tennessee.

America's Longleaf, 2018. 2018 range-wide accomplishment report.

Andrews, E.F., 1917. Agency of fire in propagation of longleaf pines. Bot. Gaz. 64, 497–508.

Armentano, T V, Doren, R.F., Platt, W.J., Mullins, T., 1995. Effects of Hurricane Andrew on coastal and interior forests of southern Florida. J. Coast. Res. 21, 111–144.

Armentano, Thomas V, Doren, R.F., Platt, W.J., Mullins, T., 1995. Effects of hurricane Andrew on coastal and interior forests of southern Florida: overview and synthesis. J. Coast. Res. 111–144.

Bale, A.M., 2009. Fire effects and litter accumulation dynamics in a montane longleaf pine ecosystem. Masters Thesis. University of Missouri, Columbia, Missouri.

Bartlein, P.J., Anderson, K.H., Anderson, P.M., Edwards, M.E., Mock, C.J., Thompson, R.S., Webb, T., Whitlock, C., 1998. Paleoclimate simulations for North America over the past 21,000 years: features of the simulated climate and comparisons with paleoenvironmental data. Quat. Sci. Rev. 17, 549–585. https://doi.org/https://doi.org/10.1016/S0277-3791(98)00012-2

Bartram, W., 1958. The Travels of William Bartram, Naturalist's Edition. Harper, F. (Ed.). Yale University Press, New Haven, Connecticut.

Batista, W.B., Platt, W.J., 1997. An old-growth definition for southern mixed hardwood forests. USDA Forest Service, Gen. Tech. Rep. SRS-9, Asheville, North Carolina.

Behm, A.L., Duryea, M.L., Long, A.J., Zipperer, W.C., 2004. Flammability of native understory species in pine flatwood and hardwood hammock ecosystems and implications for the wildland-urban interface. Int. J. Wildl. Fire 13, 355–365. https://doi.org/https://doi.org/10.1071/WF03075

Bentley, M.L., Stallins, J.A., 2005. Climatology of cloud-to-ground lightning in Georgia, USA, 1992 - 2003. Int. J. Climatol. 25, 1979–1996. https://doi.org/10.1002/joc.1227

Bishop, D.A., Williams, A.P., Seager, R., 2019. Increased fall precipitation in the southeastern United States driven by higher-intensity, frontal precipitation. Geophys. Res. Lett. 46, 8300–8309. https://doi.org/10.1029/2019GL083177

Black, B.A., Ruffner, C.M., Abrams, M.D., 2006. Native American influences on the forest composition of the Allegheny Plateau, northwest Pennsylvania. Can. J. For. Res. 36, 1266–1275. https://doi.org/Doi 10.1139/X06-027

Bowman, K.A., Chen, X., 2022. Current standing of longleaf pine trees under climate change. J. Bot. Res. 4, 28–39. https://doi.org/10.30564/jbr.v4i1.4350

Brockway, D.G., Lewis, C.E., 1997. Long-term effects of dormant-season prescribed fire on plant community diversity, structure and productivity in a longleaf pine wiregrass ecosystem. For. Ecol. Manage. 96, 167–183. https://doi.org/https://doi.org/10.1016/S0378-1127(96)03939-4

Brose, P., Wade, D., 2002. Potential fire behavior in pine flatwood forests following three different fuel reduction techniques. For. Ecol. Manage. 163, 71–84. https://doi.org/https://doi.org/10.1016/S0378-1127(01)00528-X

Brown, L.N., 1997. Mammals of Florida. Windward Publishing Co., Miami, Florida.

Brown, R.B., Stone, E.L., Carlisle, V.W., 1990. Soils, in: Myers, R.L., Ewel, J.J. (Eds.), Ecosystems of Florida. University of Central Floridas Press, Orlando, Florida, pp. 35–69.

Brudvig, L.A., Orrock, J.L., Damschen, E.I., Collins, C.D., Hahn, P.G., Mattingly, W.B., Veldman, J.W., Walker, J.L., 2014. Land-use history and contemporary management inform an ecological reference model for longleaf pine woodland understory plant communities. PLoS One 9. https://doi.org/10.1371/journal.pone.0086604

Bryant, C.M., Kulhavy, D.L., Billings, R.F., Clarke, S.R., 2006. Characteristics of bark beetle infestations in east Texas during a period of low southern pine beetle activity. Southwest. Entomol. 31, 187–199.

Buckner, E., 2000. Summary: fire in the evolution of the eastern landscape - a timeline, in: Yaussy, D. (Ed.), Proceedings: Workshop on Fire, People, and the Central Hardwoods Landscape. USDA Forest Service, Gen. Tech. Rep. NE-274, Newton Square, Pennsylvania. https://doi.org/https://doi.org/10.2737/NE-GTR-274

Burton, H.S., Smith, F.T., 2008. Colonial Natchitoches: a Creole community on the Louisiana-Texas frontier. Texas A & M University Press, College Station, Texas.

Chen, E., Gerber, J.F., 1990. Climate, in: Myers, R.L., Ewel, J.J. (Eds.), Ecosystems of Florida. University of Central Florida Press, Orlando, Florida, pp. 11–34.

Christian, H.J., Blakeslee, R.J., Boccippio, D.J., Boeck, W.L., Buechler, D.E., Driscoll, K.T., Goodman, S.J., Hall, J.M., Koshak, W.J., Mach, D.M., Stewart, M.F., 2003. Global frequency and distribution of lightning as observed from space by the Optical Transient Detector. J. Geophys. Res. 108. https://doi.org/10.1029/2002JD002347

Clark, K.E., Chin, E., Peterson, M.N., Lackstrom, K., Dow, K., Foster, M., Cubbage, F., 2018.

Evaluating climate change planning for longleaf pine ecosystems in the Southeast United States. J. Southeast. Assoc. Fish Wildl. Agencies 5, 160–168.

Clark, P.U., Dyke, A.S., Shakun, J.D., Carlson, A.E., Clark, J., Wohlfarth, B., Mitrovica, J.X., Hostetler, S.W., McCabe, A.M., 2009. The last glacial maximum. Science 325, 710–714. https://doi.org/10.1126/science.1172873

Clarke, S.R., Riggins, J.J., Stephen, F.M., 2016. Forest management and southern pine beetle outbreaks: a historical perspective. For. Sci. 62, 166–180. https://doi.org/10.5849/forsci.15-071

CLIMAP Project Members, 1976. The surface of the ice-age Earth. Science 191, 1131–1137. https://doi.org/10.1126/science.191.4232.1131

Conner, R.N., Rudolph, D.C., 1995. Excavation dynamics and use patterns of red-cockaded woodpecker cavities: relationships with cooperative breeding, in: Kulhavy, D.L., Hooper, R.G., Costa, R. (Eds.), Red-Cockaded Woodpecker: Recovery, Ecology and Management. Austin State University, Nacogdoches, Texas, pp. 343–352.

Coulson, R.N., Klepzig, K.D., 2011. Southern pine beetle II. USDA Forest Service, Gen. Tech. Rep. SRS-140, Asheville, North Carolina.

Cowell, C.M., 1995. Presettlement piedmont forests - patterns of composition and disturbance in central Georgia. Ann. Assoc. Am. Geogr. 85, 65–83. https://doi.org/https://doi.org/10.1111/j.1467-8306.1995.tb01795.x

Crocker, T.C., 1987. Longleaf pine: a history of man and a forest. USDA Forest Service, Forestry Report F8-FR 7, Atlanta, Georgia. https://doi.org/https://doi.org/10.5962/bhl.title.85034

Custer, G., 2011. Growing season prescribed fire on the Ocala National Forest [Presentation].

Pinelands Alliance, Southampton, New Jersey.

Dai, A., 2011. Drought under global warming: a review. WIREs Clim. Chang. 2, 45–65. https://doi.org/10.1002/wcc.81

Day, G.M., 1953. The Indian as an ecological factor in the northeastern forest. Ecology 34, 329–346. https://doi.org/Doi 10.2307/1930900

Delcourt, H.R., 1987. The impact of prehistoric agriculture and land occupation on natural vegetation. Tree 2, 39–44. https://doi.org/https://doi.org/10.1016/0169-5347(87)90097-8

Delcourt, H.R., Delcourt, P.A., 1997. Pre-Columbian Native American use of fire on southern Appalachian landscapes. Conserv. Biol. 11, 1010–1014. https://doi.org/10.1046/j.1523-1739.1997.96338.x

Delcourt, H.R., Delcourt, P.A., 1985. Quaternary playnology and vegetational history of the southeastern United States, in: Bryant, V.M.J., Holloway, R.G. (Eds.), Pollen Records of the Late-Quaternary North American Sediments. American Association of Stratigraphic Palynologists Foundation, Dallas, Texas, pp. 1–37.

Delcourt, P.A., Delcourt, H.R., 1998. The influence of prehistoric human-set fires on oak-chestnut forests in the southern Appalachians. Castanea 63, 335–337.

Delcourt, P.A., Delcourt, H.R., 1984. Late Quaternary paleoclimates and biotic responses in eastern North America and the western North Atlantic Ocean. Palaeogeogr. Palaeoclimatol. Palaeoecol. 48, 263–284. https://doi.org/10.1016/0031-0182(84)90048-8

Delcourt, P.A., Delcourt, H.R., Ison, C.R., Sharp, W.E., Henderson, A.G., 1998. Forests, forest fires, and their makers. Kentucky Archeological Survey, Lexington, Kentucky.

Derr, H.J., Melder, T.W., 1969. Brown-spot resistance in longleaf pine. For. Sci. 16, 204–209. https://doi.org/https://doi.org/10.1093/forestscience/16.2.204

Dyke, A.S., Prest, V.K., 1987. Late Wisconsinan and Holocene history of the Laurentide Ice Sheet. Geol. Surv. Canada.

Earley, L.S., 2004. Looking for Longleaf: The Fall and Rise of an American Forest. The University of North Carolina Press, Chapel Hill, North Carolina.

Emanuel, K., 2005. Divine Wind—The History and Science of Hurricanes. Oxford University Press, New York. https://doi.org/https://doi.org/10.1093/oso/9780195149418.001.0001

Emery, R.K., Hart, J.L., 2020. Flammability characteristics of surface fuels in a longleaf pine (*Pinus palustris* Mill.) woodland. Fire 3, 1–18. https://doi.org/10.3390/fire3030039

Engstrom, R., 1993. Characteristic mammals and birds of longleaf pine forests, in: Hermann, S.M. (Ed.), Proceedings of the Tall Timbers Fire Ecology Conference No. 18. Tall Timbers Research Station, Tallahassee, Florida, pp. 127–138.

Estill, J.C., Cruzan, M.B., 2001. Phytogeography of rare plant species endemic to the southeastern United States. Castanea 66, 3–23.

Fagan, B.M., 1991. Ancient North America: The Archaeology of a Continent. Thames and Hudson, London.

Fenneman, N.M., Johnson, D.W., 1946. Physiographic divisions of the conterminous US [Map]. US Geological Survey, Reston, Virginia. https://doi.org/https://doi.org/10.5066/P9B1S3K8

Ferguson, J.P., 1998. Prescribed fire on the Apalachicola Ranger District: the shift from dormant season to growing season and effects on wildfire suppression, in: Pruden, T.L., Brennan, L.A. (Eds.), Fire in Ecosystem Management: Shifting the Paradigm from Suppression to Prescription, Tall Timbers Fire Ecology Conference Proceedings No. 20. Tall Timbers Research Station, Tallahassee, Florida, pp. 120–126. https://doi.org/https://doi.org/10.1046/j.1526-100x.2000.80045.x

Fesenmyer, K.A., Christensen, N.L., 2010. Reconstructing Holocene fire history in a southern Appalachian forest using soil charcoal. Ecology 91, 662–670. https://doi.org/Doi 10.1890/09-0230.1

Folkerts, G.W., Deyrup, M.A., Sisson, D.C., 1993. Arthropods associated with xeric longleaf pine habitats in the southeastern United States: a brief overview, in: Hermann, S.M. (Ed.), Tall Timbers Fire Ecology Conference Proceedings No. 18. Tall Timbers Research Station, Tallahassee, Florida, pp. 159–192.

Ford, C.R., Minor, E.S., Fox, G.A., 2010. Long-term effects of fire and fire-return interval on population structure and growth of longleaf pine (*Pinus palustris*). Can. J. For. Res. 40, 1410–1420. https://doi.org/10.1139/X10-080

Foster, H.T., Black, B., Abrams, M.D., 2004. A witness tree analysis of the effects of Native American Indians on the pre-European settlement forests in East-Central Alabama. Hum. Ecol. 32, 27–47. https://doi.org/10.1023/B:HUEC.0000015211.98991.9c

Foster, H.T., Cohen, A.D., 2007. Palynological evidence of the effects of the deerskin trade on forest fires during the eighteenth century in southeastern North America. Am. Antiq. 72, 35–51. https://doi.org/https://doi.org/10.2307/40035297

Foster, M., Peterson, M.N., Cubbage, F., McMahon, G., 2019. Evaluating natural resource planning for longleaf pine ecosystems in the Southeast United States. For. Policy Econ. 100, 142–153. https://doi.org/10.1016/j.forpol.2018.11.008

Fowler, C., Konopik, E., 2007. The history of fire in the southern United States. Hum. Ecol. Rev. 14, 165–176.

Frost, C.C., 2006. History and future of the longleaf pine ecosystem, in: Jose, S., Jokela, E.J., Miller, D.L. (Eds.), The Longleaf Pine Ecosystem. Springer, New York, pp. 9–48.

https://doi.org/10.1007/978-0-387-30687-2_2

Frost, C.C., 2000. Studies in landscape fire ecology and presettlement vegetation of the southeastern United States. Dissertation. University of North Carolina, Chapel Hill, North Carolina.

Frost, C.C., 1993. Four centuries of changing landscape patterns in the longleaf pine ecosystem, in: Hermann, S. (Ed.), Tall Timbers Fire Ecology Conference Proceedings No. 18. Tall Timbers Research Station, Tallahassee, Florida, pp. 17–44.

Gang, C., Pan, S., Tian, H., Wang, Z., Xu, R., Bian, Z., Pan, N., Yao, Y., Shi, H., 2020. Satellite observations of forest resilience to hurricanes along the northern Gulf of Mexico. For. Ecol. Manage. 472, 118243. https://doi.org/10.1016/j.foreco.2020.118243

Garren, K.H., 1943. Effects of fire on vegetation of the southeastern United States. Bot. Rev. 9, 617–654. https://doi.org/https://doi.org/10.1007/BF02872506

Gilliam, F.S., 2021. Impacts of tropical cyclones on longleaf pine ecosystems of Florida: tropical cyclogenesis, landfall frequencies, and climate change. Front. Ecol. Evol. 9, 1–15. https://doi.org/10.3389/fevo.2021.595791

Glitzenstein, J.S., Harcombe, P.A., 1988. Effects of the December 1983 tornado on forest vegetation of the big thicket, southeast Texas, U.S.A. For. Ecol. Manage. 25, 269–290. https://doi.org/10.1016/0378-1127(88)90092-8

Glitzenstein, J.S., Streng, D.R., Wade, D.D., 2003. Fire frequency effects on longleaf pine (*Pinus palustris*, P. Miller) vegetation in South Carolina and northeast Florida, USA. Nat. Areas J. 23, 22–37.

Gordon, J.S., Willis, J.L., Grala, R.K., 2020. Public and forest landowner attitudes towards longleaf pine ecosystem restoration using prescribed fire. Can. J. For. Res. 50, 917–924.

https://doi.org/10.1139/cjfr-2019-0415

Graham, A., 1999. Late Cretaceous and Cenozoic History of North American Vegetation North of Mexico. Oxford University Press, New York. https://doi.org/10.2307/3515520

Grazulis, T.P., 1982. Violent tornado climatography, 1880-1982. US Nuclear Regulatory Commision, NUREG/CR-3670, Washington, DC.

Greene, S.W., 1931. The forest that fire made. Am. For. 37, 583-584,618.

Greller, A.M., 1989. Correlation of warmth and temperateness with the distributional limits of zonal forests in eastern North America. J. Torrey Bot. Soc. 116, 145–163. https://doi.org/https://doi.org/10.2307/2997197

Guyer, C., Bailey, M.A., 1993. Amphibians and reptiles of longleaf pine communities, in: Hermann, S.M. (Ed.), Proceedings of the Tall Timbers Fire Ecology Conference No. 18. Tall Timbers Research Station, Tallahassee, Florida, pp. 139–158.

Guyette, R.P., Stambaugh, M.C., Dey, D.C., Muzika, R.M., 2012. Predicting fire frequency with chemistry and climate. Ecosystems 15, 322–335. https://doi.org/10.1007/s10021-011-9512-0

Haines, T.K., Busby, R.L., Cleaves, D.A., 2001. Prescribed burning in the South: trends, purpose, and barriers. South. J. Appl. For. 25, 149–153. https://doi.org/10.1093/sjaf/25.4.149

Hanula, J.L., Meeker, J.R., Miller, D.R., Barnard, E.L., 2002. Association of wildfire with tree health and numbers of pine bark beetles, reproduction weevils and their associates in Florida. For. Ecol. Manage. 170, 233–247. https://doi.org/https://doi.org/10.1016/S0378-1127(01)00752-6

Harcombe, P.A., Glitzenstein, J.S., Knox, R.G., Orzell, S.L., Bridges, E.L., 1993. Vegetation of the longleaf pine region of the West Gulf Coastal Plain, in: Hermann, S.M. (Ed.), Proceedings of the Tall Timbers Fire Ecology Conference No. 18. Tall Timbers Research Station, Tallahassee, Florida, pp. 83–104.

Hardin, E.D., White, D.L., 1989. Rare vascular plant taxa associated with wiregrass (*Aristida stricta*) in the southeastern United States. Nat. Areas J. 9, 234–245.

Harley, G.L., Grissino-Mayer, H.D., Horn, S.P., 2013. Fire history and forest structure of an endangered subtropical ecosystem in the Florida Keys, USA. Int. J. Wildl. Fire 22, 394–404. https://doi.org/10.1071/WF12071

Haywood, J.D., Harris, F.L., Grelen, H.E., Pearson, H.A., 2001. Vegetative response to 37 years of seasonal burning on a Louisiana longleaf pine site. South. J. Appl. For. 25, 122–130. https://doi.org/10.1093/sjaf/25.3.122

He, T., Pausas, J.G., Belcher, C.M., Schwilk, D.W., Lamont, B.B., 2012. Fire-adapted traits of Pinus arose in the fiery Cretaceous. New Phytol. 194, 751–759. https://doi.org/10.1111/j.1469-8137.2012.04079.x

Henderson, J.P., 2006. Dendroclimatological analysis and fire history of longleaf pine (*Pinus palustris* Mill.) in the Atlantic and Gulf Coastal Plain. Dissertation. University of Tennessee, Knoxville, Tennessee.

Heyward, F., 1939. The relation of fire to stand composition of longleaf pine forests. Ecology 20, 287–304. https://doi.org/https://doi.org/10.2307/1930747

Hicks Jr, R.R., 2000. Humans and fire: a history of the central hardwoods, in: Yaussy, D. (Ed.), Proceedings: Workshop on Fire, People, and the Central Hardwoods Landscape. USDA Forest Service, Gen. Tech. Rep. NE-274, Newton Square, Pennsylvania, pp. 3–18. https://doi.org/https://doi.org/10.2737/NE-GTR-274

Ho, F.P., Su, J.C., Hanevich, K.L., Smith, R.J., Richards, F.P., 1987. Hurricane climatology for the Atlantic and Gulf Coasts of the United States. USDC, National Oceanic and Atmospheric Administration, National Weather Service, NOAA Technical Report NWS 38, Silver Spring, Maryland.

Hodanish, S., Sharp, D., Collins, W., Paxton, C., Orville, R.E., 1997. A 10-yr monthly lightning climatology of Florida : 1986-95. Weather Forecast. 12, 439–448. https://doi.org/https://doi.org/10.1175/1520-0434(1997)012%3C0439:AYMLCO%3E2.0.CO;2

Hodges, J.D., Elam, W.W., Watson, W.F., 1977. Physical properties of the oleoresin system of the four major southern pines. Can. J. For. Res. 4, 88–100. https://doi.org/10.1139/x77-067

Hodges, J.D., Elam, W.W., Watson, W.F., Nebeker, E.T., 1979. Oleoresin characteristics and susceptibilitty of four southern pines to souther beetle (Coleoptera: Scolytidae) attacks. Can. Entomol. 889–896. https://doi.org/https://doi.org/10.4039/Ent111889-8

Holman, J.A., 1991. North American Peistocene herpetological stability and its impact on interpretation of modern herpetofaunas: an overview. Ill State Mus Sci Pap 23, 227–235.

Huffman, J.M., 2006. Historical fire regimes in southeastern pine savannas. Dissertation, Louisiana State University, Baton Rouge, Louisiana.

Huffman, J.M., Platt, W.J., 2014. Fire history of the Avon Park Air Force Range: evidence from tree-rings. Louisiana State University, Baton Rouge, Louisiana.

Huffman, J.M., Platt, W.J., Grissino-Mayer, H., Boyce, C.J., 2004. Fire history of a barrier island slash pine (*Pinus elliottii*) savanna. Nat. Areas J. 24, 258–268.

Humphrey, S.R., 1992. Recently extinct Goff’s pocket gopher, Geomys pinetis goffi, in: Humphrey, S.R. (Ed.), Rare and Endangered Biota of Florida, Vol. 1. University Press of

Florida, Gainesville, Florida, pp. 11–18.

Jackson, Dale R, Milstrey, E.G., 1989. The fauna of gopher tortoise burrows, in: Diemer, J.E., Jackson, D. R., Landers, J.L., Layne, J.N., Wood, D.A. (Eds.), Gopher Tortoise Relocation Symposium Proceedings. Florida Game and Fresh Water Fish Commission, Nongame Wildlife Program, Technical Report No. 5, Gainesville, Florida, pp. 86–98.

Jackson, S.., Webb, R.S., Anderson, K.., Overpeck, J.., Webb, T., Williams, J.W., Hansen, B.C.S., 2000. Vegetation and environment in eastern North America during the last glacial maximum. Quat. Sci. Rev. 19, 489–508. https://doi.org/https://doi.org/10.1016/S0277-3791(99)00093-1

Johnson, A.S., Hale, P.E., 2002. The historical foundations of prescribed burning for wildlife: a southeastern perspective, in: Ford, W.M., Russell, K.R., Moorman, C.E. (Eds.), The Role of Fire in Nongame Wildlife Management and Community Restoration: Traditional Uses and New Directions Proceedings of a Special Workshop. USDA Forest Service, Gen. Tech. Rep. NE-288, Newtown Square, Pennsylvania, pp. 11–23. https://doi.org/https://doi.org/10.2737/NE-GTR-288

Johnson, E.D., Spector, T., Hiers, J.K., Pearson, D., Varner, J.M., 2018. Defining old-growth stand characteristics in fragmented natural landscapes: a case study of old-growth pine in Florida (USA) State Parks. Nat. Areas J. 38, 88–98.

Jones, R.A., Jackson, S.T., 2012. Did Native American fires maintain the longleaf pine ecosystem? A paleoecological approach, in: 97th Ecological Society of America Annual Meeting. Portland, Oregon.

Kane, J.M., Varner, J.M., Hiers, J.K., 2008. The burning characteristics of southeastern oaks: discriminating fire facilitators from fire impeders. For. Ecol. Manage. 256, 2039–2045.

https://doi.org/10.1016/j.foreco.2008.07.039

Kay, C.E., 2000. Native burning in western North America: implications for hardwood forest management, in: Yaussy, D. (Ed.), Proceedings: Workshop on Fire, People, and the Central Hardwoods Landscape. USDA Forest Service, Gen. Tech. Rep. NE-274, Newton Square, Pennsylvania, pp. 19–27. https://doi.org/https://doi.org/10.2737/NE-GTR-274

Keim, B.D., Muller, R.A., Stone, G.W., 2007. Spatiotemporal patterns and return periods of tropical storm and hurricane strikes from Texas to Maine. J. Clim. 20, 3498–3509. https://doi.org/10.1175/JCLI4187.1

Kenney, G., Staudhammer, C.L., Wiesner, S., Brantley, S.T., Bigelow, S.W., Starr, G., 2021. Hurricane Michael altered the structure and function of longleaf pine woodlands. J. Geophys. Res. Biogeosciences 126. https://doi.org/10.1029/2021JG006452

Kiester, A.R., 1971. Species density of North American amphibians and reptiles. Syst. Zool. 20, 127–137. https://doi.org/https://doi.org/10.2307/2412053

Klaus, N., 2019. Fire history of a Georgia montane longleaf pine (*Pinus palustris*) community. Georg. J. Sci. 77, 1–13.

Kocis, D.L., 2012. Reconstruction of fire history in the National Key Deer Refuge, Monroe County, Florida, U.S.A.: the Palmetto Pond macroscopic charcoal record. Masters Thesis. University of Tennessee, Knoxville, Tennessee.

Komarek, R.O.Y., 1963. Fire and the changing wildlife habitat, in: Proceedings of the 2nd Tall Timbers Fire Ecology Conference. Tall Timbers Research Station, Tallahassee, Florida, pp. 35–44.

Komarek, E. V., 1974. Effects of fire on temperate forests and related ecosystems: southeastern United States., in: Kozlowski, T.T., Ahlgren, C.E. (Eds.), Fire and Ecosystems. Academic

Press, New York, pp. 251–277.

Komarek, E. V, 1968. Lightning and lightning fires as ecological forces, in: Proceedings of 8th Tall Timbers Fire Ecology Conference. Tall Timbers Research Station, Tallahassee, Florida, pp. 169–197.

Komarek, E. V, 1964. The natural history of lightning, in: Tall Timbers Fire Ecology Conference Proceedings No. 3. Tall Timbers Research Station, Tallahassee, Florida, pp. 139–183.

Kruk, M.C., Gibney, E.J., Levinson, D.H., Squires, M., 2010. A climatology of inland winds from tropical cyclones for the eastern United States. J. Appl. Meteorol. Climatol. 49, 1538–1547. https://doi.org/10.1175/2010JAMC2389.1

Krusac, D.L., Dabney, J.M., Petrick, J.J., 1995. An ecological approach to recovering the red-cockaded woodpecker on southern national forests, in: Kulhavy, D.L., Hooper, R.G., Costa, R. (Eds.), Red-Cockaded Woodpecker: Recovery, Ecology and Management. Stephen F. Austin State University, College of Forestry, Center for Applied Studies in Forestry, Nacogdoches, Texas, pp. 61–66.

Kunkel, K.E., Stevens, L.E., Stevens, S.E., Sun, L., Janssen, E., Wuebbles, D., Konrad, C.E., Fuhrman, C.M., Keim, B.D., Dobson, J.G., 2013. Regional climate trends and scenarios for the U.S. National Climate Assessment: Part 2. Climate of the Southeast U.S. USDC National Oceanic and Atmospheric Administration, NOAA Technical Report NESDIS 142-2, Washington, DC.

Lafon, C.W., 2010. Fire in the American South: vegetation impacts, history, and climatic relations. Geogr. Compass 4, 919–944. https://doi.org/https://doi.org/10.1111/j.1749-8198.2010.00363.x

LaMoreaux, H.K., Brook, G.A., Knox, J.A., 2009. Late Pleistocene and Holocene environments of the southeastern United States from the stratigraphy and pollen content of a peat deposit on the Georgia Coastal Plain. Palaeogeogr. Palaeoclimatol. Palaeoecol. 280, 300–312. https://doi.org/DOI 10.1016/j.palaeo.2009.06.017

Lawson, J., 1709. A new voyage to Carolina. University of North Carolina, Chapel Hill, North Carolina.

Layne, J.N., Jackson, R.J., 1994. Burrow use by the Florida Mouse (Podomys floridanus) in south-central Florida. Am. Midl. Nat. 131, 17–23. https://doi.org/https://doi.org/10.2307/2426604

Liu, K.B., Lu, H.Y., Shen, C.M., 2008. A 1200-year proxy record of hurricanes and fires from the Gulf of Mexico coast: testing the hypothesis of hurricane-fire interactions. Quat. Res. 69, 29–41. https://doi.org/DOI 10.1016/j.yqres.2007.10.011

Loomis, J.B., Bair, L.S., Gonzalez-Caban, A., 2001. Prescribed fire and public support: knowledge gained, attitudes changed in Florida. J. For. 99, 18–22. https://doi.org/https://doi.org/10.1093/jof/99.11.18

Lorimer, C.G., 2001. Historical and ecological roles of disturbance in eastern North American forests: 9,000 years of change. Wildl. Soc. Bull. 29, 425–439. https://doi.org/10.2307/3784167

Lucash, M.S., Weiss, S., Duveneck, M.J., Scheller, R.M., 2022. Managing for red-cockaded woodpeckers is more complicated under climate change. J. Wildl. Manage. 1–17. https://doi.org/10.1002/jwmg.22309

Maliakal, S.K., Menges, E.S., Denslow, J.S., 2000. Community composition and regeneration of Lake Wales Ridge wiregrass flatwoods in relation to time-since-fire. J. Torrey Bot. Soc. 127, 125–138. https://doi.org/10.2307/3088690

Mann, R.B., 2000. Fire in the central hardwoods: Why are we concerned?, in: Yaussy, D. (Ed.), Proceedings: Workshop on Fire, People, and the Central Hardwoods Landscape. USDA Forest Service, Gen. Tech. Rep. NE-274, Newton Square, Pennsylvania, pp. 1–2. https://doi.org/https://doi.org/10.2737/NE-GTR-274

Margold, M., Stokes, C.R., Clark, C.D., 2018. Reconciling records of ice streaming and ice margin retreat to produce a palaeogeographic reconstruction of the deglaciation of the Laurentide Ice Sheet. Quat. Sci. Rev. 189, 1–30. https://doi.org/10.1016/j.quascirev.2018.03.013

Martin, P.S., 1967. Prehistoric overkill, in: Martin, P.S., Wright, H.E. (Eds.), Pleistocene Extinctions. Yale University Press, New Haven, Connecticut, pp. 75–120.

Martinson, S., Hofstetter, R.W., Ayres, M.P., 2007. Why does longleaf pine have low susceptibility to southern pine beetle? Can. J. For. Res. 37, 1966–1977. https://doi.org/10.1139/X07-066

Matthews, J.M., Hinchee, J., Guldin, J.M., 2020. Restoration of longleaf pine in the southern region of the U.S. Forest Service: an overview of the million-acre challenge, in: Bragg, Don C.; Koerth, Nancy E.; Holley, A.G. (Ed.), Proceedings of the 20th Biennial Southern Silvicultural Research Conference. USDA Forest Service, e–Gen. Tech. Rep. SRS–253, Asheville, North Carolina, pp. 112–119.

Matusick, G., Eckhardt, L.G., Somers, G.L., 2010. Susceptibility of longleaf pine roots to infection and damage by four root-inhabiting ophiostomatoid fungi. For. Ecol. Manage. 260, 2189–2195. https://doi.org/10.1016/j.foreco.2010.09.018

McCay, D.H., 2000. Effects of chronic human activities on invasion of longleaf pine forests by sand pine. Ecosystems 3, 283–292. https://doi.org/DOI 10.1007/s100210000026

McIntyre, R.K., Guldin, J.M., Ettel, T., Ware, C., Jones, K., 2018. Restoration of longleaf pine in the southern United States: a status report, in: Kirschman, J.E. (Ed.), Proceedings of the 19th Biennial Southern Silvicultural Research Conference. USDA Forest Service, e-Gen. Tech. Rep. SRS-234, Asheville, North Carolina, pp. 297–302. https://doi.org/https://doi.org/10.2737/SRS-GTR-234

Means, D.B., 2006. Vertebrate faunal diversity of longleaf pine ecosystems, in: Jose, S., Jokela, E.J., Miller, D.L. (Eds.), The Longleaf Pine Ecosystem: Ecology, Silviculture, and Restoration. Springer, New York, pp. 157–213. https://doi.org/10.1007/978-0-387-30687-2

Meltzer, D.J., 2003. Peopling of North America. Dev. Quat. Sci. 1, 539–563. https://doi.org/10.1016/S1571-0866(03)01026-1

Melvin, M.A., 2020. 2020 national prescribed fire use report. Coalition of Prescribed Fire Councils, Inc., Technical Bulletin 04-20, Newton, Georgia.

Melvin, M.A., 2012. 2012 national prescribed fire use survey report. Coalition of Prescribed Fire Councils, Inc., Tech. Rep. 01-12, Newton, Georgia.

Mitchener, L.J., Parker, A.J., 2005. Climate, lightning, and wildfire in the national forests of the southeastern United States: 1989-1998. Phys. Geogr. 26, 147–162. https://doi.org/Doi 10.2747/0272-3646.26.2.147

Mohr, C.T., 1896. The timber pines of the southern United States. USDA, Division of Forestry, Bulletin No. 13, Washington DC.

Mutch, R.W., 1970. Wildland fires and ecosystems - a hypothesis. Ecology 51, 1046–1051. https://doi.org/10.2307/1933631

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature 403, 853–858.

https://doi.org/10.1080/21564574.1998.9650003

Myers, R.K., van Lear, D.H., 1998. Hurricane-fire interactions in coastal forests of the south: a review and hypothesis. For. Ecol. Manage. 103, 265–276. https://doi.org/Doi 10.1016/S0378-1127(97)00223-5

Mylavarapu, R., Mitchell, C.C., Savoy, H.J., 2014. Soils of the southeastern US, in: Sikora, F.J., Moore, K.P. (Eds.), Soil Test Methods From the Southeastern United States. Clemson University, K.P. Moore Agricultural Service Laboratory, Southern Cooperative Series Bulletin No. 419, Clemson, South Carolina, pp. 2–10.

National Oceanic and Atmospheric Administration. Climate at a glance: city time series. Accessed December 5, 2022. https://www.ncei.noaa.gov/access/monitoring/climate-at-a-glance/city/time-series.

Noss, R.F., Platt, W.J., Sorrie, B.A., Weakley, A.S., Means, D.B., Costanza, J., Peet, R.K., 2015. How global biodiversity hotspots may go unrecognized: lessons from the North American Coastal Plain. Divers. Distrib. 21, 236–244. https://doi.org/10.1111/ddi.12278

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/Doi 10.1641/B580207

Ojha, S.K., Dimov, L.D., Tadesse, W., 2021. Growth, proportion, and distribution pattern of longleaf pine across southeastern forests and disturbance types: A change assessment for the period 1997-2018. PLoS One 16, 1–24. https://doi.org/10.1371/journal.pone.0245218

Orville, R.E., 1991. Lightning ground flash density in the contiguous United States - 1989. Mon. Weather Rev. 119, 573–577. https://doi.org/https://doi.org/10.1175/1520-0493(1991)119%3C0573:LGFDIT%3E2.0.CO;2

Oswalt, C.M., Cooper, J.A., Brockway, D.G., Brooks, H.W., Walker, J.L., Connor, K.F., Oswalt, S.N., Conner, R.C., 2012. History and current condition of longleaf pine in the southern United States. USDA Forest Service, Gen. Tech. Rep. SRS–166, Asheville, North Carolina.

Otrosina, W.J., Bannwart, D., Roncadori, R.W., 1999. Root-infecting fungi associated with a decline of longleaf pine in the southeastern United States. Plant Soil 217, 145–150. https://doi.org/10.1023/a:1004645115446

Otto, J.S., Anderson, N.E., 1982. Agricultural history slash-and-burn cultivation in the Highlands South: a problem in comparative agricultural history. Comp. Stud. Soc. Hist. 24, 131–147. https://doi.org/https://doi.org/10.1017/S0010417500009816

Outcalt, K.W., 2000. Occurrence of fire in longleaf pine stands in the southeastern United States, in: Moser, K.W., Moser, C.F. (Eds.), Tall Timbers Fire Ecology Conference Proceedings No. 21. Tall Timbers Research Station, Tallahassee, Florida, pp. 1781–82.

Outcalt, K.W., 1998. Needs and opportunities for longleaf pine ecosystem restoration in Florida, in: Kush, J.S. (Ed.), Ecological Restoration and Regional Conservation Strategies. Longleaf Alliance, Report. No. 3, Andalusia, Alabama, pp. 38–43.

Outcalt, K.W., Brockway, D.G., 2010. Structure and composition changes following restoration treatments of longleaf pine forests on the Gulf Coastal Plain of Alabama. For. Ecol. Manage. 259, 1615–1623. https://doi.org/10.1016/j.foreco.2010.01.039

Outcalt, K.W., Sheffield, R.M., 1996. The longleaf pine forest: trends and current conditions. USDA Forest Service, Res. Bull. SRS-9, Asheville, North Carolina.

Patterson, W.A., Edwards, K.J., Maguire, D.J., 1987. Microscopic charcoal as a fossil indicator of fire. Quat. Sci. Rev. 6, 3–23. https://doi.org/https://doi.org/10.1016/0277-3791(87)90012-6

Peet, R.K., 2006. Ecological classification of longleaf pine woodlands, in: Jose, S., Jokela, E.J., Miller, D.L. (Eds.), The Longleaf Pine Ecosystem: Ecology, Silviculture, and Restoration. Springer, New York, pp. 51–93. https://doi.org/10.1007/978-0-387-30687-2

Peet, R.K., Allard, D.J., 1993. Longleaf pine vegetation of the southern Atlantic and eastern Gulf coast regions: a preliminary classification, in: Hermann, S.M. (Ed.), Tall Timbers Fire Ecology Conference Proceedings No. 18. Tall Timbers Research Station, Tallahassee, Florida, pp. 45–81. https://doi.org/10.1086/284833

Pinchot, G., Ashe, W.W., 1897. Timber Trees and Forests of North Carolina. M.I. & J.C. Stewart, Public Printers, Winston, North Carolina. https://doi.org/https://doi.org/10.5962/bhl.title.56350

Platt, W.J., 1999. Southeastern pine savannas, in: Andserson, R.C., Fralish, J.S., Baskin, J.M. (Eds.), Savannas, Barrens, and Rock Outcrop Plant Communities of North America. Cambridge University Press, Cambridge, pp. 23–51. https://doi.org/https://doi.org/10.1017/CBO9780511574627

Platt, W.J., Ellair, D.P., Huffman, J.M., Potts, S.E., Beckage, B., 2016. Pyrogenic fuels produced by savanna trees can engineer humid savannas. Ecol. Monogr. 86, 352–372. https://doi.org/https://doi.org/10.1002/ecm.1224

Platt, W.J., Rathburn, S.L., 1993. Dynamics of an old growth longleaf pine population, in: Hermann, S.M. (Ed.), Tall Timbers Fire Ecology Conference Proceedings No. 18. Tall Timbers Research Station, Tallahassee, Florida, pp. 275–297.

Portmann, R.W., Solomon, S., Hegerl, G.C., 2009. Spatial and seasonal patterns in climate change, temperatures, and precipitation across the United States. Proc. Natl. Acad. Sci. U. S. A. 106, 7324–7329. https://doi.org/10.1073/pnas.0808533106

Powell, E.J., Keim, B.D., 2015. Trends in daily temperature and precipitation extremes for the southeastern United States: 1948-2012. J. Clim. 28, 1592–1612. https://doi.org/10.1175/JCLI-D-14-00410.1

Prunty, M.C., 1965. Some geographic views of the role of fire in settlement processes in The South, in: Tall Timbers Fire Ecology Conference Proceedings No. 4. Tall Timbers Research Station, Tallahassee, Florida, pp. 161–168.

Puhlick, J.J., Brantley, S.T., O'Halloran, T.L., Clay, L., Klepzig, K.D., 2022. Perspectives: carbon markets might incentivize poorer ecological outcomes in longleaf pine ecosystems. For. Ecol. Manage. 520, 120421. https://doi.org/10.1016/j.foreco.2022.120421

Pyne, S.J., 1982. Fire in America. Princeton University Press, Princeton, New Jersey.

Riebold, R.J., 1971. The early history of wildfires and prescribed burning, in: Prescribed Burning Symposium Proceedings. USDA Forest Service, Asheville, North Carolina, pp. 11–20.

Rosche, S.B., Moorman, C.E., Deperno, C.S., Jones, J.G., 2017. Effects of growing season fire on northern bobwhite nest site selection and survival, in: National Quail Symposium Proceedings. https://doi.org/https://doi.org/10.7290/nqsp08mwgx

Rother, M.T., Huffman, J.M., Guiterman, C.H., Robertson, K.M., Jones, N., 2020. A history of recurrent, low-severity fire without fire exclusion in southeastern pine savannas, USA. For. Ecol. Manage. 475, 118406. https://doi.org/10.1016/j.foreco.2020.118406

Rother, M.T., Huffman, J.M., Harley, G.L., Platt, W.J., Jones, N., Robertson, K.M., Orzell, S.L., 2018. Cambial phenology informs tree-ring analysis of fire seasonality in coastal plain pine savannas. Fire Ecol. 14, 164–185. https://doi.org/10.4996/fireecology.140116418

Rudolph, D.C., Conner, R.N., 1991. Cavity tree selection by red-cockaded woodpeckers in relation to tree age. Wilson Bull. 103, 458–467.

Samuelson, L.J., Stokes, T.A., Ramirez, M.R., Mendonca, C.C., 2019. Drought tolerance of a

*Pinus palustris* plantation. For. Ecol. Manage. 451, 117557. https://doi.org/10.1016/j.foreco.2019.117557

Scharf, E.A., 2010. Archaeology, land use, pollen and restoration in the Yazoo Basin (Mississippi, USA). Veg. Hist. Archaeobot. 19, 159–175. https://doi.org/DOI 10.1007/s00334-010-0241-7

Schmidtling, R.C., 2003. The southern pines during the Pleistocene. Acta Hortic. 615, 203–209. https://doi.org/https://doi.org/10.17660/ActaHortic.2003.615.19

Schmidtling, R.C., Hipkins, V., 1998. Genetic diversity in longleaf pine (Pinus palustris): influence of historical and prehistorical events. Can. J. For. Res. 28, 1135–1145. https://doi.org/https://doi.org/10.1139/x98-102

Schultz, R., 1997. Loblolly pine: the ecology and culture of loblollv pine (*Pinus taeda* L.). USDA Forest Service, Agricultural Handbook 713, New Orleans, Louisiana.

Sheehan, T.N., Klepzig, K.D., 2022. Arthropods and fire within the biologically diverse longleaf pine ecosystem. Ann. Entomol. Soc. Am. 115, 69–94. https://doi.org/10.1093/aesa/saab037

Simpson, R.H., Lawrence, M.B., 1971. Atlantic hurricane frequencies along the U.S. coastline. USDC National Oceanic and Atmospheric Administration, NOAA Technical Memorandum NWS TM SR-58, Coral Gables, Florida.

Slobodin, S., 2001. Western Beringia at the end of the ice age. Arctic Anthropol. 38, 31–47.

Smith, J., 1910. Travels and Works of Captain John Smith. Arber, E. (Ed.). John Grant, Edinburgh.

Sobel, A.H., Camargo, S.J., Hall, T.M., Lee, C., Tippett, M.K., Wing, A.A., 2016. Human influence on tropical cyclone intensity. Science 353, 242–246. https://doi.org/https://doi.org/10.1126/science.aaf6574

South, D.B., Buckner, E.R., 2004. Population growth and the decline of natural southern yellow pine forests, in: Rauscher, H. Michael; Johnsen, K. (Ed.), Southern Forest Science: Past, Present, and Future. USDA Forest Service, Gen. Tech. Rep. SRS 75, Asheville, North Carolina, pp. 307–317. https://doi.org/https://doi.org/10.2737/SRS-GTR-75

Sparks, J.C., Masters, R.E., Engle, D.M., Bukenhofer, G.A., 2002. Season of burn influences fire behavior and fuel consumption in restored shortleaf pine-grassland communities. Restor. Ecol. 10, 714–722. https://doi.org/https://ui.adsabs.harvard.edu/link_gateway/2002ResEc..10..714S/doi:10.1046/j.1526-100X.2002.01052.x

Spencer, J., Jones, K.B., Gamble, D.W., Benedetti, M.M., Taylor, A.K., Lane, C.S., 2017. Late-Quaternary records of vegetation and fire in southeastern North Carolina from Jones Lake and Singletary Lake. Quat. Sci. Rev. 174, 33–53. https://doi.org/10.1016/j.quascirev.2017.09.001

Springer, G.S., White, D.M., Rowe, H.D., Hardt, B., Mihimdukulasooriya, L.N., Cheng, H., Edwards, R.L., 2010. Multiproxy evidence from caves of Native Americans altering the overlying landscape during the late Holocene of east-central North America. Holocene 20, 275–283. https://doi.org/Doi 10.1177/0959683609350395

Stambaugh, M.C., Guyette, R.P., Marschall, J.M., 2011. Longleaf pine (*Pinus palustris* Mill.) fire scars reveal new details of a frequent fire regime. J. Veg. Sci. 22, 1094–1104. https://doi.org/10.1111/j.1654-1103.2011.01322.x

Stanturf, J.A., Wade, D.D., Waldrop, T.A., Kennard, D.K., Achtemeier, G.L., 2002. Background paper: fire in southern forest landscapes, in: Wear, D.N., Greis, J.G. (Eds.), Southern Forest Resource Assessment. USDA Forest Service, Gen. Tech. Rep. SRS-53, Asheville, North

Carolina, pp. 607–630. https://doi.org/https://doi.org/10.2737/SRS-GTR-53

Stein, B.A., Kutner, L.S., Adams, J.S., 2000. Precious heritage: the status of biodiversity in the United States. Oxford University Press, New York.

Stober, J., Merry, K., Bettinger, P., 2020. Analysis of fire frequency on the Talladega National Forest, USA, 1998-2018. Int. J. Wildl. Fire 29, 943–949. https://doi.org/10.1071/WF20022

Stoddard, H.L., 1931. The Bobwhite Quail: Its Habits, Preservation and Increase. Charles Scribner's Sons, New York.

Stout, J.I., Marion, W.R., 1993. Pine flatwoods and xeric pine forersts of the southern (lower) coastal plain, in: Martin, W.H., Boyce, S.G., Echternacht, A.C. (Eds.), Biodiversity of the Southeastern United States: Lowland Terrestrial Communities1. John Wiley & Sons, Inc., New York.

Tanner, B., Douglas, M., Greenberg, C.H., Chamberlin, J., Styers, D., 2018. A macroscopic charcoal and multiproxy record from peat recovered from depression marshes in longleaf pine sandhills, Florida, USA. Quaternary 1, 1–20. https://doi.org/10.3390/quat1030025

Tebeau, C.W., 1980. A History of Florida (revised). University of Miami Press, Miami, Florida.

Thornton, R., 2002. Health, disease, and demography, in: Deloria, P.J., Salisbury, N. (Eds.), A Companion to American Indian History. pp. 68–84. https://doi.org/10.1002/9780470996461

Toribio-Diaz, M.H., Carr, S., Putz, F.E., 2019. Pine savanna plant community disassembly after fire suppression. J. Veg. Sci. 0–3. https://doi.org/10.1111/jvs.12843

Trani-Griep, M.K., 2002. Maintaining species in the south, in: Wear, D.N., Greis, J.G. (Eds.), Southern Forest Resource Assessment. USDA Forest Service, Gen. Tech. Rep. SRS-53, Asheville, North Carolina, pp. 113–150. https://doi.org/https://doi.org/10.2737/SRS-GTR-53

US Fish and Wildlife Service, 2003. Recovery Plan for the Red-Cockaded Woodpecker (*Picoides borealis*) Second Revision. US Fish and Wildlife Service, Atlanta, Georgia.

Van Balen, J.B., Doerr, P.D., 1978. The relationship of understory vegetation to red-cockaded woodpecker activity, in: Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies. pp. 82–92.

Van Lear, D.H., Carroll, W.D., Kapeluck, P.R., Johnson, R., 2005. History and restoration.of the longleaf pine-grassland ecosystem: implications for species at risk. For. Ecol. Manage. 211, 150–165. https://doi.org/DOI 10.1016/j.foreco.2005.02.014

Vasil'ev, S.A., 2001. The final Paleolithic in northern Asia: lithic assemblage diversity and explanatory models. Arctic Anthropol. 38, 3–30.

Wade, D.D., Brock, B.L., Brose, P.H., Grace, J.B., Hoch, G.A., Patterson III, W.A., 2000. Fire in eastern ecosystems, in: Brown, J.K., Smith, J.K. (Eds.), Wildland Fire in Ecosystems: Effects of Fire on Flora. USDA Forest Service, Gen. Tech. Rep. RMRS-GTR-42 Vol. 2, Ogden, Utah, pp. 53–96. https://doi.org/https://doi.org/10.2737/RMRS-GTR-42-V2

Wade, D.D., Lunsford, J.D., 1989. A guide for prescribed fire in southern forests. USDA Forest Service, Tech. Pub. R8-TP 11, Atlanta, Georgia.

Wahlenberg, W.G., 1946. Longleaf Pine: Its Use, Ecology, Regeneration, Protection, Growth, and Management, 1st ed. Charles Lathrop Pack Forestry Foundation, Washington, DC.

Wakeley, P.C., 1954. Planting the southern pines. USDA Forest Service, Agricultural Monograph No. 18, Washington, DC.

Waldrop, T.A., Van Lear, D.H., Lloyd, F.T., Harms, W.R., 1987. Long-term studies of prescribed burning in loblolly pine forests of the Southeastern Coastal Plain. USDA Forest Service, Gen. Tech. Rep. SE-45, Asheville, North Carolina.

https://doi.org/https://doi.org/10.2737/SE-GTR-45

Waldrop, T.A., White, D.L., Jones, S.M., 1992. Fire regimes for pine grassland communities in the southeastern United States. For. Ecol. Manage. 47, 195–210. https://doi.org/https://doi.org/10.1016/0378-1127(92)90274-D

Walker, J., Peet, R.K., 1984. Composition and species diversity of pine-wiregrass savannas of the Green Swamp, North Carolina. Vegetatio 55, 163–179. https://doi.org/https://doi.org/10.1007/978-94-009-5526-4_20

Wall, W.A., Hohmann, M.G., Just, M.G., Hoffmann, W.A., 2021. Characterizing past fire occurrence in longleaf pine ecosystems with the mid-infrared burn index and a random forest classifier. For. Ecol. Manage. 500, 119635. https://doi.org/10.1016/j.foreco.2021.119635

Walsh, K.J.E., Mcbride, J.L., Klotzbach, P.J., Balachandran, S., Camargo, S.J., Holland, G., Knutson, T.R., Kossin, J.P., Lee, T., 2016. Tropical cyclones and climate change. WIREs Clim. Chang. 7. https://doi.org/10.1002/wcc.371

Ward, J.D., Mistretta, P.A., 2006. Impact of pests on forest health, in: Wear, D.N., Greis, J.G. (Eds.), Southern Forest Resource Assessment. USDA Forest Service, Gen. Tech. Rep. SRS-53, Asheville, North Carolina, pp. 403–428. https://doi.org/https://doi.org/10.2737/SRS-GTR-53

Ware, S., Frost, C.C., Doerr, P.D., 1993. Southern mixed hardwood forest: the former longleaf pine forest, in: Martin, W.H., Boyce, S.G., Echternacht, A.C. (Eds.), Biodiversity of the Southeastern United States: Lowland Terrestrial Communities. John Wiley & Sons, Inc, New York.

Waters, C.G., 2020. The historic fire return interval and the ecological effects of fire suppression on montane longleaf pine dominated ecosystems in northwestern Georgia . Masters Thesis. Kennesaw State University, Kennesaw, Georgia.

Watts, W.A., 1980. Late-Quaternary vegetation history at White Pond on the inner coastal plain of South Carolina. Quat. Res. 13, 187–199. https://doi.org/10.1016/0033-5894(80)90028-9

Watts, W.A., 1971. Postglacial and interglacial vegetation history of southern Georgia and central Florida. Ecology 52, 676–690. https://doi.org/https://doi.org/10.2307/1934159

Watts, W.A., 1970. The full-glacial vegetation of northwestern Georgia. Ecology 51, 17–33. https://doi.org/https://doi.org/10.2307/1933597

Watts, W.A., 1969. A pollen diagram from Mud Lake, Marion County, north-central Florida. Geol. Soc. Am. Bull. 80, 631–642. https://doi.org/https://doi.org/10.1130/0016-7606(1969)80[631:APDFML]2.0.CO;2

Watts, W.A., Hansen, B.C.S., Grimm, E.C., 1992. Camel Lake: a 40 000-yr record of vegetational and forest history from northwest Florida. Ecology 73, 1056–1066. https://doi.org/https://doi.org/10.2307/1940180

Webb, T., Bartlein, P.J., Kutzbach, J.E., 1987. Climatic change in eastern North America during the past 18,000 years: comparisons of pollen data with model results, in: Ruddiman, W.F., Wright Jr., H.E. (Ed.), The Geology of North America: North America and Adjacent Oceans during the Last Deglaciation. The Geological Society of America, Boulder, Colorado, pp. 447–462. https://doi.org/https://doi.org/10.1130/DNAG-GNA-K3.447

Wells, O.O., Switzer, G.L., Schmidtling, R.C., 1991. Geographic variation in Mississppi loblolly pine and sweetgum. Silvae Genet. 40, 105–119.

West, D.N., 2007. Late holocene charcoal stratigraphy and modern charcoal deposition in the pine rocklands of Great Abaco Island, the Bahamas. Masters Thesis. University of

Tennessee, Knoxville, Tennessee.

White, C.R., Harley, G.L., 2016. Historical fire in longleaf pine (*Pinus palustris*) forests of south Mississippi and its relation to land use and climate. Ecosphere 7. https://doi.org/10.1002/ecs2.1458

White, D.L., Waldrop, T.A., Jones, S.M., 1991. Forty years of prescribed burning on the Santee Fire Plots: effects on understory vegetation. USDA Forest Service, Gen. Tech. Rep. SE-69, Asheville, North Carolina.

White, D.M., 2007. Reconstruction and analysis of Native American land use during the Late Holocene. Masters Thesis. Ohio University, Athens, Ohio.

Whitehead, D.R., 1973. Late-Wisconsin vegetational changes in unglaciated eastern North America. Quat. Res. 3, 621–631. https://doi.org/10.1016/0033-5894(73)90034-3

Whitehead, D.R., Sheehan, M.C., 1985. Holocene vegetational changes in the Tombigbee River Valley, eastern Mississippi. Am. Midl. Nat. 113, 122–137. https://doi.org/Doi 10.2307/2425354

Willard, D.A., Bernhardt, C., Brown, R., Landacre, B., Townsend, P.A., 2010. Development and application of a pollen-based paleohydrologic reconstruction from the Lower Roanoke River Basin, North Carolina, USA. The Holocene 21, 305–317. https://doi.org/10.1177/0959683610378876

Willard, D.A., Bernhardt, C.E., Brooks, G.R., Cronin, T.M., Edgar, T., Larson, R., 2007. Deglacial climate variability in central florida, USA. Palaeogeogr. Palaeoclimatol. Palaeoecol. 251, 366–382. https://doi.org/DOI 10.1016/j.palaeo.2007.04.016

Willard, D.A., Bernhardt, C.E., Holmes, C.W., Landacre, B., Marot, M., 2006. Response of Everglades tree islands to environmental change. Ecol. Monogr. 76, 565–583.

https://doi.org/10.1890/0012-9615(2006)076

Williams, A.P., Cook, B.I., Smerdon, J.E., Bishop, D.A., Seager, R., Mankin, J.S., 2017. The 2016 southeastern U.S. drought: an extreme departure from centennial wetting and cooling. J. Geophys. Res. Atmos. 122, 10,888-10,905. https://doi.org/10.1002/2017JD027523

Williams, J.W., Shuman, B.N., Webb, T., Bartlein, P.J., Leduc, P.L., 2004. Late-quaternary vegetation dynamics in North America: scaling from taxa to biomes. Ecol. Monogr. 74, 309–334. https://doi.org/https://doi.org/10.1890/02-4045

Zampieri, N.E., Pau, S., Okamoto, D.K., 2020. The impact of Hurricane Michael on longleaf pine habitats in Florida. Sci. Rep. 10, 1–11. https://doi.org/10.1038/s41598-020-65436-9

# Chapter 3. Effects of dormant and growing season burning on surface fuels and potential fire behavior in northern Florida longleaf pine (*Pinus palustris*) flatwoods[1]

## 3.1 Abstract

Prescribed fire is widely used to manage fuels in high-frequency, low-severity fire regimes including pine flatwoods of the southeastern US where prescribed burning during the growing season (the frost-free period during the calendar year) has become more common in recent decades. Growing season prescribed fires address ecological management objectives that focus on increasing herb cover and decreasing shrub cover. The shift from shrub to herb dominance due to burning in the growing season corresponds to a change in surface fuels that could affect fire behavior, yet little has been done to assess the potential effects. We examined the effects of season-of-burn on shrub and herbaceous fuel layers and predicted fire behavior at replicate plots on frequently burned mesic pine flatwoods for two season-of-burn treatments (growing and dormant season prescribed fires) in two geographic regions in northern Florida. The Fuel Characteristic Classification System was used to construct a representative fuelbed for each plot at each sampling time to predict fire behavior. Predicted fire behavior was tested for correlation with measured surface fuel properties to determine if there was an effect from differences in fuels characteristics across treatments. In addition, fire temperature was measured

---

[1] Cronan, J.B., Wright, C.S., Petrova, M., 2015. Effects of dormant and growing season burning on surface fuels and potential fire behavior in northern Florida longleaf pine (*Pinus palustris*) flatwoods. For. Ecol. Manage. 354, 318–333. https://doi.org/10.1016/j.foreco.2015.05.018

*in situ* as a proxy for fire intensity and tested for treatment effects on the re-growth of live surface fuels. Compared to single dormant season burns, our single growing season burns caused no changes to live understory fuels and had no detectable effect on fire behavior, although predicted rate of spread and flame length were significantly reduced after all prescribed burns. Shrub cover and predicted fire behavior were, however, significantly different between geographic regions, and shrub height was significantly affected by fire temperature. Predicted fire behavior was strongly correlated with measures of the litter and herb strata. Results from this study suggest that land managers should not initially expect large changes in understory fuel properties or potential fire behavior from a shift to burning during the growing season and show that geographic location and fire intensity had significant effects on live fuels and potential fire behavior.

## 3.2. **Introduction**

Throughout the United States (US), prescribed fire is used to manage fuels (Schwilk et al., 2009; Stephens et al., 2012) and is recommended to counter the negative ecological effects of human activities, such as fire suppression and climate change, in ecosystems with high-frequency, low-severity fire regimes (Ryan et al., 2013; Stephens et al., 2012; Stephens and Ruth, 2005). Using prescribed fire requires an understanding of how variation in its application affects ecosystem properties, fuel characteristics, and potential fire behavior (Agee and Skinner, 2005; O’Brien et al., 2010). Shifting season-of-burn from the dormant season to the growing season has been gaining attention as a treatment option because doing so can affect vegetation dynamics and produce ecological benefits (Knapp et al., 2009). In the southeastern US, prescribed fire is widely used to control fuels, particularly understory shrubs and hardwood trees in fire-adapted pine forests (O'Brien et al., 2010). While much research has been focused on the ecological effects of season-of-burn (e.g. Robbins and Myers, 1992), scant attention has been given to the effects on fuels and wildfire risk, important considerations given that managing fire potential is often a primary goal of prescribed burning in this region (Marshall et al., 2008; O'Brien et al., 2010).

The pine flatwoods ecosystem is widespread throughout the coastal plain of the southeastern US. When frequently burned, it is characterized by an open canopy of pines, most commonly longleaf pine (*Pinus palustris* Mill.), and a biologically diverse understory of herbs and shrubs (Hardin and White, 1989). Prior to European settlement, the mean fire-return interval for longleaf pine forests was 2.2 to 3.2 years, with a shorter median, and most fires occurred during the growing season (Bale, 2009; Henderson, 2006; Stambaugh et al., 2011). Fire frequency drives understory composition in pine flatwoods with herbs favored at shorter fire-return intervals (Brockway and Lewis, 1997). This effect is enhanced by growing season fires when fire-return intervals are less than two years, however, the magnitude of the seasonal effect appears to vary geographically (Glitzenstein et al., 2003; Haywood et al., 2001).

The use of prescribed fire in the pine flatwoods ecosystem has shifted seasonally over the past several decades. The dormant season was the preferred burning period when fire was reintroduced as a management tool in the 1940s (Stanturf et al., 2002). Burns during the dormant season were favored because dry air and predictable winds following wetting rains produced manageable fire behavior and good smoke dispersion. A more recent focus on endangered species preservation and maintenance of biological diversity has prompted land management agencies to increase the frequency of burning and extend burning operations into the growing season with the goal of reducing the shrub component and increasing abundance of bunchgrasses and other herbaceous species (Ferguson, 1998; McWhite et al., 1999). This shift in understory composition is desirable because herb-dominated understories have greater plant diversity (Glitzenstein et al., 2012), and provide habitat for the gopher tortoise (*Gopherus polyphemus* Daudin, 1801; Cox et al., 1987)) and the red cockaded woodpecker (*Picoides borealis* Vieillot, 1809; James et al., 1997; Van Balen and Doerr, 1978), two vulnerable keystone species (Conner et al., 2004; Eisenberg, 1983); and the northern bobwhite quail (*Colinus virginianus* Linnaeus, 1758), an important game species (Schroeder, 1985).

Manipulating season-of-burn to alter the understory has implications for potential fire behavior because the amount and structure of surface fuels differ between shrub- and herb-dominated types (Anderson, 1982). Measures of fire behavior can be high for shrub-dominated vegetation (Andreu et al., 2012; Hough and Albini, 1978; Saglam et al., 2008). Because biomass of fine-dead and volatile-live fuels accumulate rapidly, shrub-dominated fuelbeds can support intense fires that are difficult to control. In forested areas, taller shrub-dominated fuelbeds decrease the gap between surface fuels and the tree canopy increasing the probability of crown fire. In pine flatwoods, the shrub understory component can be managed with regular prescribed burning. Without regular burning, however, the rapid growth of shrubs (Figure 3-1) contributes to surface fuel levels that can support high-intensity fires (Brose and Wade, 2002; Kreye et al., 2014). In contrast, herb-dominated fuel types tend not to support high-intensity fires because herb biomass does not accumulate to the same level as shrubs and fuel height remains relatively low (Yospin et al., 2012). Herb-dominated fuel types can affect fire behavior in other respects, however. Higher surface area-to-volume (SAV) ratio and near-optimal packing of continuous herbaceous fuelbeds can support high rates of fire spread. In addition, as herbaceous fuels cure and their moisture content decreases towards the end of their phenological growth cycle, they can have a high probability of ignition.

The goal of this study was to determine how season-of-burning influences live fuel characteristics and therefore potential fire behavior in the pine flatwoods ecosystem. The objectives were to: (1) quantify the effects of prescribed burning in the dormant and growing seasons on post-burn fuel loading, cover, and height of live understory fuels, and (2) determine the extent to which differences in post-burn live surface fuel recovery influences fire behavior in stands managed with prescribed fire in different seasons.

**Figure 3-1.** Prescribed burn demonstration plot at St. Marks National Wildlife Refuge, Florida, US showing biennially burned (left) and unburned (right) fuels in mesic longleaf pine flatwoods.

We hypothesized that, relative to dormant season burns, growing season burns would cause a small shift towards herbs and away from shrubs with a similarly minor decline in fire behavior. The hypothesized direction and magnitude of expected change in live understory fuels was based on results from other published experiments in similar ecosystems in the southeastern US where the effects of dormant season and growing season burns have been compared.

Although the effects were minor, single growing season burns were found to increase herb production in an upland longleaf pine forest in central Louisiana (Grelen and Epps, 1967), decrease understory hardwoods in an oak-hickory (*Quercus*-*Carya*) forest in central Virginia (Brose, 2010), and decrease saw palmetto (*Serenoa repens* (W. Bartram) Small) in pine flatwoods in central and southern Florida (Willcox and Giuliano, 2010). The direction and magnitude of our hypothesized shift in live understory fuels is also suggested by long-term studies of season-of-burning in fire-adapted loblolly (*P. taeda* L.) and longleaf pine ecosystems (Glitzenstein et al., 2003; Haywood et al., 2001; Waldrop et al., 1987). These long-term studies show that individual growing season fires cause incremental shifts that favor herbs, and when applied consistently at short intervals, in some cases, can cause a large shift from shrub- to herb-dominated understory vegetation. Relative to dormant season fires we expect predicted fire behavior following growing season fires to decline based on known differences in fire behavior between shrub- and herb-dominated fuel types, namely that herbaceous fuel loading is typically lower than shrub fuel loading which tends to reduce measures of fire intensity (Brose and Wade, 2002; Kreye et al., 2014).

## 3.3 **Methods**

### 3.3.1 *Study area*

The study area encompasses mesic, mature pine flatwoods on federally managed lands in northern Florida (Figure 3-2). The climate in northern Florida is humid-subtropical (Kottek et al., 2006) and temperatures range from an average minimum of 5°C in January to an average maximum of 33°C in July. Average annual precipitation is 1525–1650 mm with peak rainfall in July associated with convective thunderstorm activity. Dry periods occur in October-November and April-May. Eglin Air Force Base (EAFB) is characterized by broad plateaus dissected by dendritic streams to the north and flat coastal lowlands to the south; soils in pine flatwoods are generally somewhat poorly to moderately well-drained Entisols (Overing et al., 1995; Overing and Watts, 1989). Topography of the Apalachicola National Forest and St. Marks National Wildlife Refuge (APSM) is flat and where pine flatwoods are present soils are commonly poorly drained sandy Spodosols (Allen, 1991; Sanders, 1981). Pine flatwoods in the study area are characterized by an overstory dominated by longleaf pine, an open midstory, and an understory of shrubs and herbs, including saw palmetto, gallberry (*Ilex glabra* (L.) A. Gray), dwarf live oak (*Q. minima* (Sarg.) Small), Darrow's blueberry (*Vaccinium darrowii* Camp), wiregrass (*Aristida stricta* Michx.), bluestem (*Andropogon* L. and *Schizachyrium* Nees), hairy trilisa (*Carphephorus paniculatus* (J.F. Gmel.) Herb.), and silk-grass (*Pityopsis graminifolia* (Michx.) Nutt.).

### 3.3.2 *Study design*

Growing and dormant season burn treatments were replicated eight times across the study and evenly allocated between two geographic regions (i.e., four replicates per region; Figure 3-2). Repeated measurements of understory fuels were conducted during the dormant season no more than five months before treatment, and immediately (within one month), one year, and two years post-treatment. The dormant season was defined as the period between October 15 and March 14, and the growing season was March 15 to October 14 which corresponds to the typical frost-free period for northern Florida. Burns were conducted between December 2009 and July 2010 (Table 3-1). Replicates, or treatment plots, ranged from 2 to 4.5 ha in area and were located in mature, mesic longleaf pine stands that were at least 2 ha and were part of larger (10s to 100s of ha) administrative units. To reduce the influence of confounding variables, plots were located in stands with similar age, vegetation composition (characteristic mesic pine flatwoods vegetation, as described above), time-since-last-fire, and disturbance history that included at least 20 years of prescribed burning at 3–5 year intervals and no evidence of other past disturbances (i.e., high severity fires, grazing, silvicultural treatments, or agriculture). This study utilized operational prescribed burns conducted on administrative units as treatments. We identified and measured pre-fire fuels in 22 stands of mature longleaf pine that met these selection criteria throughout the study area. Six stands were excluded from the analysis because burns were not conducted within the treatment window (*n* = 3), were conducted on the same day (*n* = 2), or plots

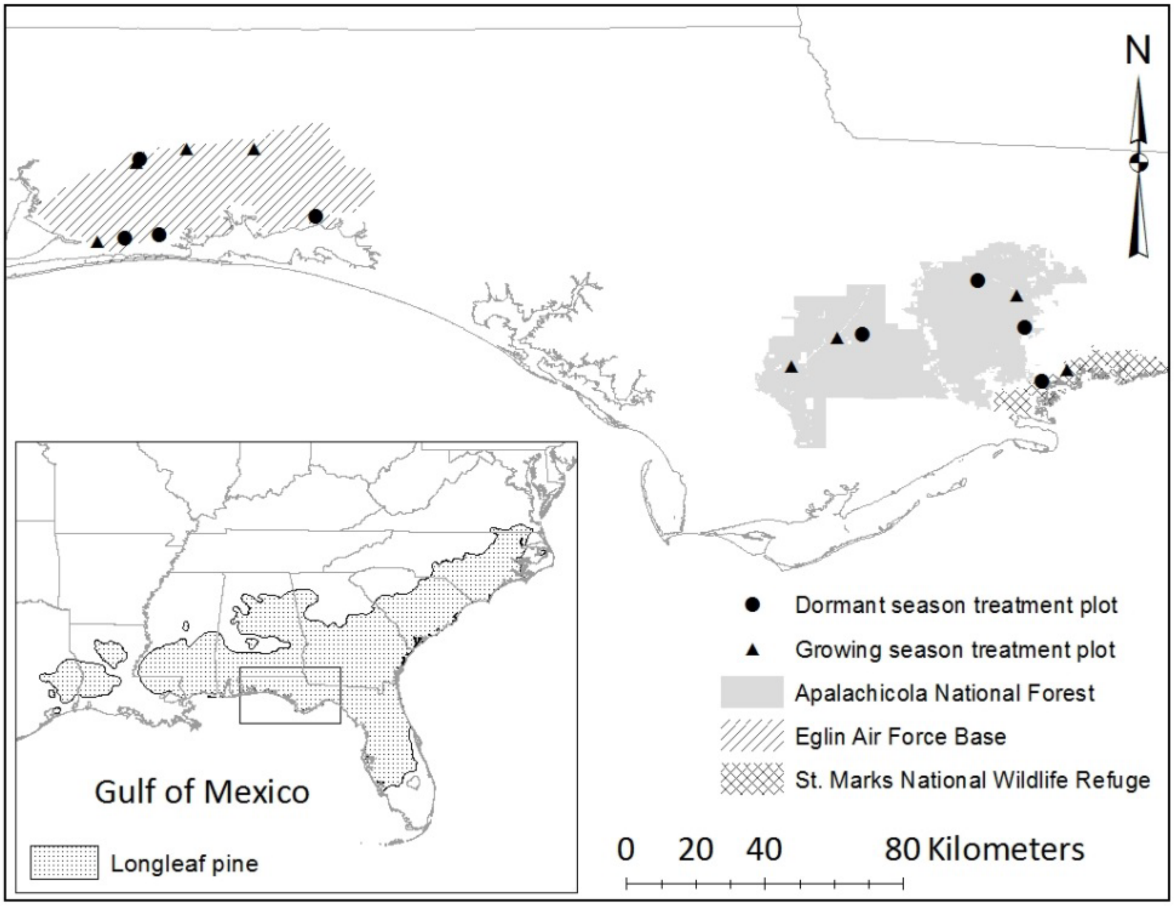


**Figure 3-2.** Location of 2-4.5 hectare mesic longleaf pine flatwoods season-of-burn treatment plots in northern Florida. Inset: box shows general area of treatment plots relative to the historic distribution of longleaf pine in the southeastern US.

were burned again before the final repeated measurement was conducted (*n* = 1). Within each plot, subplot markers (*n* = 20) were systematically established on a 40-m grid arranged to provide a buffer of the same distance from sources of edge effect including stand boundaries (e.g., changes in forest age, composition, or structure) and roads (Figure 3-3). As we were interested in how vegetation and fuels recover following fires in different seasons, immediate post-burn data were not used in this study.

### 3.3.3 *Fuel sampling*

Data were collected to test the effect of season-of-burn treatments on live surface fuels. Fuel loading of understory vegetation by life form (i.e., shrubs and herbs), litter, and 1-hr (< 0.64 cm diameter) and 10-hr (0.64-2.54 cm diameter) timelag fuel classes for downed-woody fuels were inventoried using standard destructive methods (Wright, 2013) from 20 biomass subplots at each of the four sampling times. Biomass subplots were located 10 m apart along a 40 m line between subplot markers and assignment of sampling time was based on consecutive order (Figure 3-3). The sampling area for biomass subplots varied (0.5 $m^2$, 1 $m^2$, and 4 $m^2$) according to the fuel type to balance precision, accuracy, and sampling effort. Coverage of understory vegetation by life form, and 100-hr (2.64-7.62 cm) and 1000-hr (> 7.62 cm) timelag fuel classes for downed-woody fuel loading were measured at each sampling time on two 20-m transects of random azimuth originating from subplot markers by using line intercept (Canfield, 1941; Stephenson and Buell, 1965) and planar intersect (Brown, 1974) sampling methods, respectively. Transect endpoints were marked so that they could be remeasured at each sampling time. Three points were established along each transect (for a total of 120 points per treatment plot) to estimate litter and duff depth, vegetation height by life form, and canopy cover at each sampling

**Table 3-1.** Geographic region, fire history, burn date, season-of-burn, day-of-burn weather, and thermocouple data ($\bar{x} \pm \mathrm{SE}$) for season-of-burn treatment plots in northern Florida, US. Except where noted ambient temperature data were collected on site from portable weather stations. A total of 15 thermocouples were deployed at each plot.

| | | Fire history[a] | | Treatment burn | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Plot No. | Geographic region | Season-of-last-burn | Time-since-last-fire (years) | Burn date | Season-of-burn | Air temp. (°C)[b] | Relative humidity (percent) | MTT (°C)[c] | Residence time (seconds)[c] | Thermocouples exposed to flame |
| 1[d] | EAFB | Dormant | 2.9 | 12 Jan 2010 | Dormant | 9 | 46 | 437 ± 26 | 29 ± 3 | 13 |
| 2[e] | EAFB | Growing | 4.5 | 23 Dec 2009 | Dormant | 17 | 73 | 400 ± 33 | 25 ± 5 | 2 |
| 3 | EAFB | Dormant | 1.9 | 23 Jan 2010 | Dormant | 14 | 85 | 356 ± 42 | 20 ± 10 | 14 |
| 4 | EAFB | Growing | 4.9 | 21 Feb 2010 | Dormant | 3 | 33 | 504 ± 33 | 41 ± 5 | 12 |
| 5 | EAFB | Dormant | 3.2 | 8 May 2010 | Growing | 29 | 70 | 332 ± 57 | 19 ± 8 | 8 |
| 6 | EAFB | Dormant | 2.1 | 30 Mar 2010 | Growing | 21 | 28 | 371 ± 23 | 20 ± 3 | 13 |
| 7 | EAFB | Dormant | 2.2 | 8 May 2010 | Growing | 30 | 65 | 438 ± 32 | 35 ± 7 | 9 |
| 8 | EAFB | Dormant | 5.2 | 19 Mar 2010 | Growing | 20 | 41 | 395 ± 45 | 28 ± 6 | 10 |
| 9 | APSM | Dormant | 3.3 | 18 Feb 2010 | Dormant | 14 | 27 | 430 ± 42 | 34 ± 8 | 7 |
| 10 | APSM | Dormant | 5.0 | 11 Feb 2010 | Dormant | 6 | 52 | 389 ± 42 | 22 ± 4 | 11 |
| 11[d] | APSM | Dormant | 2.9 | 14 Jan 2010 | Dormant | 12 | 58 | 485 ± 24 | 31 ± 3 | 14 |
| 12 | APSM | Dormant | 2.3 | 17 Feb 2010 | Dormant | 8 | 42 | 522 ± 35 | 34 ± 4 | 15 |
| 13 | APSM | Dormant | 2.3 | 19 May 2010 | Growing | 26 | 65 | 472 ± 37 | 33 ± 5 | 10 |
| 14 | APSM | Dormant | 2.6 | 2 Jun 2010 | Growing | 29 | 66 | 332 ± 28 | 20 ± 5 | 8 |
| 15 | APSM | Growing | 2.0 | 22 Jul 2010 | Growing | 34 | 57 | 460 ± 27 | 31 ± 4 | 13 |
| 16 | APSM | Dormant | 2.5 | 9 Jul 2010 | Growing | 36 | 47 | 423 ± 40 | 30 ± 5 | 13 |

[a] Information about most recent prescribed fire prior to treatment burn.

[b] Air temperature at time of burn treatment.

[c] Maximum thermocouple temperature (MTT) and residence time is the average value from thermocouples exposed to flame.

[d] Weather data collected with handheld instruments.

[e] Weather data from Eglin Air Force Base Remote Automated Weather Station B-75 (N30° 33.22′ W86° 45.61′) located 9.8 km from plot.

time. Vegetation height was estimated as the average height of plants within a 1 m radius of the measurement point (Burgan and Rothermel, 1984) and canopy cover was estimated by using the vertical tube method (Johansson, 1985). Subplot data were averaged for each sampling time for each treatment plot.

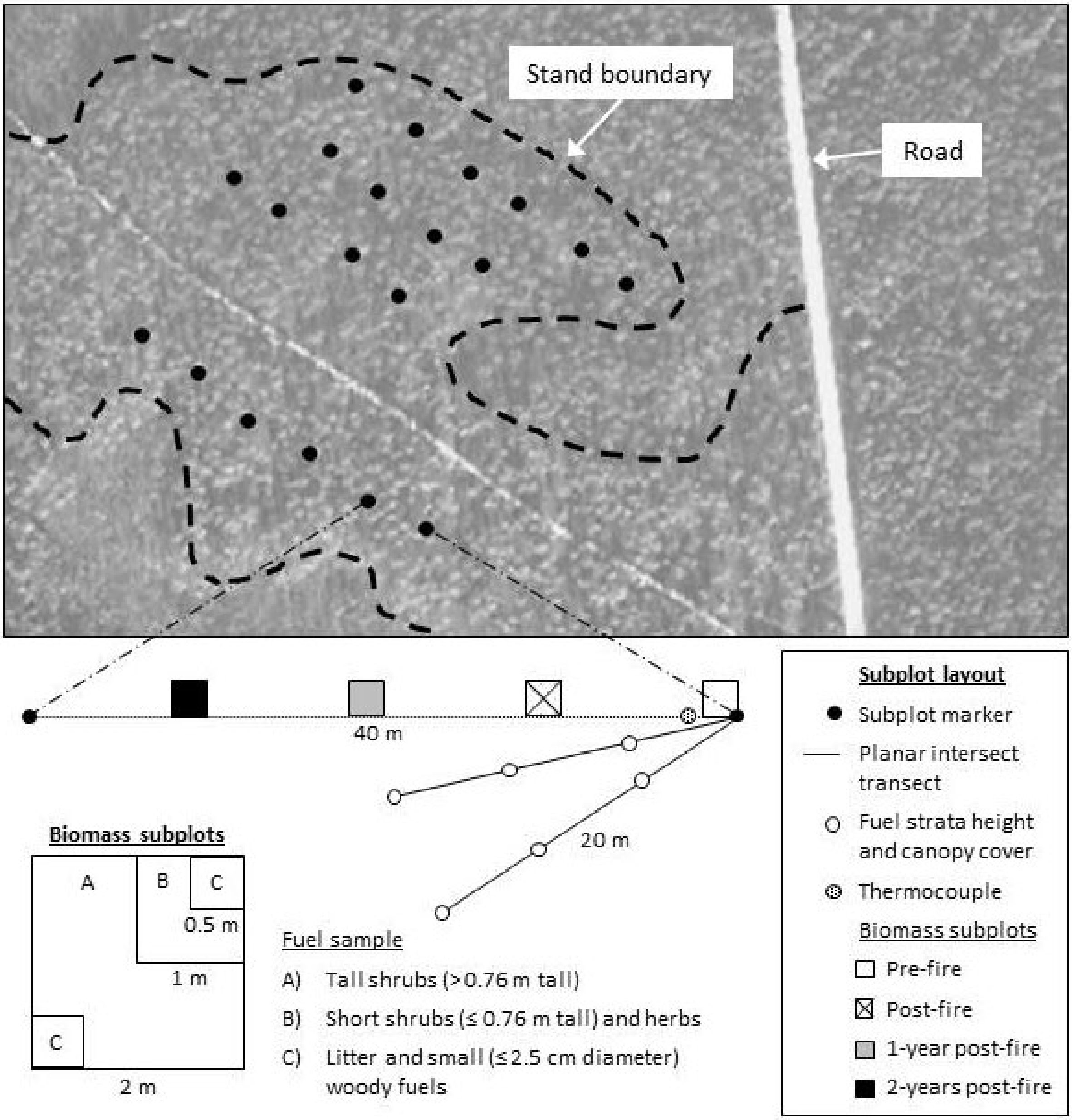


**Figure 3-3.** Aerial photo showing systematic arrangement of subplots (*n* = 20) within stand boundaries of a mesic pine flatwoods plot. Schematic illustration shows fuel sampling design within a subplot.

### 3.3.4 *Fire weather and in-fire temperature observations*

To document day-of-burn weather conditions, temperature, relative humidity, wind speed, and wind direction were measured adjacent to each plot using portable weather stations (WatchDog 2000 Series, Spectrum Technologies Inc., Aurora, IL). In three instances observations were collected with handheld instruments (Kestrel® 4000, Nielsen-Kellerman, Birmingham, MI) or inferred from nearby remote automated weather stations (Table 3-1). To adjust for the effects of fire intensity on post-fire herb and shrub growth, in-fire temperature was recorded *in situ* at each plot with an array of 15 thermocouples. Thermocouples provide a useful gauge of the physiological effects of fire by recording heat duration and flame temperature (Kennard et al., 2005). During burn treatments temperature was measured at 3–5 second intervals with 20-gauge wire, type-K thermocouples insulated with ceramic fiber (XCIB-K-2-7-3, OMEGA® Engineering, Stamford, CT) connected to single-channel data loggers (EL-USB-TC-LCD, Lascar Electronics, Ltd., Salisbury, UK; HOBO® U12-014, Onset® Corp., Bourne, MA). Thermocouples were arrayed systematically 3 m from the first 15 subplots and sensors were suspended 5 cm above the litter surface (Figure 3-3). Temperature time series were used to calculate flame residence time (RT), defined as seconds with temperature readings above 300°C (Wotton et al., 2012), and maximum thermocouple temperature (MTT; Wally et al., 2006). RT and MTT were averaged for each treatment plot for all thermocouples exposed to flame.

### 3.3.5 *Fire behavior predictions*

The Fuels Characteristic Classification System (FCCS; Ottmar et al., 2007) was used to construct custom fuelbeds from measured surface fuel characteristics and to predict fire behavior for each plot at pre-fire, 1-year, and 2-year post-fire sampling times (48 custom fuelbeds).

Reaction intensity (RI; kW m$^{-2}$), rate-of-spread (ROS; m min$^{-1}$), and flame length (FL; m) were compared between treatments and geographic regions over time. The FCCS is a fire management decision support tool that includes a surface fire behavior prediction model based on a reformulation of the Rothermel quasi-steady-state fire spread model (Rothermel, 1972; Sandberg et al., 2007). The FCCS surface fire spread model differs from the Rothermel model by explicitly modeling the heat sink and heat source for each surface fuel stratum, providing a framework to evaluate differences in fire behavior among fuelbeds constructed with field data as direct inputs (Sandberg et al., 2007). FCCS fuelbeds are divided into six strata that represent unique combustion environments and include tree canopies, shrubs, herbs, woody fuels, litter, and duff (Riccardi et al., 2007a).

To characterize fuelbeds we used an existing FCCS fuelbed, "Longleaf pine-slash pine (*P. elliottii* Engelm.)/gallberry forest" (FCCS fuelbed 191), as a template for the canopy fuel stratum and for intrinsic fuel properties such as heat content and bulk density. This fuelbed was selected because its characteristics were a close match to the dominant overstory and understory species, and the 20-year mean fire-return interval (4.3 years) at our plots. We customized the inputs of the surface fuel strata for each fuelbed with our fuel inventory measurements (Table 3-2). All input data for plots were averaged from subplots and are included in Appendix A. Fire behavior was simulated for all resulting fuelbeds under the same benchmark environmental conditions of no slope, 6.4 km hr$^{-1}$ wind speed, and fuel moisture contents of 6 percent for 1-hr fuels, 7 percent for 10-hr fuels, 8 percent for 100-hr fuels, 60 percent for graminoids and forbs, and 90 percent for shrubs; (i.e. D2L2 scenario; Scott and Burgan, 2005). Benchmark environmental conditions were used so that we could compare relative differences in fire behavior associated with differences in fuels; predictions do not necessarily represent prescribed burning conditions.

**Table 3-2.** Data source and measurement unit by input variable used to build FCCS fuelbeds to represent treatment plots at different sampling times in northern Florida (see Appendix A for input values)

| Input variables | Data source | Measurement units |
|---|---|---|
| Fuelbed FCCS191: Longleaf pine -slash pine/gallberry forest (2-3 year prescribed fire rotation) | Selected based on vegetation type, mean fire rotation period, and mean canopy cover for treatment plot from measured values from canopy cover points. | |
| **Canopy** | Used default values for FCCS191 | |
| **Shrubs** | | |
| Cover | Mean cover value for treatment plot from measured values from line intercept transects. | Percent |
| Height | Mean height value from height sampling points | Meters |
| Loading | Mean biomass for treatment plots from 1- and 4-$m^2$ biomass subplots | Megagrams $hectare^{-1}$ |
| **Herbs** | | |
| Cover | Mean cover value for treatment plot from measured values from planar intersect transects. | Percent |
| Height | Mean height value from height sampling points | Meters |
| Loading | Mean biomass for treatment plots from $1m^2$ biomass subplots | Megagrams $hectare^{-1}$ |
| **Woody fuels** | | |
| 1-hr and 10-hr loading | Mean loading value for treatment plot from 0.5-$m^2$ biomass subplots | Megagrams $hectare^{-1}$ |
| 100-hr and 1000-hr loading | Mean loading value for treatment plot from measured planar intersect inventory | Megagrams $hectare^{-1}$ |
| **Litter** | | |
| Cover | Mean cover value for treatment plot from measured values from line intercept transects. | Percent |
| Depth | Mean depth value from depth sampling points | Millimeters |
| Loading | Calculated from cover and depth. | Megagrams $hectare^{-1}$ |
| **Duff** | | |
| Cover | Percent of depth sampling points with duff present (depth > 1 mm) | Percent |
| Depth | Mean depth value from depth sampling points | Millimeters |

### 3.3.6 *Data analysis*

Repeated measures analysis of variance (Crawley, 2007) with season-of-burn and geographic region as explanatory variables, and sampling time as a repeated measure was used to test the effect of dormant and growing season burns on the difference between pre- and post-fire shrub and herb fuels and measures of predicted fire behavior. Interaction terms were limited to two-way interactions (i.e., season-of-burn × time, region × time, season-of-burn × region). Tukey's Honestly Significant Difference post-hoc multiple comparison tests (Tukey, 1953) were conducted to examine change within treatment levels across sampling time and between treatment levels for each sampling time. MTT was assessed for significant correlation with live fuel variables and incorporated into the repeated measures model as a covariate when significant. Model residuals were assessed for homogeneity of variance and normality; assumptions were met for each. Outliers were identified by flagging absolute standardized residuals that lie outside the 95 percent confidence interval of the standard normal distribution. If outliers were present, statistical tests were repeated without them to determine their influence on model interpretation. To determine if fire intensity was different between the season-of-burn treatments or geographic region, MTT for each variable was tested with a two-sample $t$ test (Appendix B). Because of its high correlation with MTT ($\rho = 0.915$, $P < 0.001$), RT was not used as a proxy for fire intensity. The effect of live fuels on predicted fire behavior over the range of sampled conditions was studied using correlation and regression analysis. Litter fuel loading is calculated as a function of depth, type, and coverage in FCCS v 2.2 (Riccardi et al., 2007b) and therefore excluded from the correlation analysis as the FCCS did not accept direct input of measured litter loading. Phenological differences (i.e., the presence of leaves on deciduous species) in live fuels at plots burned and sampled in the growing season introduced a potentially confounding variable that was assessed by adjusting live fuel measurements with paired plot data (Appendix C).

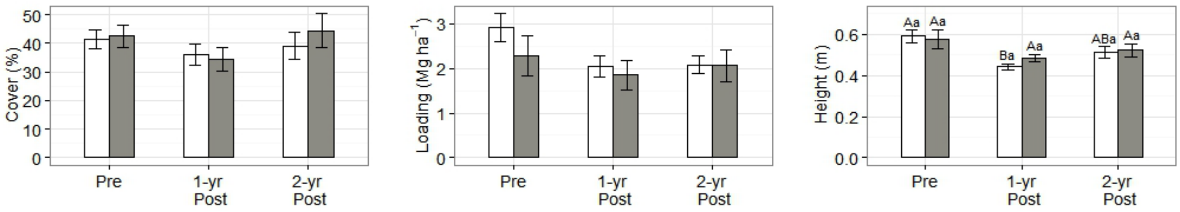
Given the small sample size and high probability of Type II error, statistical significance for all tests was evaluated at $\alpha = 0.1$. A Bonferroni correction was made on $t$ tests and Tukey $P$ values in instances where two analyses were conducted on the same data (i.e., separate tests for the effect of season-of-burn and region on MTT and separate post-hoc tests for the effect of season-of-burn × time and region × time interactions on shrub cover, shrub height, ROS, and FL). Thus, $\alpha = 0.1 \div 2$, or 0.05, was used as a level of significance. Statistical analyses were conducted with R version 3.1.1 (R Development Core Team, 2014). Except when noted, results are presented as the plot mean ± standard error.

## 3.4 **Results**

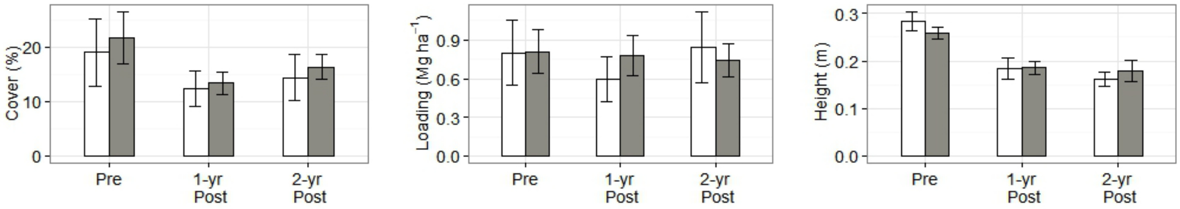
### 3.4.1 *Shrub fuels*

Pre-fire shrub cover did not differ (Tukey $P = 1.000$; Figure 3-4) between plots burned in the dormant (41.2 ± 3.3 percent) and growing (42.6 ± 4.0 percent) seasons. There was a season-of-burn × time interaction ($P = 0.057$) indicating that reduction of shrub cover one year after treatment was slightly greater at plots burned in the growing season, but variability within each season-of-burn treatment group was high, and as a result, the slightly greater reduction of shrub cover at plots burned during the growing season was not significant (Tukey $P \geq 0.955$). An interaction between geographic region and time ($P < 0.001$) suggested that prescribed burning reduced shrub cover more at EAFB (Figure 3-5). Within each region changes in shrub cover over time were not significant (Tukey $P = 0.307$). There was, however, a significant difference between regions. A nonsignificant difference between APSM (44.7 ± 4.7 percent) and EAFB (39.1 ± 1.5 percent) before (Tukey $P = 0.876$) and one year after (Tukey $P = 0.110$) treatment became significant the second year after treatment (Tukey $P = 0.004$) when shrub cover was 19.9 ± 6.3 percent lower at EAFB. MTT did not explain a significant amount of variation in post-fire shrub cover ($P = 0.609$) and was not included as a covariate in the test for the effect of season-of-burn.

a) Shrub Fuels



b) Herbaceous Fuels



c) Predicted Fire Behavior

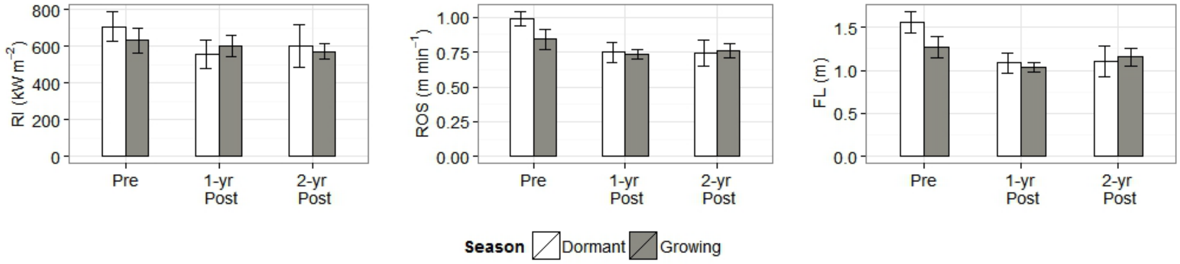
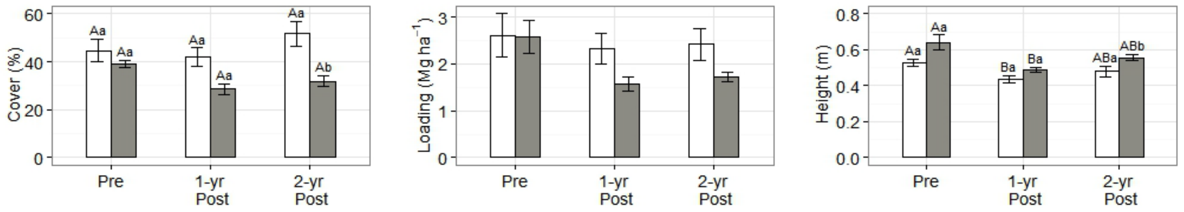


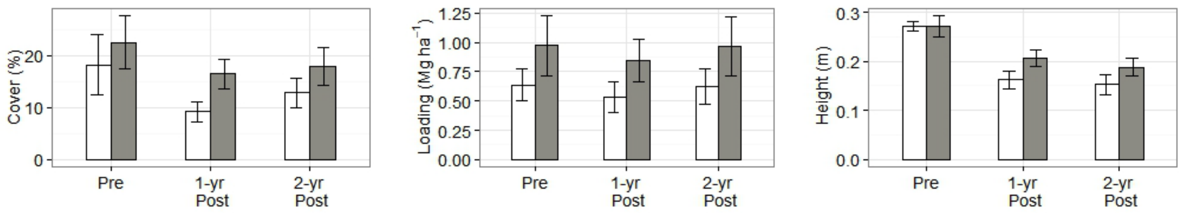
Figure 3-4. Live fuel cover, loading, and height for understory a) shrub and b) herbaceous fuel layers, and c) fire behavior predictions from custom FCCS fuelbeds for pre-fire, 1-year post-fire, and 2-years post-fire at treatment plots grouped by season-of-burn. Means with the same uppercase letter are not significantly different among sample times within season-of-burn treatments and means with the same lowercase letter are not significantly different between season-of-burn treatments for a sample time (Tukey $P \leq 0.1$). Bars without letters are not significantly different.

Pre-fire shrub fuel loading averaged across all plots was 2.59 ± 0.28 Mg ha$^{-1}$ and there was no season-of-burn treatment effect on post-fire shrub growth; season-of-burn alone and season-of-burn × time and season-of-burn × region interactions were not significant ($P \geq 0.221$; Figure 3-4). For geographic region, pre-fire shrub fuel loading was not different (Tukey $P$ = 1.000) between APSM (2.60 ± 0.46 Mg ha$^{-1}$) and EAFB (2.58 ± 0.35 Mg ha$^{-1}$) but there was a significant region × time interaction ($P = 0.091$). Mean shrub fuel loading appeared to decline more at EAFB after burning (Figure 3-5), but variability among plots was high and post-hoc

**a) Shrub Fuels**



**b) Herbaceous Fuels**



**c) Predicted Fire Behavior**

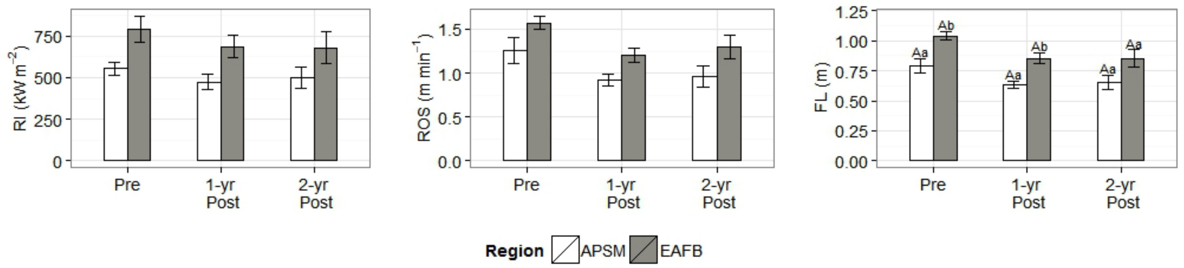


Figure 3-5. Live fuel cover, loading, and height for understory a) shrub and b) herbaceous fuel layers, and c) fire behavior predictions from custom FCCS fuelbeds for pre-fire, 1-year post-fire, and 2-years post-fire at treatment plots grouped by geographic region. Means with the same uppercase letter are not significantly different among sample times within geographic region and means with the same lowercase letter are not significantly different between geographic regions for a sample time (Tukey $P \leq 0.1$). Bars without letters are not significantly different.

testing showed that the change in shrub fuel loading over time was not significant for either geographic region (Tukey $P \geq 0.232$) and that shrub fuel loading the first and second years after treatment at EAFB was not lower than APSM (Tukey $P \geq 0.559$). MTT did not explain a significant amount of variation in post-fire shrub fuel loading ($P = 0.160$) and was not included as a covariate in season-of-burn tests.

Pre-fire shrub height averaged across all plots was 0.58 ± 0.03 m. Season-of-burn alone and season-of-burn × time and season-of-burn × region interactions were not significant ($P \geq$

0.265; Figure 3-4). Shrub height differed significantly regionally (*P* = 0.057), based on significant differences for the second year after treatment (Tukey *P* = 0.026), when mean shrub height was 0.48 ± 0.03 m at APSM and 0.56 ± 0.02 m at EAFB. Mean shrub height at APSM was lower than at EAFB across all times (Figure 3-5), which was the opposite of the regional trend that was observed for shrub cover and fuel loading. Although mean shrub height was slightly lower at APSM before and one year after treatment, these differences were not significant (Tukey $P \geq 0.158$). As one might expect, shrub height declined significantly by 0.09 ± 0.02 m at APSM (Tukey *P* = 0.016) and by 0.15 ± 0.04 m at EAFB (Tukey *P* = 0.004) from pre-fire to 1-yr post-fire. By the second year after treatment, however, mean shrub height was no longer significantly different from pre-fire means for either geographic region (Tukey $P \geq 0.262$). MTT explained a significant amount of variation in post-fire shrub height (*P* = 0.060), which declined with increasing MTT, and was included as a covariate in season-of-burn tests.

### 3.4.2 *Herb fuels*

Pre-fire herb cover averaged across treatments was 20.3 ± 3.8 percent. Season-of-burn alone and season-of-burn × time and season-of-burn × region interactions were not significant ($P \geq 0.462$; Figure 3-4). Mean herb cover tended to decrease after burning and although time was a significant term in the overall model (*P* = 0.005), variability among plots was high and post-hoc testing was unable to identify significant changes in herb cover among sampling times (Tukey $P \geq 0.149$). Mean herb cover was slightly lower at APSM for each sampling time (Figure 3-5), but this difference was not significant (*P* = 0.316). MTT did not explain a significant amount of variation in post-fire herb cover (*P* = 0.867) and was not included as a covariate to test for the effect of season-of-burn.

Pre-fire herb fuel loading averaged across all plots was 0.81 ± 0.15 Mg $ha^{-1}$. Season-of-burn alone and season-of-burn × time and season-of-burn × region interactions were not significant ($P \geq 0.189$; Figure 3-4). Sampling time was not significant ($P = 0.243$) and suggested that herb fuel loading recovered to pre-treatment levels within the first post-treatment sampling time. As with herb cover, mean herb fuel loading was consistently lower at APSM for all sampling times (Figure 3-5), however, this difference between geographic regions was not significant ($P = 0.246$). MTT did not explain a significant amount of variation in post-fire herb fuel loading ($P = 0.585$) and was not included as a covariate in season-of-burn tests.

Pre-fire herb height averaged across treatments was 0.27 ± 0.10 m. Season-of-burn alone and season-of-burn × time and season-of-burn × region interactions were not significant ($P \geq 0.168$; Figure 3-4). Mean herb height tended to decrease after burning and post-hoc testing showed that herb height the first (0.18 ± 0.01 m) and second (0.17 ± 0.01) years after treatment was significantly lower (Tukey $P < 0.001$) than pre-fire herb height. As with herb cover and fuel loading, mean herb height was slightly lower at APSM for each sampling time (Figure 3-5), but this difference was not significant ($P = 0.179$).

### 3.4.3 *Predicted fire behavior*

Prior to treatment, predicted RI, ROS, and FL averaged across all plots was 670 ± 52 kW $m^{-2}$, 1.41 ± 0.09 m $min^{-1}$, and 0.91 ± 0.05 m, respectively. All three predicted fire behavior metrics decreased after burning but season-of-burn alone and season-of-burn × time and season-of-burn × region interactions were not significant ($P \geq 0.126$; Figure 3-4). Predicted RI, ROS, and FL differed significantly regionally ($P \leq 0.035$). For all sampling times the mean predicted RI, ROS, and FL at APSM were lower than at EAFB (Figure 3-5), however post-hoc testing showed that, except for predicted FL, these differences were not significant (Tukey $P \geq 0.165$). Relative to EAFB, predicted FL at APSM was 0.25 ± 0.07 m lower before treatment (Tukey $P = 0.021$) and 0.22 ± 0.07 m lower the first year after treatment (Tukey $P = 0.055$). Although predicted FL at APSM was 0.20 ± 0.11 m lower than EAFB the second year after treatment, this difference was not significant (Tukey $P = 0.105$).

### 3.4.4 *In-fire temperatures*

Distribution of MTT and RT were weakly bimodal and the average MTT was 423°C with a range of 332–524°C (Table 3-1). Average RT was 28 seconds and ranged from 19 to 43 seconds. No differences in MTT were observed between dormant season and growing season burns or between geographic regions (see Appendix B).

### 3.4.5 *Correlation between predicted fire behavior and surface fuel properties*

Measures of the litter and herb fuel strata were most strongly correlated with predicted fire behavior, while correlation coefficients for the shrub layer were consistently low (Table 3-3). Herbaceous fuel loading was strongly correlated with predicted RI. Cover of herbs and litter, which were additive categories in our sample data, had opposite relationships with predicted RI. Other surface fuel measures correlated with predicted RI included litter depth and herb height. Litter depth was well correlated with predicted ROS, however, predicted ROS stopped increasing when litter depth exceeded 20 mm. Other fuel variables correlated with predicted ROS included 1-hr and 100-hr downed woody fuel loading and duff depth. Litter depth was strongly correlated with predicted FL, however, the relationship between litter depth and predicted FL did not flatten as was observed with litter depth and ROS. Other fuel variables correlated with predicted FL included 1-hr, 10-hr, and 1000-hr downed woody fuel loading and duff depth. No live fuel measures were correlated with predicted ROS or FL.

**Table 3-3.** Correlation of FCCS fire behavior predictions with fuel characteristics measured at season-of-burn treatment plots by sampling time.

| Input variable | Reaction intensity (kW $m^{-2}$) | Rate of spread (m $min^{-1}$) | Flame length (m) |
|---|---|---|---|
| **Shrubs** | | | |
| Percent cover | -0.425** | 0.005 | -0.172 |
| Fuel loading | -0.132 | 0.289* | 0.237 |
| Height | 0.321* | 0.227 | 0.325* |
| **Herbs** | | | |
| Percent cover | 0.693*** | -0.137 | 0.162 |
| Fuel loading | 0.871*** | -0.169 | 0.215 |
| Height | 0.481*** | 0.343* | 0.480*** |
| **Litter** | | | |
| Percent cover | -0.743*** | 0.098 | -0.229 |
| Fuel loading | -- | -- | -- |
| Depth | 0.487*** | 0.919*** | 0.927*** |
| **Duff** | | | |
| Percent cover | -0.087 | 0.465*** | 0.364* |
| Depth | 0.099 | 0.597*** | 0.554*** |
| **Woody fuels** | | | |
| 1-hr fuel loading | 0.094 | 0.514*** | 0.500*** |
| 10-hr fuel loading | 0.143 | 0.479*** | 0.500*** |
| 100-hr fuel loading | 0.067 | 0.548*** | 0.490*** |
| 1000-hr fuel loading | 0.428** | 0.404** | 0.562*** |

Significance levels:
*** $P < 0.0001$; ** $0.001 < P < 0.01$; * $0.01 < P < 0.05$; **.** $0.05 < P < 0.1$

## 3.5 Discussion

### 3.5.1 *Shrub fuels*

We did not detect a difference in the shrub fuel stratum between single dormant and growing season burns in mature pine flatwoods. This result agrees with past studies in which observed individual growing season burns in pine flatwoods had only small (Robertson and Hmielowski, 2014; Willcox and Giuliano, 2010) or negligible (Boyer, 1990; Hughes and Knox, 1964; Olson and Platt, 1995) negative effects on the shrub layer relative to dormant season burns. Growing season burning is thought to have a greater negative effect on shrubs than dormant season burning in fire-adapted pine forests of the southeastern US because fires in the growing season coincide with a period of low carbohydrate reserves in root structures of understory shrubs. When plants are top-killed by fire during this time of the year less energy is available for regrowth, and recovery is delayed (Ferguson, 1957). Reduced recovery following growing season burning relative to burns in the dormant season has been observed for saw palmetto (Willcox and Giuliano, 2010) in pine flatwoods, and deciduous hardwoods in mixed southern pine woodlands (Robertson and Hmielowski, 2014), but not gallberry in slash pine forests (Hughes and Knox, 1964). Carbohydrate reserves for saw palmetto and gallberry, two of the most common shrub species at our plots in both geographic regions, are lowest during the mid- to late-summer (Hough, 1968; Hughes and Knox, 1964). The growing season burns at our plots occurred during the first half of the growing season, from mid-March to late-July (Table 3-1) and did not align well with the period of depleted carbohydrate reserves, which could help to explain the lack of a significant effect in our results. Higher fire intensity during the growing season has also been suggested as a possible cause of shrub reduction relative to dormant season burning (Waldrop et al., 1987), although other studies have found that dormant season fires burn at higher intensity than those in the growing season (Sparks et al., 2002). We did not detect a difference in MTT, used as a proxy measure for fire intensity, between season-of-burn treatments, so we were unable to examine the putative relationships between shrub response and seasonally influenced fire intensity.

We found that other factors, aside from the season of burn, influence post-fire recovery of the shrub fuel layer in pine flatwoods. Greater reduction of shrubs at EAFB relative to APSM suggests that prescribed fires can have differential effects on post-fire shrub dynamics in pine flatwoods across geographic regions. Differences in post-fire recovery of shrubs in longleaf pine forests between geographic regions and habitat types have been observed and attributed to fire intensity (Liu et al., 2004), soil moisture (Olson and Platt, 1995), and soil texture (Glitzenstein et al., 2003). Differences in fire intensity were not observed between plots at APSM and EAFB and therefore it is unlikely this factor contributed to our observed differences in shrub cover reduction. Olson and Platt (1995) observed that shrubs at upland pine savanna sites were slower to recover after burning relative to shrubs at more poorly drained seepage savannas while Glitzenstein et al. (2003) noted that pine flatwoods understory shrub cover was unaffected by high-frequency repeated burning at sites on Spodosols in northern Florida and significantly reduced at sites with finely textured Ultisols in South Carolina. Our results are consistent with the observation by Glitzenstein et al. (2003) that shrubs growing on Spodosols are less affected by burning, but inconsistent with their hypothesis that coarser soil texture increases resistance of shrubs to stress as soils at EAFB soils are generally more well-drained and coarsely textured than Spodosol soils at APSM. For our study, post-fire recovery of the shrub layer was slower on coarse-textured, well-drained soils (e.g. EAFB) and reflects observations by Olson and Platt (1995). The relationship between soils and post-fire shrub recovery at our plots is equivocal, however, as we lack specific soil typing, so are relying on published soil surveys which may not accurately represent the actual soil type at our treatment plots owing to the spatial variability within geographic regions.

The shrub stratum is an important determinant of fire behavior in southeastern pine forest types (Andreu et al., 2012). Relevant characteristics of this stratum include fuel loading, cover, and height (Brose and Wade, 2002; Hough and Albini, 1978). In pine flatwoods, resprouting shrub stems recover height and accumulate biomass quickly following disturbance, which, over several years without burning can contribute a large fraction to the surface fuel load (Kreye et al., 2014; McNab et al., 1978). In stands with a shrub-dominated understory, as is typical for pine flatwoods, potential fire behavior can increase to undesirable levels within five years of treatment due to high fuel loading of shrubs and litter (Brose and Wade, 2002). To control accumulations of hazardous fuels, including shrubs, management activities focus on: (1) continually top-killing shrubs to keep fuel loading and heights low, or (2) contributing to shrub mortality to reduce the capacity of vegetation to fully recover and thereby reduce the maximum level of accumulation that is possible between treatments. Frequent prescribed burning over the past 20 years at our plots has maintained relatively low loading and height of shrubs relative to long-unburned pine flatwoods where shrub fuel loading can be considerably higher (Kreye et al., 2014). Given the recent management history of our plots, initial fuel loads, and therefore the total amount that could be reduced following prescribed burns, were well below those associated with a high difficulty of fire suppression (Brose and Wade, 2002). Changes in shrub cover before and after treatment for growing and dormant season burns (Figure 3-4) were also well below Hough and Albini's (1978) 15, 50, and 85 percent palmetto cover categories that correspond to saw palmetto quantities above which marked changes in fire behavior are expected. Furthermore, pre- and post-treatment shrub cover for both season-of-burn treatments was not significantly different suggesting shrub cover returns to pre-fire levels rapidly.

### 3.5.2 *Herb dynamics*

Measures of the herb fuel layer did not differ between season-of-burn treatments. Other studies in southeastern pine-dominated ecosystems show there to be wide variability in herb response to single burns (e.g., Brewer, 2006; Hiers et al., 2000) suggesting that it can be difficult to assess a treatment effect when species with different phenology and response to fire are grouped together by life form. Variability in post-fire regrowth has also been observed within a single species (Sparks et al., 1998) suggesting that multiple factors can influence herb growth following a single fire. While we attempted to control for some factors by selecting compositionally comparable plots and using in-fire temperature measurements to adjust for differences in fire intensity, other confounding factors may have been present. For instance, our study locations were substantially colder and wetter than normal during the dormant season burn treatments, and warmer and slightly drier than normal during the growing season burn treatments (Figure 3-6). Since precipitation during the growing season is known to affect herb growth in pine flatwoods (Grelen and Lohrey, 1978), effects of season-of-burn may have been overwhelmed by a departure from normal precipitation levels from the dormant to the growing season. In addition, we may not have detected a season-of-burn effect on herbaceous fuels due to the coarse temporal scale (i.e., annual) of our post-treatment measurements. Although one year is a relevant time-step for prescribed fire and fuels management, detecting the effect of a single season-of-burn treatment on herbs may require weekly or monthly sampling as was conducted in other studies that did observe effects related to season-of-burning (Hiers et al., 2000; Platt et al., 1988; Shepherd et al., 2012).

Potential fire behavior is unlikely to be affected by the small variations in the herb layer we observed because, as with the shrub layer, herb cover, fuel loading, and height were well below thresholds known to produce extreme fire behavior. By virtue of its overall lower fuel loading, the herb fuel stratum in pine flatwoods does not contribute to fire behavior to the same degree as other fuels that comprise a greater portion of the total fuelbed such as shrubs and litter. Fire behavior observations in grasslands (Cheney et al., 1998; Setterfield et al., 2010) and laboratory settings (Kreye et al., 2013) show that fuel loading must change by several megagrams per hectare to substantially affect fire behavior. At our plots herb loading ranged from 0.10 to 2.39 Mg $ha^{-1}$ and on average comprised only 13.7 ± 1.4 percent of the total fine fuel loading.

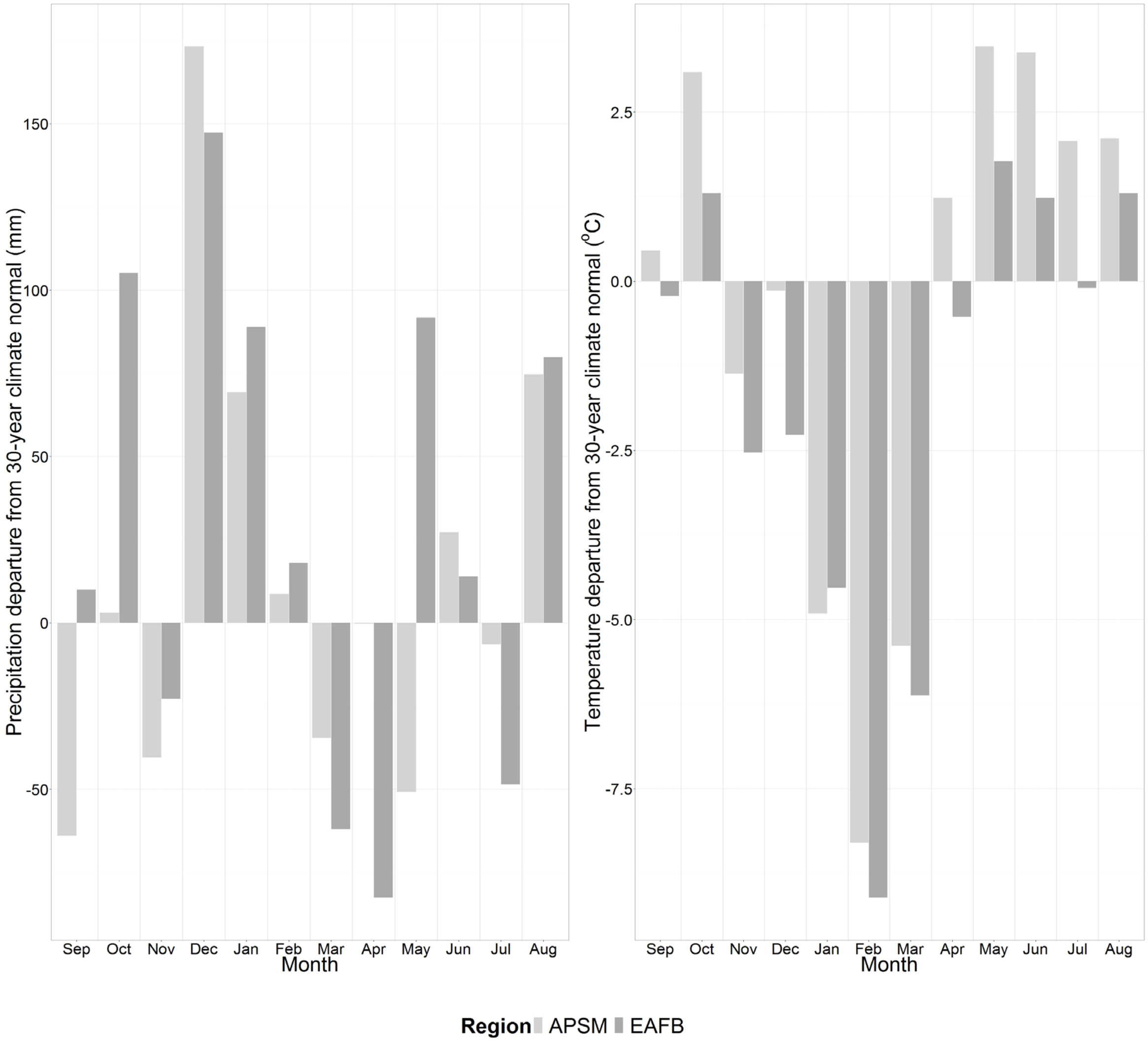


**Figure 3-6.** Departure from 1971-2000 precipitation and temperature climate normals (National Oceanic and Atmospheric Association (NOAA) 2002) for APSM (NOAA Cooperative Station ID 088758, Tallahassee, Florida) and EAFB (NOAA Cooperative Station ID 086240, Niceville, Florida) in study area during a 12-month period surrounding the burn treatments from September 2009 to August 2010.

### 3.5.3 *Predicted fire behavior*

Predicted fire behavior for post-treatment fuelbeds for plots burned in the dormant and growing seasons were not different. This not only reflects the nonsignificant effects of season-of-burn on the recovery of live fuels at our plots, but also the relatively low loading of total fine surface fuels in frequently burned pine flatwoods. The range of biomass of total fine surface fuels (i.e., shrubs, herbs, litter, and downed-woody fuels < 2.54 cm in diameter) for all plots and sampling times in this study ranged from 4.25 to 10.41 Mg ha$^{-1}$ and represents the lower end of sampled fuel conditions in studies that have assessed fire behavior in forested ecosystems in the US. For instance, Brose and Wade (2002) sampled fuels before and after fuels reduction treatments in pine plantations and pine flatwoods in northern Florida and found that total fine surface fuel loading ranged from 4.46 to 60.87 Mg ha$^{-1}$. They also report that predicted fire behavior would result in low difficulty of fire suppression for plots with total fine surface fuel loading up to 26.77 Mg ha$^{-1}$. Other studies throughout the US have examined the effect of fuel treatments on fire behavior and found that substantial differences in fire behavior were associated with changes in total fine surface fuel loading on the order of 10s of Mg ha$^{-1}$ (McGinnis et al., 2010; Youngblood et al., 2008), further highlighting the narrow range of sampled fuel conditions and fire potential at the low end of the continuum that our plots represent. In their current state the fuels on our plots are what would be considered well-managed, and any changes associated with season-of-burn treatments would not influence fire behavior on a scale likely to affect fire control efforts.

The litter layer plays an important role in fire behavior for fuel types with a longleaf pine overstory (Mitchell et al., 2009; Wahlenberg, 1946), such as pine flatwoods, and pine-dominated ecosystems with a low severity fire regime, in general (Agee, 1998). Pine litter is important in the longleaf pine flatwoods fuel type because needles have high energy content (Reid and Robertson, 2012) and the overstory can quickly produce enough litterfall annually to create a continuous fine dead fuel layer that will readily carry fire.  There is also a synergistic effect with the herb fuel layer, primarily bunchgrasses, which, when dominant, can loft litter and orient individual needles vertically (Hendricks et al., 2002). This orientation of the litter increases the rate of litter drying (Nelson and Hiers, 2008) and the probability of ignition. Litter depth was highly correlated with predicted ROS and FL and litter fuel loading, while not a direct input into FCCS, would have been highly correlated with these measures of fire behavior. Cover of litter was less correlated with predicted fire behavior because there was little variation in coverage (86.3 ± 1.6 percent) among plots for each sampling time. For this study litter was the dominant fine surface fuel, accounting for 47.9 ± 1.7 percent of total fine surface fuel loading on average. In other studies of fuels in pine flatwoods, litter accounted for an even larger fraction of total fine surface fuels. Kreye et al. (2014) recorded litter fuel loading of 11.1 to 14.3 Mg ha$^{-1}$ which was 74.1 and 69.4 percent, respectively, of total fine surface fuel loading, 1-2 years after mowing treatments in burned, mature pine flatwoods on the Osceola National Forest in northern Florida, approximately 170 km east of our easternmost plots. The high correlation we observed between herb cover and loading with RI is surprising as herbs were a relatively minor component of the surface fuel complex on our plots. The high herb layer correlation with predicted RI was a function of the manner in which the FCCS fire spread model partitions RI calculations by individual fuelbed strata making it sensitive to different fuel moisture levels for each stratum. In our environmental benchmark scenario, herb fuel moisture was lower than shrub fuel moisture (60 percent v. 90 percent), which may have over-weighted the influence of the herb fuel layer.

### 3.6 Management implications

Existing literature consistently points to the length of the fire-free interval as a driver of fuel composition and amount, and of potential fire behavior in pine flatwoods (Brose and Wade, 2002; Hough and Albini, 1978; Kreye et al., 2014), and suggests that land managers should prioritize frequent burning (< 5 years) to maintain low fuel loading (O'Brien et al., 2010). Our results showed that a single growing season prescribed fire did not affect live fuel recovery or predicted fire behavior differentially than a dormant season prescribed fire for up to two years following burning for frequently burned pine flatwoods. Based on this study, managers should not expect dramatic changes in fuel amounts, composition, structure, or fire behavior in this ecosystem regardless of season-of-burn following a single prescribed fire.

This study examined the effects of burning in the dormant and growing seasons on fuel recovery and found only subtle differences; management decisions should carefully weigh treatment goals, not just on the effects on potential fire behavior. For instance, the decision to use prescribed fire in pine flatwoods to restore or maintain habitat characteristics or understory plant diversity may take precedence over simply maintaining low fuel loading levels. An open understory with a large wiregrass component is desirable for some rare species that prefer an open herbaceous understory such as the red-cockaded woodpecker (James et al., 1997; Van Balen and Doerr, 1978) and gopher tortoise (Cox et al., 1987). For ecological goals such as these, a single growing season burn may produce beneficial effects. For example, Shepherd et al. (2012) found that relative to dormant season burning, a single growing season burn increased seed production for some grass species common to pine savannas. While decades of dormant season prescribed burning have shown that hazardous fuels in pine flatwoods can be managed effectively with prescribed fire, incorporating growing season prescribed fire may help to achieve ecological goals while maintaining acceptable surface fuel levels if burns can be conducted with sufficient frequency (i.e., at least once every 5 years).

Pine flatwoods typically occur as part of a mosaic of multiple vegetation types with different fire regimes and management goals within operational prescribed fire boundaries. Design and implementation of prescribed fire burning regimes should incorporate frequency and season-of-burn and should consider management objectives for all vegetation types.

Based on other published work (Glitzenstein et al., 2003; Haywood et al., 2001) we expect that multiple burns spaced at short intervals (1–3 years) and consistently applied in the growing season may incrementally change the composition, amount, and structure of live surface fuels and alter potential fire behavior. While initial changes associated with growing season burning may initially be subtle, managers should monitor live fuels as cumulative incremental changes may produce a fuel complex with different fire behavior characteristics. Over longer periods of time, however, repeated burning at short fire-return intervals (1–2 years) has been shown to substantially reduce shrubs (Brockway and Lewis, 1997), especially for burns conducted in the growing season in some geographic regions in the pine flatwoods ecosystem (Glitzenstein et al., 2003; Haywood et al., 2001).

## 3.7 **References**

Agee, J.K., 1998. Fire and pine ecosystems, in: Richardson, D.M. (Ed.), Ecology and Biogeography of the *Pinus*. Cambridge University Press, Cambridge, United Kingdom, pp. 193–218.

Agee, J.K., Skinner, C.N., 2005. Basic principles of forest fuel reduction treatments. For. Ecol. Manage. 211, 83–96. https://doi.org/10.1016/j.foreco.2005.01.034

Allen, W.J., 1991. Soil survey of Wakulla County, Florida. USDA Soil Conservation Service, Washington, DC.

Anderson, H.E., 1982. Aids to determining fuel models for estimating fire behavior. USDA Forest Service, Gen. Tech. Rep. INT-122, Ogden, Utah. https://doi.org/https://doi.org/10.2737/INT-GTR-122

Andreu, A.G., Shea, D., Parresol, B.R., Ottmar, R.D., 2012. Evaluating fuel complexes for fire hazard mitigation planning in the southeastern United States. For. Ecol. Manage. 273, 4–16. https://doi.org/DOI 10.1016/j.foreco.2011.06.040

Bale, A.M., 2009. Fire effects and litter accumulation dynamics in a montane longleaf pine ecosystem. Masters Thesis. University of Missouri, Columbia, Missouri.

Boyer, W.D., 1990. *Pinus palustris* Mill. (longleaf pine), in: Burns, R.M., Honkala, B.H. (Eds.), Silvics in North America, Volume 1, Conifers. USDA, Forest Service, Washington, DC, pp. 405–412.

Brewer, J.S., 2006. Long-term population changes of a fire-adapted plant subjected to different fire seasons. Nat. Areas J. 26, 267–273. https://doi.org/10.3375/0885-8608(2006)26[267:lpcoaf]2.0.co;2

Brockway, D.G., Lewis, C.E., 1997. Long-term effects of dormant-season prescribed fire on plant community diversity, structure and productivity in a longleaf pine wiregrass ecosystem. For. Ecol. Manage. 96, 167–183. https://doi.org/https://doi.org/10.1016/S0378-1127(96)03939-4

Brose, P., 2010. Long-term effects of single prescribed fires on hardwood regeneration in oak shelterwood stands. For. Ecol. Manage. 260, 1516–1524. https://doi.org/10.1016/j.foreco.2010.07.050

Brose, P., Wade, D., 2002. Potential fire behavior in pine flatwood forests following three different fuel reduction techniques. For. Ecol. Manage. 163, 71–84.

https://doi.org/https://doi.org/10.1016/S0378-1127(01)00528-X

Brown, J.K., 1974. Handbook for inventorying downed woody material. USDA Forest Service, Gen. Tech. Rep. INT-16, Ogden, Utah.

Burgan, R.E., Rothermel, R.C., 1984. BEHAVE: fire behavior prediction and fuel modeling system: FUEL subsystem. USDA Forest Service, Gen. Tech. Rep. INT-167, Ogden, Utah. https://doi.org/https://doi.org/10.2737/INT-GTR-167

Canfield, R.H., 1941. Application of the line interception method in sampling range vegetation. J. For. 39, 388–394. https://doi.org/https://doi.org/10.1093/jof/39.4.388

Cheney, N.P., Gould, J.S., Catchpole, W.R., 1998. Prediction of fire spread in grasslands. Int. J. Wildl. Fire 8, 1–13. https://doi.org/10.1071/wf9980001

Conner, R.N., Saenz, D., Rudolph, D.C., 2004. The red-cockaded woodpecker: interactions with fire, snags, fungi, rat snakes and pileated woodpeckers. Texas J. Sci. 56, 415–426.

Cox, J., Inkley, D., Kautz, R., 1987. Ecology and habitat needs of gopher tortoise (*Gopherus polyphemus*) populations found on lands slated for large-scale development in Florida. Florida Game and Fresh Water Fish Commission, Nongame Wildlife Program Technical Report No. 4, Tallahassee, Florida.

Crawley, M.J., 2007. Mixed effect models, in: The R Book. Wiley, Chichester, England; Hoboken, NJ, USA, pp. 627–660. https://doi.org/DOI:10.1007/s00362-008-0118-3

Eisenberg, J., 1983. The gopher tortoise as a keystone species, in: Bryant, R.J., Franz, R. (Eds.), The Gopher Tortoise: A Keystone Species: Proceedings of the 4th Annual Meeting of the Gopher Tortoise Council. Gopher Tortoise Council, Valdosta, Georgia, pp. 1–4.

Ferguson, E.R., 1957. Stem-kill and sprouting following prescribed fires in a pine-hardwood stand in Texas. J. For. 55, 426–429.

Ferguson, J.P., 1998. Prescribed fire on the Apalachicola Ranger District: the shift from dormant season to growing season and effects on wildfire suppression, in: Pruden, T.L., Brennan, L.A. (Eds.), Fire in Ecosystem Management: Shifting the Paradigm from Suppression to Prescription, Tall Timbers Fire Ecology Conference Proceedings No. 20. Tall Timbers Research Station, Tallahassee, Florida, pp. 120–126. https://doi.org/https://doi.org/10.1046/j.1526-100x.2000.80045.x

Glitzenstein, J.S., Streng, D.R., Masters, R.E., Robertson, K.M., Hermann, S.M., 2012. Fire-frequency effects on vegetation in north Florida pinelands: another look at the long-term Stoddard Fire Research Plots at Tall Timbers Research Station. For. Ecol. Manage. 264, 197–209. https://doi.org/DOI 10.1016/j.foreco.2011.10.014

Glitzenstein, J.S., Streng, D.R., Wade, D.D., 2003. Fire frequency effects on longleaf pine (*Pinus palustris*, P. Miller) vegetation in South Carolina and northeast Florida, USA. Nat. Areas J. 23, 22–37.

Grelen, H.E., Epps, E.A., 1967. Season of burning affects herbage quality and yield on pine-bluestem range. J. Range Manag. 20, 31–33. https://doi.org/http://dx.doi.org/10.2307/3896287

Grelen, H.E., Lohrey, R.E., 1978. Herbage yield related to basal area and rainfall in a thinned longleaf plantation. USDA Forest Service, Res. Note SO-232, New Orleans, Louisiana.

Hardin, E.D., White, D.L., 1989. Rare vascular plant taxa associated with wiregrass (*Aristida stricta*) in the southeastern United States. Nat. Areas J. 9, 234–245.

Haywood, J.D., Harris, F.L., Grelen, H.E., Pearson, H.A., 2001. Vegetative response to 37 years of seasonal burning on a Louisiana longleaf pine site. South. J. Appl. For. 25, 122–130. https://doi.org/10.1093/sjaf/25.3.122

Henderson, J.P., 2006. Dendroclimatological analysis and fire history of longleaf pine (*Pinus palustris* Mill.) in the Atlantic and Gulf Coastal Plain. Dissertation. University of Tennessee, Knoxville, Tennessee.

Hendricks, J.J., Wilson, C.A., Boring, L.R., 2002. Foliar litter position and decomposition in a fire-maintained longleaf pine-wiregrass ecosystem. Can. J. For. Res. 32, 928–941. https://doi.org/Doi 10.1139/X02-020

Hiers, J.K., Wyatt, R., Mitchell, R.J., 2000. The effects of fire regime on legume reproduction in longleaf pine savannas: Is a season selective? Oecologia 125, 521–530. https://doi.org/https://doi.org/10.1007/s004420000469

Hough, W.A., 1968. Carbohydrate reserves of saw-palmetto: seasonal variation and effects of burning. For. Sci. 14, 399–405. https://doi.org/https://doi.org/10.1093/forestscience/14.4.399

Hough, W.A., Albini, F.A., 1978. Predicting fire behavior in palmetto-gallberry fuel complexes. USDA Forest Service, Res. Pap. SE-174, Asheville, North Carolina.

Hughes, R.H., Knox, F.E., 1964. Response of gallberry to seasonal burning. USDA Forest Service, Res. Note SE-21, Asheville, North Carolina.

James, F.C., Hess, C.A., Kufrin, D., 1997. Species-centered environmental analysis: indirect effects of fire history on red-cockaded woodpeckers. Ecol. Appl. 7, 118–129. https://doi.org/10.2307/2269411

Johansson, T., 1985. Estimating canopy density by the vertical tube method. For. Ecol. Manage. 11, 139–144. https://doi.org/10.1016/0378-1127(85)90063-5

Kennard, D.K., Outcalt, K.W., Jones, D., OBrien, J.J., 2005. Comparing techniques for estimating flame temperature of prescribed fires. Fire Ecol. 1, 75–84. https://doi.org/DOI:

10.4996/fireecology.0101075

Knapp, E.E., Estes, B.L., Skinner, C.N., 2009. Ecological effects of prescribed fire season: a literature review and synthesis for managers. USDA Forest Service, Gen. Tech. Rep. PSW-224, Redding, California. https://doi.org/https://doi.org/10.2737/PSW-GTR-224

Kottek, M., Grieser, J., Beck, C., Rudolf, B., Rubel, F., 2006. World map of the Koppen-Geiger climate classification updated. Meteorol. Zeitschrift 15, 259–263. https://doi.org/10.1127/0941-2948/2006/0130

Kreye, J.K., Kobziar, L.N., Camp, J.M., 2014. Immediate and short-term response of understory fuels following mechanical mastication in a pine flatwoods site of Florida, USA. For. Ecol. Manage. 313, 340–354. https://doi.org/10.1016/j.foreco.2013.10.034

Kreye, J.K., Kobziar, L.N., Zipperer, W.C., 2013. Effects of fuel load and moisture content on fire behaviour and heating in masticated litter-dominated fuels. Int. J. Wildl. Fire 22, 440–445. https://doi.org/10.1071/wf12147

Liu, C.X., Harcombe, P.A., Knox, R.G., 2004. Structural changes after prescribed fire in woody plant communities of southeastern Texas. Texas J. Sci. 56, 319–334.

Marshall, D.J., Wimberly, M., Bettinger, P., Stanturf, J.A., 2008. Synthesis of knowledge of hazardous fuels management in loblolly pine forests. USDA Forest Service, Gen. Tech. Rep. SRS-110, Asheville, North Carolina. https://doi.org/https://doi.org/10.2737/SRS-GTR-110

McGinnis, T.W., Keeley, J.E., Stephens, S.L., Roller, G.B., 2010. Fuel buildup and potential fire behavior after stand-replacing fires, logging fire-killed trees and herbicide shrub removal in Sierra Nevada forests. For. Ecol. Manage. 260, 22–35. https://doi.org/DOI 10.1016/j.foreco.2010.03.026

McNab, W.H., Edwards, M.B., Hough, W.A., 1978. Estimating fuel weights in slash pine-palmetto stands. For. Sci. 24, 345–358. https://doi.org/https://doi.org/10.1093/forestscience/24.3.345

McWhite, R.W., Furman, J., Petrick, C.J., 1999. Eglin Air Force Base integrated natural resources transitional plan 1998-2001. US Department of Defense, Air Force, Natural Resources Management Branch, Niceville, Florida.

Mitchell, R.J., Hiers, J.K., O'Brien, J.J., Starr, G., 2009. Ecological forestry in the Southeast: understanding the ecology of fuels. J. For. 107, 391–397. https://doi.org/https://doi.org/10.1093/jof/107.8.391

Nelson, R.M., Hiers, J.K., 2008. The influence of fuelbed properties on moisture drying rates and timelags of longleaf pine litter. Can. J. For. Res. 38, 2394–2404. https://doi.org/https://doi.org/10.1139/X08-078

O'Brien, J.J., Mordecai, K.A., Wolcott, L., Snyder, J., Outcalt, K.W., 2010. Fuel managers field guide: hazardous fuels management in subtropical pine flatwoods and tropical pine rocklands. USDA Forest Service, Gen. Tech. Rep. SRS-123, Asheville, North Carolina. https://doi.org/https://doi.org/10.2737/SRS-GTR-123

Olson, M.S., Platt, W.J., 1995. Effects of habitat and growing-season fires on resprouting of shrubs in longleaf pine savannas. Vegetatio 119, 101–118. https://doi.org/https://doi.org/10.1007/BF00045593

Ottmar, R.D., Sandberg, D.V., Riccardi, C.L., Prichard, S.J., 2007. An overview of the Fuel Characteristic Classification System - quantifying, classifying, and creating fuelbeds for resource planning. Can. J. For. Res. 37, 2383–2393. https://doi.org/https://doi.org/10.1139/X07-077

Overing, J.D., Watts, F.C., 1989. Soil survey of Walton County, Florida. USDA Soil Conservation Service, Washington, DC.

Overing, J.D., Weeks, H.H., Wilson Jr., J.P., Sullivan, J., Ford, R.D., 1995. Soil survey of Okaloosa County, Florida. USDA Soil Conservation Service, Washington, DC.

Platt, W.J., Evans, G.W., Davis, M.M., 1988. Effects of fire season on flowering of forbs and shrubs in longleaf pine forests. Oecologia 76, 353–363. https://doi.org/https://doi.org/10.1007/BF00377029

R Development Core Team, 2014. R: A language and environment for statistical computing [Computer software]. Foundation for Statistical Computing, Vienna. https://www.r-project.org/.

Reid, A.M., Robertson, K.M., 2012. Energy content of common fuels in upland pine savannas of the south-eastern US and their application to fire behaviour modelling. Int. J. Wildl. Fire 21, 591–595. https://doi.org/http://dx.doi.org/10.1071/WF10139

Riccardi, C.L., Ottmar, R.D., Sandberg, D.V., Andreu, A.G., Elman, E., Kopper, K., Long, J., 2007a. The fuelbed: a key element of the Fuel Characteristic Classification System. Can. J. For. Res. 37, 2394–2412. https://doi.org/https://doi.org/10.1139/X07-143

Riccardi, C.L., Prichard, S.J., Sandberg, D.V., Ottmar, R.D., 2007b. Quantifying physical characteristics of wildland fuels using the Fuel Characteristic Classification System. Can. J. For. Res. 37, 2413–2420. https://doi.org/https://doi.org/10.1139/X07-175

Robbins, L.E., Myers, R.L., 1992. Seasonal effects of prescribed burning in Florida: a review. Tall Timbers Research Station, Miscellaneous Publication No. 8, Tallahassee, Florida.

Robertson, K.M., Hmielowski, T.L., 2014. Effects of fire frequency and season on resprouting of woody plants in southeastern US pine-grassland communities. Oecologia 174, 765–776.

https://doi.org/DOI 10.1007/s00442-013-2823-4

Rothermel, R.C., 1972. A mathematical model for predicting fire spread in wildland fuels. USDA Forest Service, Res. Pap. INT-115, Ogden, Utah.

Ryan, K.C., Knapp, E.E., Varner, J.M., 2013. Prescribed fire in North American forests and woodlands: history, current practice, and challenges. Front. Ecol. Environ. 11, e15–e24. https://doi.org/10.1890/120329

Saglam, B., Bilgili, E., Kucuk, O., Durmaz, B.D., 2008. Fire behavior in Mediterranean shrub species (Maquis). African J. Biotechnol. 7, 4122–4129. https://doi.org/https://doi.org/10.4314/ajb.v7i22.59536

Sandberg, D.V., Riccardi, C.L., Schaaf, M.D., 2007. Reformulation of Rothermel's wildland fire behaviour model for heterogeneous fuelbeds. Can. J. For. Res. 37, 2438–2455. https://doi.org/10.1139/x07-094

Sanders, T.E., 1981. Soil survey of Leon County, Florida. USDA Soil Conservation Service, Washington, DC.

Schroeder, R.L., 1985. Habitat suitability index models: northern bobwhite. USDI Fish and Wildlife Service, Bio. Rep. 82 (10.104), Washington, DC.

Schwilk, D.W., Keeley, J.E., Knapp, E.E., McIver, J., Bailey, J.D., Fettig, C.J., Fiedler, C.E., Harrod, R.J., Moghaddas, J.J., Outcalt, K.W., Skinner, C.N., Stephens, S.L., Waldrop, T.A., Yaussy, D.A., Youngblood, A., 2009. The national Fire and Fire Surrogate study: effects of fuel reduction methods on forest vegetation structure and fuels. Ecol. Appl. 19, 285–304. https://doi.org/https://doi.org/10.1890/07-1747.1

Scott, J.H., Burgan, R.E., 2005. Standard fire behavior fuel models: a comprehensive set for use with Rothermel's surface fire spread model. USDA Forest Service, Gen. Tech. Rep. RMRS-

153, Fort Collins, Colorado. https://doi.org/https://doi.org/10.2737/RMRS-GTR-153

Setterfield, S.A., Rossiter-Rachor, N.A., Hutley, L.B., Douglas, M.M., Williams, R.J., 2010. Turning up the heat: the impacts of *Andropogon gayanus* (gamba grass) invasion on fire behaviour in northern Australian savannas. Divers. Distrib. 16, 854–861. https://doi.org/DOI 10.1111/j.1472-4642.2010.00688.x

Shepherd, B.J., Miller, D.L., Thetford, M., 2012. Fire season effects on flowering characteristics and germination of longleaf pine (*Pinus palustris*) savanna grasses. Restor. Ecol. 20, 268–276. https://doi.org/10.1111/j.1526-100X.2010.00759.x

Sparks, J.C., Masters, R.E., Engle, D.M., Bukenhofer, G.A., 2002. Season of burn influences fire behavior and fuel consumption in restored shortleaf pine-grassland communities. Restor. Ecol. 10, 714–722. https://doi.org/https://ui.adsabs.harvard.edu/link_gateway/2002ResEc..10..714S/doi:10.1046/j.1526-100X.2002.01052.x

Sparks, J.C., Masters, R.E., Engle, D.M., Palmer, M.W., Bukenhofer, G.A., 1998. Effects of late growing-season and late dormant-season prescribed fire on herbaceous vegetation in restored pine-grassland communities. J. Veg. Sci. 9, 133–142. https://doi.org/https://doi.org/10.2307/3237231

Stambaugh, M.C., Guyette, R.P., Marschall, J.M., 2011. Longleaf pine (*Pinus palustris* Mill.) fire scars reveal new details of a frequent fire regime. J. Veg. Sci. 22, 1094–1104. https://doi.org/10.1111/j.1654-1103.2011.01322.x

Stanturf, J.A., Wade, D.D., Waldrop, T.A., Kennard, D.K., Achtemeier, G.L., 2002. Background paper: fire in southern forest landscapes, in: Wear, D.N., Greis, J.G. (Eds.), Southern Forest Resource Assessment. USDA Forest Service, Gen. Tech. Rep. SRS-53, Asheville, North

Carolina, pp. 607–630. https://doi.org/https://doi.org/10.2737/SRS-GTR-53

Stephens, S.L., McIver, J.D., Boerner, R.E.J., Fettig, C.J., Fontaine, J.B., Hartsough, B.R., Kennedy, P.L., Schwilk, D.W., 2012. The effects of forest fuel-reduction treatments in the United States. Bioscience 62, 549–560. https://doi.org/DOI 10.1525/bio.2012.62.6.6

Stephens, S.L., Ruth, L.W., 2005. Federal forest-fire policy in the United States. Ecol. Appl. 15, 532–542. https://doi.org/https://doi.org/10.1890/04-0545

Stephenson, S.N., Buell, M.F., 1965. The reproducibility of shrub cover sampling. Ecology 46, 379–380. https://doi.org/Doi 10.2307/1936352

Tukey, J.W., 1953. The problem of multiple comparisons.

Van Balen, J.B., Doerr, P.D., 1978. The relationship of understory vegetation to red-cockaded woodpecker activity, in: Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies. pp. 82–92.

Wahlenberg, W.G., 1946. Longleaf Pine: Its Use, Ecology, Regeneration, Protection, Growth, and Management, 1st ed. Charles Lathrop Pack Forestry Foundation, Washington, DC.

Waldrop, T.A., Van Lear, D.H., Lloyd, F.T., Harms, W.R., 1987. Long-term studies of prescribed burning in loblolly pine forests of the Southeastern Coastal Plain. USDA Forest Service, Gen. Tech. Rep. SE-45, Asheville, North Carolina. https://doi.org/https://doi.org/10.2737/SE-GTR-45

Wally, A.L., Menges, E.S., Weekley, C.W., 2006. Comparison of three devices for estimating fire temperatures in ecological studies. Appl. Veg. Sci. 9, 97–108. https://doi.org/10.1658/1402-2001(2006)9[97:cotdfe]2.0.co;2

Willcox, E.V., Giuliano, W.M., 2010. Seasonal effects of prescribed burning and roller chopping on saw palmetto in flatwoods. For. Ecol. Manage. 259, 1580–1585.

https://doi.org/10.1016/j.foreco.2010.01.034

Wotton, B.M., Gould, J.S., McCaw, W.L., Cheney, N.P., Taylor, S.W., 2012. Flame temperature and residence time of fires in dry eucalypt forest. Int. J. Wildl. Fire 21, 270–281. https://doi.org/Doi 10.1071/Wf10127

Wright, C.S., 2013. Fuel consumption models for pine flatwoods fuel types in the southeastern United States. South. J. Appl. For. 37, 148–159. https://doi.org/Doi 10.5849/Sjaf.12-006

Yospin, G.I., Bridgham, S.D., Kertis, J., Johnson, B.R., 2012. Ecological correlates of fuel dynamics and potential fire behavior in former upland prairie and oak savanna. For. Ecol. Manage. 266, 54–65. https://doi.org/DOI 10.1016/j.foreco.2011.10.046

Youngblood, A., Wright, C.S., Ottmar, R.D., McIver, J.D., 2008. Changes in fuelbed characteristics and resulting fire potentials after fuel reduction treatments in dry forests of the Blue Mountains, northeastern Oregon. For. Ecol. Manage. 255, 3151–3169. https://doi.org/https://doi.org/10.1016/j.foreco.2007.09.032

# Chapter 4. Effects of a managed fire regime and forest structure on understory composition in frequently burned mesic flatwoods in northwestern Florida

## 4.1 **Abstract**

Grass-dominated ecosystems including grasslands, savannas, and woodlands are a globally important biome. Their ecological functions and species diversity are in large part maintained by frequent, low intensity fire. Longleaf pine (*Pinus palustris*) ecosystems are part of this biome, and the fire regime has been maintained with prescribed fire for several decades. Land managers utilize prescribed fire that to some extent emulates historic fire regimes, which sustained low-density stands with an open understory and high diversity and abundance of understory grasses and forbs. Long-term, controlled experiments applying prescribed fire in longleaf pine stands provide consistent evidence that frequent annual or biennial burning, especially when combined with growing season burns, shifts plant abundance from woody to herbaceous plants: a response observed in fire-adapted ecosystems globally. The goal of this study was to evaluate the effects of frequent prescribed fire and forest structure on understory composition in mesic longleaf pine flatwoods. I measured understory biomass and forest structure in 22 stands representing a range of understory vegetation states, from herb to shrub dominance. A 20-year history of prescribed burns and wildfire for each stand was compiled from management records. Constrained multivariate ordination was used to test whether explanatory variables (i.e., prescribed fire history and forest structure) affected understory biomass, grouped by genera and plant functional groups. Boundary line regression further assessed effects on individual species and plant functional groups. Mean fire interval (MFI) and coarse woody debris biomass had marginally significant effects on understory composition. These variables, though

uncorrelated, weakly aligned with the first Principal Components axis where sites were arranged along a compositional gradient from typical understory shrubs and the dominant grass *Aristida beyrichiana* to sites characterized by vines and understory hardwoods. Boundary line regression showed a significant negative relationship between forbs and MFI, however this relationship did not extend to graminoids. Boundary line regression did not show any significant effects of MFI on measures of woody plant biomass. Season-of-burn had no significant effects on understory plants in the constrained ordination or boundary line regression. These results suggest that other environmental factors in concert with fire regime characteristics more favorable to fire sensitive species were insufficient to significantly influence understory vegetation dynamics. Managers tasked with shifting understory vegetation toward greater herb abundance in longleaf pine flatwoods may find that longer fire frequencies (i.e., more than the annual and biennial burns used to produce such effects in controlled studies) will be insufficient. Even with consistently applied annual or biennial prescribed fire, small-scale trials or frequent monitoring will still be necessary to ensure progress as other environmental factors may hinder efforts to shift understory composition.

## 4.2 Introduction

Grass-dominated ecosystems cover 37 percent of the Earth’s land area (O’Mara, 2012). They provide habitat for large mammals (Fritz and Loison, 2006; Vynne et al., 2022), harbor extensive biodiversity (Roleček et al., 2019; Wilson et al., 2012), are the source of commercially important grain crops (Zohary et al., 2000), support the livelihood of one fifth of global human population (Suttie et al., 2005), and play a major role in carbon storage and wildfire emissions (Grace et al., 2006; van der Werf et al., 2017). Accounting for *c.* 80 percent of global annual area burned (Fernández-García and Alonso-González, 2023), these ecosystems are dependent on frequent fire (Frost and Robertson, 1987). Plants have evolved uniquely fire-adapted traits (Maurin et al., 2014; Simon and Pennington, 2012; Wahlenberg, 1946) in response to millions of years of coexistence with fire (Cerling et al., 1997; Edwards et al., 2010; Scheiter et al., 2012). When climate or soil conditions are not limiting to tree growth, the persistence of these ecosystems is dependent on regularly occurring fires (Bond and Keeley, 2005). Fire plays an important role in promoting biodiversity (He et al., 2019; Pausas and Ribeiro, 2017). This relationship has been observed across grass-dominated ecosystems including grasslands in South Africa (Gordijn and O'Connor, 2021), the Brazilian cerrado (Teixeira et al., 2022), grasslands of the mid-western United States (US; Alstad et al., 2016) , and the pine savannas of the southeastern US (Abrahamson et al., 2021). Plant diversity in these ecosystems is concentrated in the herbaceous layer (Veldman et al., 2015) and is threatened by fire exclusion which permits encroachment of woody vegetation. Woody plants outcompete herbaceous species and can ultimately lead to localized extinction (Lehmann et al., 2014; Nayak et al., 2014; Toribio-Diaz et al., 2019). The conversion of grass-dominated systems to closed-canopy forests or shrublands can further diminish biological diversity by degrading wildlife habitat (Bowles et al., 2003; Brudvig et al., 2014; Leach and Givnish, 1996; Teixeira et al., 2022; Titshall et al., 2000). While fire exclusion is a major source of ecological degradation in these ecosystems (Bond et al., 2005; Gold et al., 2023), less dramatic changes in the fire regime can also have important impacts on biodiversity and habitat on lands where fire is frequent enough to control woody encroachment (Palmquist et al., 2014).

Relatively small changes in fire regime characteristics, such as a mean fire interval (MFI) of just a few years outside the historical range of variability and shifting burn seasonality, have been linked to changes in biodiversity in grass-dominated ecosystems. The intermediate disturbance hypothesis (IDH), which posits that a moderate level of disturbance optimizes diversity by favoring both r- and K-selected species (Connell, 1978), is often cited as a conceptual framework for understanding how small changes in MFI can affect plant composition (Dee and Menges, 2014; Gordijn et al., 2018; Nayak et al., 2014). However, it is worth noting that other relationships between fire frequency and plant diversity have also been observed. Plant diversity was maximized by the highest frequency of fire permitted by fuels in pine savannas of the southeastern US (Brewer, 2023; Glitzenstein et al., 2003). Conversely species richness in tallgrass prairies of the upper mid-western US increased as the fire interval lengthened from one to four years (Collins et al., 1995) and measures of diversity in jarrah forests of Australia were unaffected by large changes in fire frequency (Burrows et al., 2019). These observations show a range of sensitivity to fire frequency that, in some cases, shift species richness and understory plant composition when deviations are a few years on either side of historical MFIs. Understory diversity and composition can be sensitive to small changes in fire frequency because reproduction and survival of woody species and longer-lived perennial herbs are increasingly limited as MFI falls below 3–5 years. In such cases dominant understory vegetation can shift from woody, to perennial, and then to annual species as MFI shortens. The inverse happens as MFI lengthens. The combined effect of increased shade and decreased mineral soil cover can reduce the presence of annual herbs. Fire exclusion frequently results in a type shift to woody plant-dominated communities and localized extinctions of herbaceous species (Archer et al., 2017). Seasonality of fires can also influence species richness (Gordijn and O’Connor, 2021) and understory composition (Meller et al., 2022; White et al., 1991), although to a lesser extent than MFI. Other environmental factors, including moisture, soils, nutrient availability, herbivory, and evolutionary adaptations of plant species have interactions with fire to influence the degree that fire frequency and seasonality affect understory plant composition and measures of diversity (Frost and Robertson, 1987).

The longleaf pine (*Pinus palustris* Mill.) ecosystem historically included 37 million ha of mostly fire-maintained vegetation across the southeastern US (Jose et al., 2006). Intensive land use across the region following European settlement reduced the extent of this ecosystem by 98 percent (Frost, 2006). Today, remaining areas are highly fragmented, and where fire was excluded, woody plant encroachment (Gilliam and Platt, 1999; Maliakal et al., 2000) and subsequent decline of the species-rich herb layer has been observed (Brewer, 2017; Hardin and White, 1989; Toribio-Diaz et al., 2019). Frequent, low-intensity fires prior to European settlement supported high levels of understory plant diversity and endemism across the range of longleaf pine (Hardin and White, 1989; Myers et al., 2000; Noss et al., 2015; Peet and Allard, 1993). Despite the re-introduction of fire through dormant-season prescribed burning during the mid to late 1900s (Stanturf et al., 2002), herbaceous species did not regain previous levels of cover. Understory vegetation dominated by woody plants is an enduring legacy of fire exclusion (Moser and Wade, 2005) that has been sustained by longer rotation (> 3 years) dormant-season prescribed burning (Mitchell and Duncan, 2009). Prescribed fire is used by land managers to meet ecosystem management goals (Lavoie et al., 2011; McIntyre et al., 2018) because fire exclusion and fragmentation preclude free-burning wildfires and the cultural burning practices that historically maintained this system (Brudvig et al., 2014). Results from long-term controlled experiments generally conclude that shorter fire rotations (< 3 years) and use of growing-season burns can shift understory composition from woody to herbaceous species (Glitzenstein et al., 2012, 2003; Waldrop et al., 1992) and increase biological diversity (Freeman et al., 2019; Walker and Peet, 1984). These results provided the basis for shifting management techniques to more closely emulate the historic fire regime, such as shortening fire return intervals to 1–3 years and burning during the growing season (Custer, 2011; Ferguson, 1998; McWhite et al., 1999).

This study evaluates how understory vegetation composition in longleaf pine flatwoods is affected by fire frequency and season-of-burn. These two fire regime characteristics were selected because they are known determinants of biodiversity and understory composition. Most long-term studies describe an increase in the ratio of herbaceous-to-woody plant abundance associated with more frequent fires and/or increasing number of growing-season fires in the longleaf pine ecosystem (Brockway and Lewis, 1997; Glitzenstein et al., 2012, 2003; Haywood et al., 2001; Waldrop et al., 1987) and savannas globally (de Souza et al., 2022; Mogashoa et al., 2021; Ratajczak et al., 2012). I hypothesize that a) there is a gradient of increasing herbaceous and decreasing woody understory biomass with shorter MFI values across sites and b) this effect is magnified across a gradient of increasing proportion of growing season burns. Further, I suspect these effects are muted relative to results in controlled studies based on the comparatively greater variability in application of prescribed fire over time and the presence of confounding variables associated with the large geographic area of my study. To test this hypothesis, I sampled understory vegetation in mesic longleaf pine flatwoods managed with prescribed fire that represent a range of fire frequency and proportion of growing season burns (Figure 4-1). Understory data were then tested using constrained ordination and regression. Constrained ordination identified the effects of managed fire regime characteristics on trends in understory vegetation composition. Regression provided a more detailed look into effects on individual species that may have been overlooked by constrained ordination.

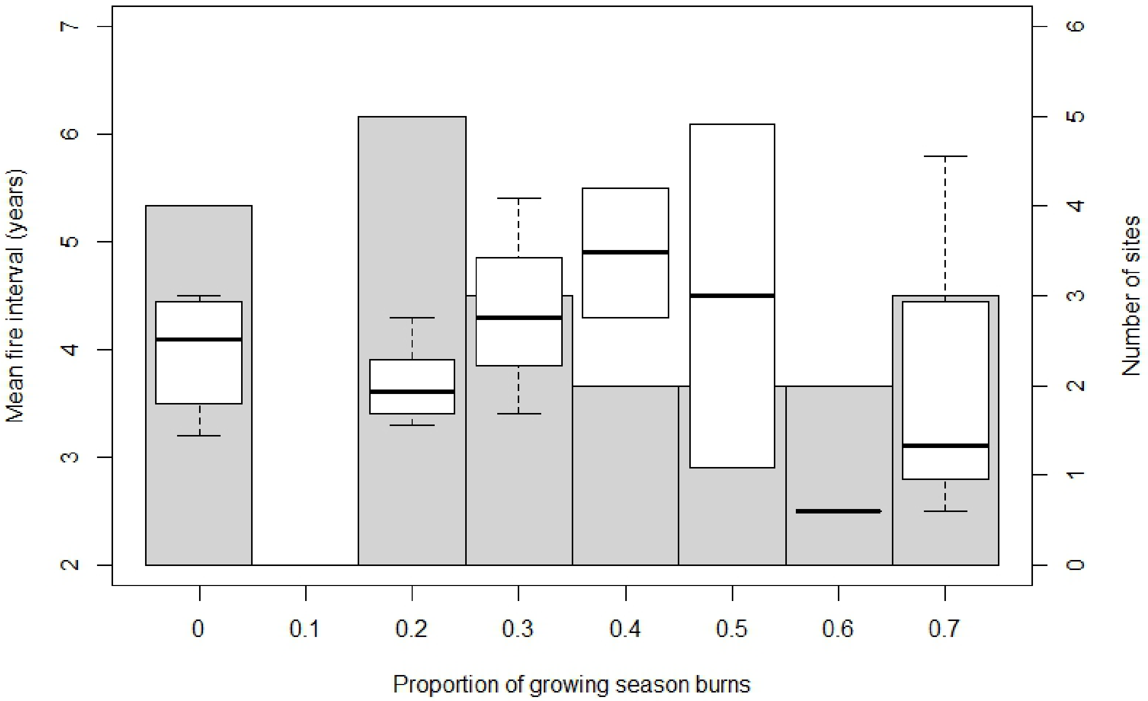


**Figure 4-1.** Variability of fire frequency as measured by the mean fire interval for the twenty-year period prior to vegetation sampling relative to percentage of growing season burns (box plots). Grey bars summarize the distribution of percentage of burns that occurred during the growing season for the twenty-year period prior to vegetation sampling.

Few studies describe how understory vegetation responds to increased frequency of burning and use of growing-season burns across the range of variability in longleaf pine managed with prescribed fire (e.g., Addington et al., 2015; Hannon et al., 2020). This type of research is important to evaluate the efficacy of prescribed fire management strategies predicated on the results of long-term controlled studies described above. While they are an important contribution to the understanding of the interactions of fire and understory vegetation, they were designed to test for direct effects and study designs utilize rigid burn schedules and cover relatively small areas to eliminate confounding variables. In practice, these confounding variables are present in a management context. The purpose of this study was not to challenge the validity of long-term controlled studies but rather to test the strength of these experimental-scale relationships at the management scale. Results will help land managers assess how the current range of prescribed fire regime characteristics are correlated with understory composition and suggest possible adjustments.

## 4.3 **Methods**

### 4.3.1 *Study sites*

I established 22 research sites in mesic, mature pine flatwoods at three locations: Eglin Air Force Base ($n = 11$), the Apalachicola National Forest ($n = 8$), and St. Marks National Wildlife Refuge ($n = 3$; Figure 4-2).

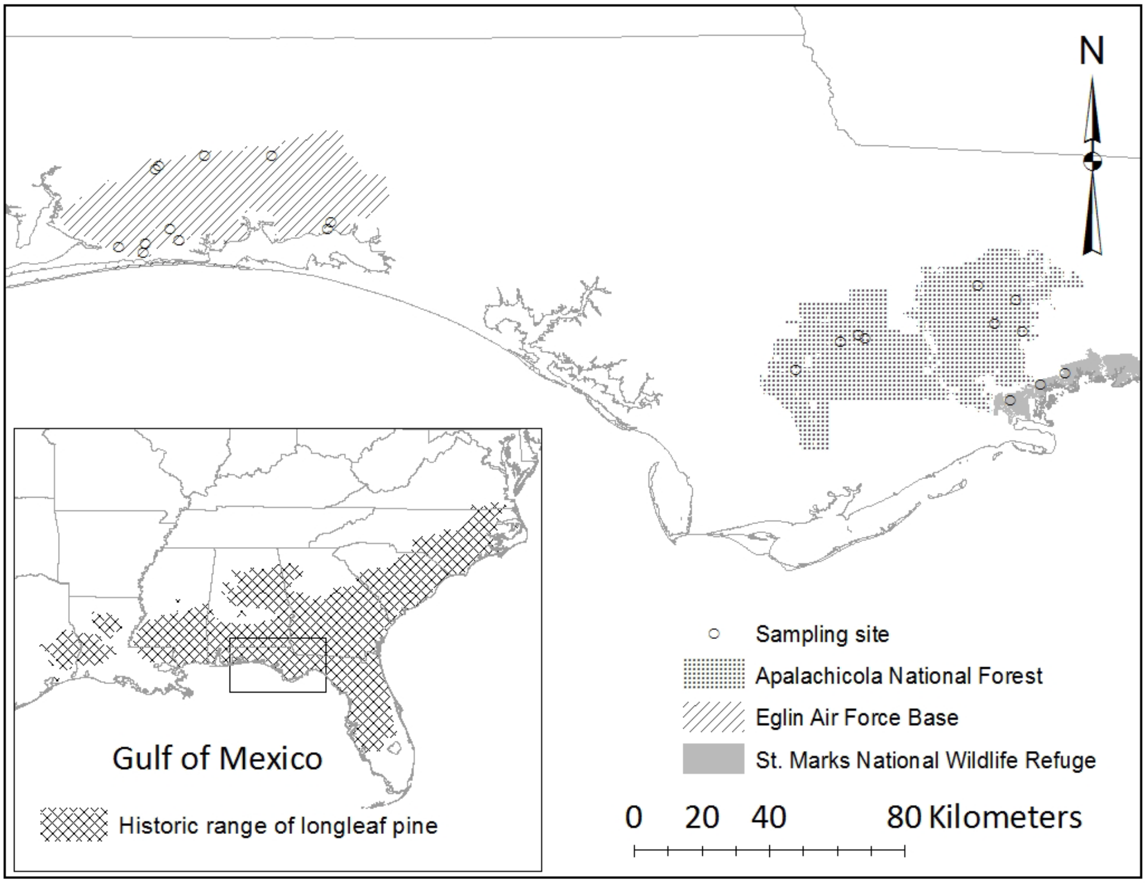


**Figure 4-2.** Historic distribution of longleaf pine forests in the southeastern United States. Study sites were located in mesic longleaf pine flatwoods in northwestern and north-central Florida.

Each site was located within a distinct prescribed burn unit so that fire management history was not replicated. These locations fell within the historical range of longleaf pine and along the border between the Southern and Southeastern Coastal Plains Ecoregions (Omernik, 1987). Vegetation communities in the longleaf pine ecosystem are classified along a soil moisture gradient with mesic flatwoods representing intermediate conditions (Peet, 2006). They are characterized by acidic sandy soils underlain by an impermeable layer of clay, an open canopy of tall pines, typically longleaf pine, and an understory of low growing shrubs and herbs. Sites with mesic longleaf pine flatwoods were chosen because they are commonly managed with prescribed fire in the southeastern US.

Eglin Air Force Base is characterized by gently rolling terrain primarily occupied by longleaf sandhills (Provencher et al., 2001) and extensively drained deep sandy Entisols (Overing et al., 1995; Overing and Watts, 1989). Apalachicola National Forest and St. Marks National Wildlife Refuge are adjacent to each other on broad flat terrain where longleaf flatwoods are prevalent and soils are poorly drained Spodosols (Allen, 1991; Sanders, 1981). At all sites, longleaf pine was the dominant overstory species. Understory composition was typical of frequently burned flatwoods (Drewa et al., 2002a) but varied across a compositional gradient from shrub to herb dominance (Figures 4-3 & 4-4). Understory species with the highest biomass included dwarf live oak (*Quercus minima* (Sarg.) Small), saw palmetto (*Serenoa repens* (W. Bartram) Small), wiregrass (*Aristida beyrichiana* Trin. & Rupr.), gallberry (*Ilex glabra* (L.) A. Gray), and rusty lyonia (*Lyonia ferruginea* (Walter) Nutt.). No sites had a substantial presence of understory hardwood trees.

**Figure 4-3.** Variability of understory vegetation among study sites showing increasing dominance of herbaceous species from left to right.

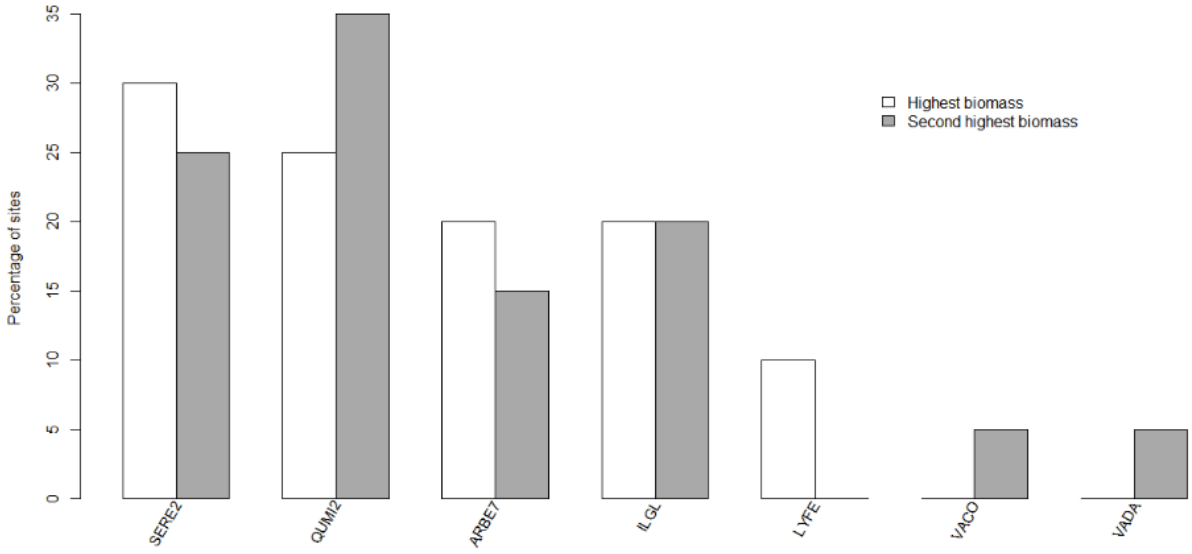


**Figure 4-4.** Frequency of occurrence among sites for species with the highest and second highest biomass. Species codes: SERE2 (*Serenoa repens*), QUMI2 (*Quercus minima*), ARBE7 (*Aristida beyrichiana*), ILGL (*Ilex glabra*), LYFE (*Lyonia ferruginea*), VACO (*Vaccinium corymbosum*), VADA (*Vaccinium darrowii*).

### 4.3.2 *Study design*

Sites were identified to satisfy the sampling protocol of a related study (Cronan et al., 2015) that included measuring understory fuel characteristics in stands managed with frequent fire. To reduce the influence of environmental factors not included as constraints I chose sites located in stands of mature, mesic longleaf pine flatwoods that were at least two hectares, had been actively managed with prescribed fire for 15–30 years, had no evidence of past ground disturbance (e.g., agriculture) that could influence understory composition (Hedman et al., 2000), and had no indications of recent overstory disturbance (e.g., silviculture, hurricane damage, or canopy damage from fire). At each site, 20 vegetation sampling plots were established on a systematic grid with 80-m spacing fit to the stand boundaries. Prescribed fire management records dating back to 1970 were used to characterize the managed fire regime at each site. To avoid the confounding effect of time-since-last-fire (TSLF) I excluded sites where field data were not collected two years after the most recent fire. Two-year TSLF field data were collected in 2010 for three sites burned in 2008 and in 2012 at 18 sites that burned in late 2009 or early 2010. Field data collection at a single site did not occur two years after the most recent burn and was dropped from the analysis. One drawback to this design is a lack of before and after treatment data. This increases the degree of uncertainty concerning the effects of prescribed fire on understory composition.

### 4.3.3 *Understory biomass data (dependent variables)*

Live, understory vegetation biomass was inventoried using standard destructive methods (Wright, 2013) from the grids of nested 0.25–4m$^2$ plots to assess abundance, composition, and structure. Vegetation was sampled at the species level for common species, whereas uncommon species were aggregated by plant functional group (Table 4-1). One exception to this approach was *Quercus.* Several species were common but only *Quercus minima* was identified by species. All other species were grouped by functional group (shrub or understory tree). Biomass values were analyzed at three levels of classification: species, genera, and functional group.

### 4.3.4 *Fire regime and forest structure data (explanatory variables)*

Prescribed fire regime and forest structure characteristics were examined as possible explanatory variables for trends in understory vegetation. A review of the prescribed fire records showed that regular application of prescribed fire did not begin until the 1980s for most sites. To maintain consistency of fire management across all sites I limited analysis to a 20-year period (1991–2010) when all sites were being regularly burned. Prescribed fire management variables used in this analysis included: growing season burns (as a percentage of total number of burns), MFI (years), standard deviation of MFI (years), and length of time each site has been regularly burned (years). Forest characteristics, including canopy cover (Bowles et al., 2011), coarse and fine downed woody debris loading (Thaxton and Platt, 2006), and forest floor depth (Sydes and Grime, 1981), affect understory vegetation in longleaf pine flatwoods and were included as explanatory variables. Coarse (particles greater than 2.5 cm in diameter) downed woody debris (cDWD) loading (Mg ha$^{-1}$) was measured along three 20-m transects originating at each of the 20 vegetation plots. Loading was estimated with the planar intersect method (Brown, 1974). Fine (particles less than 2.5 cm in diameter) downed woody debris (fDWD) loading (Mg ha$^{-1}$) was sampled directly from twenty 0.25 m$^2$ plots systematically arranged at each site coincident with the vegetation plots. Canopy cover (percent) was estimated at 180 points in each site. Points were located at three evenly spaced points along each of the 20-m transects using the vertical

**Table 4-1.** Species list. Common vegetation was sampled by species while uncommon species were categorized by plant functional groups. Percent occurrence is average for all sites. Percent occurrence for plant functional groups is for all species within each category. Plot size is area of biomass sample for each species or uncommon species represented by plant functional groups.

| Taxonomic Name | Species Code | Percent Occurrence | Plot Size ($m^2$) |
|---|---|---|---|
| Understory Trees (< 2m tall) | | 52.4 | 4 |
| *Acer rubrum* | ACRU | 0.0 | 4 |
| *Cornus florida* | *COFL2* | 4.8 | 4 |
| *Chionanthus virginicus* | *CHVI3* | 4.8 | 4 |
| *Diospyros virginiana* | *DIVI5* | 9.5 | 4 |
| *Ilex opaca* | *ILOP* | 9.5 | 4 |
| *Liquidambar styraciflua* | *LIST2* | 0.0 | 4 |
| *Magnolia grandiflora* | *MAGR4* | 4.8 | 4 |
| *Magnolia virginiana* | *MAVI2* | 28.6 | 4 |
| *Pinus elliottii* | *PIEL* | 0.0 | 4 |
| *Pinus serotina* | *PISE* | 0.0 | 4 |
| *Rhus copallinum* | *RHCO* | 9.5 | 4 |
| *Symplocos tinctoria* | *SYTI* | 4.8 | 4 |
| | | | |
| Shrubs | | 100.0 | 4 |
| *Aronia arbutifolia* | *ARAR7* | 23.8 | 4 |
| *Asimina angustifolia* | *ASAN6* | 9.5 | 4 |
| *Baccharis halimifolia* | *BAHA* | 0.0 | 4 |
| *Callicarpa americana* | *CAAM2* | 4.8 | 4 |
| *Clethra alnifolia* | *CLAL3* | 9.5 | 4 |
| *Clinopodium coccineum* | *CLCO10* | 4.8 | 4 |
| *Conradina canescens* | COCA19 | 0.0 | 4 |
| *Cyrilla racemiflora* | *CYRA* | 19.0 | 4 |
| *Garberia heterophylla* | *GAHE4* | 4.8 | 1 |
| *Hypericum hypericoides* | *HYHY* | 52.4 | 1 |
| *Hypericum tetrapetalum* | *HYTE4* | 28.6 | 1 |
| *Ilex coriacea* | *ILCO* | 33.3 | 4 |
| *Ilex glabra* | *ILGL* | 100 | 1-4[1] |
| *Ilex vomitoria* | *ILVO* | 38.1 | 4 |
| *Lyonia ferruginea* | *LYFE* | 42.9 | 1-4[1] |

[1] Plot size varied depending on abundance.

**Table 4-1 (cont.).** Species list. Common vegetation was sampled by species while uncommon species were categorized by plant functional groups. Percent occurrence is average for all sites. Percent occurrence for plant functional groups is for all species within each category. Plot size is area of biomass sample for each species or uncommon species represented by plant functional groups.

| Taxonomic Name | Species Code | Percent Occurrence | Plot Size ($m^2$) |
|---|---|---|---|
| *Lyonia lucida* | *LYLU3* | 14.3 | 1-4[1] |
| *Morella cerifera* | *MOCE2* | 42.9 | 1 |
| *Quercus minima* | *QUMI2* | 100 | 1 |
| *Quercus* spp. | QUERC | 85.7 | 4 |
| *Serenoa repens* | *SERE2* | 95.2 | 4 |
| *Vaccinium arboreum* | *VAAR* | 38.1 | 4 |
| *Vaccinium corymbosum* | *VACO* | 33.3 | 4 |
| | | | |
| Vines | | 90.5 | 1 |
| *Gelsemium sempervirens* | *GESE* | 28.6 | 1 |
| *Smilax auriculata* | *SMAU* | 90.5 | 1 |
| *Toxicodendron radicans* | *TORA2* | 0.0 | 1 |
| *Vitis rotundifolia* | *VIRO3* | 19.0 | 1 |
| | | | |
| Sub- shrubs | | 100.0 | 1 |
| *Gaylussacia dumosa* | *GADU* | 95.2 | 1 |
| *Kalmia hirsuta* | *KAHI2* | 38.1 | 1 |
| *Licania michauxii* | *LIMI5* | 33.3 | 1 |
| *Vaccinium darrowii* | *VADA* | 95.2 | 1 |
| *Yucca filamentosa* | *YUFI* | 4.8 | 4 |
| | | | |
| Graminoids | | 100.0 | 1 |
| *Andropogon glaucopsis* | *ANGL10* | 100.0 | 1 |
| *Aristida beyrichiana* | *ARBE7* | 100.0 | 1 |
| | | | |
| Forbs | | 100.0 | 1 |

[1] Plot size varied depending on abundance.

tube method (Johansson, 1985). Litter loading (Mg $ha^{-1}$) was calculated by taking the product of mean litter depth (mm) measured at three points established along each 20-m transect (180 samples per site) and published bulk density values for southeastern US long-needle pine litter types from the Fuelbed Characteristic Classification System (Prichard et al., 2013). Forest floor biomass is the sum of litter and fDWD.

### 4.3.5 *Data analysis*

Multivariate and univariate analysis techniques were used to identify measures of the managed fire regime and forest structure that described variation in the understory vegetation across the range of sampled conditions. Redundancy analysis (RDA), a type of constrained ordination (Rao, 1964) was used to identify which parameters of the fire regime or forest structure explained compositional differences in biomass of understory vegetation. Boundary line regression (Webb, 1972) was used to test for relationships between measures of the managed fire regime and measures of understory composition.

RDA was conducted with biomass data aggregated by genera and plant functional group. Partitioning the data in different ways (i.e., by genera and plant functional group) for analysis provided an opportunity to test for effects of forest characteristics and prescribed fire on general trends of plant taxa and structure of the understory. Prior to conducting RDA, a Principal Components Analysis (PCA) was performed to identify compositional patterns of understory on vegetation. The broken stick method (Frontier, 1976) was used to assess which principal component axes in the PCA to retain. This method assumes that if the total variance is divided randomly among the principal components they will yield a broken stick distribution. Principal components with observed eigenvalues are compared with this distribution and those greater than the broken stick distribution are retained. To select ordination techniques used in this analysis, Detrended Correspondence Analysis (DCA) was used to determine the gradient length of the sampling environment using the full species dataset for biomass. Results showed relatively short axis lengths of 1.5 and 0.7 for biomass data grouped by genera and plant functional groups, respectively. This is consistent with my understanding of linear responses expected across the relatively narrow environmental gradients I sampled (Section 4.3.4) and was below the threshold of 3–4 commonly used to select linear versus unimodal gradient analyses (Ter Braak and Prentice, 1988). Given the narrow environmental gradients, I selected redundancy analysis (RDA) for constrained ordination. Plot data ($n$ = 20 per site) for understory biomass and forest structure were averaged at the site level which corresponds with the scale of fire management data. Rare genera that occurred in less than 10 percent of sites were removed (Marchant, 1990; McCune and Grace, 2002), because most rare species were not captured by the sampling design (i.e. most herbaceous species were not identified) and those that remained would have added noise to statistical analyses. Excluding rare species also permitted me to focus on patterns and structure of dominant understory vegetation. This reduced the number of genera from 37 to 19. There were no plant functional groups that occurred in less than 10 percent of the sites. Biomass data were analyzed as a matrix of continuous values because the presence of null values was less than the 60 percent threshold commonly used as a cutoff for conversion to presence/absence (McCune and Grace, 2002). After removal of rare genera, the occurrence of null values was 40 percent. The percentage of null values in the plant functional group dataset was 10 percent. Biomass data classified by genera and plant functional group were log-transformed to reduce the effect of right-skewed values. Environmental variables were checked for multicollinearity. Highly correlated variables (correlation value +/- 0.55) were excluded from the analysis.

Multivariate outlier analysis characterized a single site as an outlier. This site was removed from analyses. Variables were log-transformed when they did not fit a normal distribution, then mean-centered and standardized to equalize different units of measure for each variable (McCune and Grace, 2002). Forward selection was used to sequentially add constraints to the model. A two-step process to generate models included a global test of full model evaluation of additional terms based on alpha significance and adjusted $r^2$ (Blanchet et al., 2008). Because sites were in geographically distinct regions with western sites at Eglin Air Force Base ($n$ = 10) and eastern sites at Apalachicola National Forest/St. Marks National Wildlife Refuge ($n$ = 10) a conditional term blocking the sites into two regions was added to the final model derived from the forward selection technique. To understand how explanatory variables differed between regional blocks each was tested for significant difference in mean values between the two regions with a Student's *t*-test.

Boundary line regression was conducted on important contributors to understory composition (10 species with the highest biomass and all plant functional groups) for two explanatory variables: the 20-year MFI and percentage of growing-season burns. This analysis is useful for determining a functional relationship between two factors in scenarios where other confounding variables are present. This type of regression is conducted by plotting dependent and explanatory variables and fitting a line to the upper limit of the data points. This line represents the maximum potential response to a single explanatory variable whereas points that fall below the line are assumed to be influenced by the other variables present. This technique provides the capability to analyze a univariate response in field settings where confounding variables cannot be controlled. It is primarily used in crop yield studies (Makowski et al., 2007), but is also useful for ecological experiments (e.g., Hiers et al., 2007). In the case of this study, boundary line regression serves as a secondary method for identifying relationships between fire regime characteristics and the understory plant community. This is useful because it is possible there are confounding variables that were not measured and therefore excluded from the constrained ordination. I chose the 20-year MFI and percentage of growing-season burns as explanatory variables because they are frequently used in long-term studies of fire effects on understory composition and by fire and land managers to set prescribed burning strategies and objectives. Explanatory variables were grouped into fixed-width windows, where each window was set at one tenth of the data range. In the case of the 20-year MFI this width was selected to correspond with fire return interval values rounded to the nearest year because the effects on vegetation are categorized at this level of precision. For both variables this width provides a balance between overfitting data and maintaining enough subdivisions to characterize response variable trends (Shatar and McBratney, 2004). A logarithmic regression was fit to the maximum dependent variable in each window.

All statistical tests were evaluated at $\alpha = 0.05$ and conducted with R version 3.6.2 (R Development Core Team, 2022). Outlier analysis was conducted with the mvoutlier package (Filzmoser and Gschwander, 2021) and multivariate analyses with the vegan package (Oksanen et al., 2022). Except when noted, results are presented as the plot mean ± standard error.

## 4.4 **Results**

Results indicated that variation in the forest understory was not explained by the gradient of either the fire regime or measures of forest structure among longleaf pine flatwoods sites. The explanatory variables for my sites fell within a relatively narrow range (Table 4-2). The 20-year

**Table 4-2.** Summary of fire regime and forest structure for study sites located in northern Florida. Explanatory variables used in constrained ordination. Mean fire interval was calculated by taking the average value of fire free intervals for the 20-year period preceding the most recent burn prior to field data collection.

| Explanatory variable | Units | Mean | Range |
|---|---|---|---|
| Mean fire interval (MFI) | Years | 4.0 | 2.5 – 6.1 |
| Growing season burns | Percent | 35 | 0 – 70 |
| Standard deviation of mean fire return interval | --- | 2.1 | 1.0 – 3.7 |
| Length of time under frequent burning regime | Years | 19.5 | 13.1 – 30.4 |
| Canopy cover | Percent | 40.6 | 22.5 – 61.7 |
| Litter biomass | Mg ha$^{-1}$ | 3.52 | 1.75 – 6.52 |
| Fine woody debris biomass (fDWD) | Mg ha$^{-1}$ | 0.84 | 0.24 – 1.62 |
| Coarse woody debris biomass (cDWD) | Mg ha$^{-1}$ | 2.79 | 0.57 – 11.40 |

MFI was 2.5 to 6.1 years, the percentage of growing-season burns was between 0 and 70 percent, and the duration of regular burning ranged from 13 to 30 years. Canopy coverage ranged from 23 to 62 percent. Total biomass for dead surface fuels ranged from 1.75 to 6.52 Mg ha$^{-1}$, 0.24 to 1.62 Mg ha$^{-1}$, and 0.57 to 11.40 Mg ha$^{-1}$ for litter, fDWD, and cDWD, respectively.

Field sampling produced biomass for 60 common species of woody plants and grasses. Individual forb species contributed minimally to total understory biomass and were grouped together. *Quercus minima* had the highest average percentage of live understory plant biomass (21.7 percent) with a range of 0.08 to 2.15 Mg ha$^{-1}$ across sites. Other abundant species included *S. repens* (17.8 percent; range: 0.0–1.3 Mg ha$^{-1}$), *I. glabra* (12.7 percent; range: 0.0–1.13 Mg ha$^{-1}$), *A. beyrichiana* (12.6 percent; range: 0.02–1.82 Mg ha$^{-1}$), and *L. ferruginea* (5.3 percent; range: 0.0–1.00 Mg ha$^{-1}$). Averaged across sites, the top five most abundant species accounted for 70.2 percent of the total live understory plant biomass (Table 4-3). All other species, whether collected individually or grouped into broader classes, had mean biomass values less than 0.15 Mg ha$^{-1}$.

**Table 4-3.** Biomass and percent of total understory biomass by site for the five most abundant (by relative contribution of biomass) species. See Appendix D for a complete list of results.

| Site | *Quercus minima* | | *Serenoa repens* | | *Aristida* | | *Ilex glabra* | | *Lyonia ferruginea* | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Biomass (Mg ha$^{-1}$) | % of Total | Biomass (Mg ha$^{-1}$) | % of Total | Biomass (Mg ha$^{-1}$) | % of Total | Biomass (Mg ha$^{-1}$) | % of Total | Biomass (Mg ha$^{-1}$) | % of Total |
| A01 | 0.55 | 22.4 | 0.00 | 0.0 | 0.02 | 0.8 | 0.66 | 26.4 | 0.00 | 0.0 |
| A02 | 0.95 | 25.3 | 0.95 | 25.3 | 0.05 | 1.3 | 0.10 | 2.7 | 0.52 | 14.1 |
| A03 | 0.62 | 11.5 | 1.30 | 24.1 | 0.02 | 0.4 | 1.13 | 21. | 0.84 | 15.6 |
| A04 | 0.94 | 28.7 | 0.74 | 22.6 | 0.34 | 10.4 | 0.25 | 7.6 | 0.23 | 7.0 |
| A05 | 0.70 | 18.5 | 0.45 | 11.7 | 0.59 | 15.4 | 0.11 | 3.1 | 1.00 | 25.8 |
| A06 | 0.67 | 17.8 | 0.53 | 13.7 | 0.51 | 13.2 | 0.23 | 5.9 | 0.93 | 24.0 |
| A07 | 0.94 | 30.1 | 1.30 | 41.3 | 0.19 | 6.1 | 0.20 | 6.7 | 0.05 | 1.6 |
| A08 | 1.36 | 40.5 | 0.46 | 13.7 | 0.50 | 14.6 | 0.23 | 7.1 | 0.00 | 0.0 |
| A09 | 0.46 | 17.3 | 0.58 | 21.8 | 0.55 | 20.7 | 0.06 | 2.3 | 0.00 | 0.0 |
| A10 | 1.27 | 49.8 | 0.24 | 9.4 | 0.52 | 20.4 | 0.00 | 0.0 | 0.00 | 0.0 |
| A11 | 1.33 | 51.6 | 0.51 | 19.8 | 0.07 | 2.7 | 0.16 | 6.2 | 0.19 | 7.4 |
| E01 | 0.22 | 10.6 | 0.28 | 13.5 | 0.08 | 3.8 | 0.79 | 38.0 | 0.00 | 0.0 |
| E02 | 0.15 | 5.0 | 0.47 | 15.7 | 0.17 | 5.7 | 0.46 | 15.3 | 0.00 | 0.0 |
| E03 | 0.79 | 17.1 | 0.56 | 12.3 | 0.13 | 2.9 | 0.90 | 20.0 | 0.54 | 11.8 |
| E04 | 0.12 | 3.0 | 1.07 | 27.2 | 1.23 | 31.2 | 0.74 | 18.8 | 0.00 | 0.0 |
| E05 | 0.62 | 19.2 | 0.59 | 18.3 | 0.78 | 24.1 | 0.16 | 5.0 | 0.00 | 0.0 |
| E06 | 0.09 | 2.5 | 0.16 | 4.5 | 0.81 | 50.7 | 0.80 | 22.6 | 0.00 | 0.0 |
| E07 | 0.08 | 3.7 | 0.85 | 39.5 | 0.03 | 1.4 | 0.40 | 19.1 | 0.08 | 3.7 |
| E08 | 0.62 | 21.2 | 0.40 | 14.0 | 0.72 | 24.7 | 0.60 | 20.5 | 0.00 | 0.0 |
| E09 | 0.20 | 6.0 | 0.25 | 7.4 | 0.25 | 7.4 | 0.50 | 14.9 | 0.00 | 0.0 |
| E11 | 2.15 | 54.7 | 0.70 | 18.1 | 0.27 | 6.9 | 0.30 | 7.4 | 0.00 | 0.0 |

When aggregated by plant functional group, shrubs generally contributed the highest biomass followed by either graminoids or sub-shrubs. Mean live understory biomass was 3.36 Mg ha$^{-1}$ (range: 2.09–5.40 Mg ha$^{-1}$). Shrub biomass was 68.3 percent of total above-ground biomass for total live understory vegetation with a range of 1.11 to 4.31 Mg ha$^{-1}$. Shrubs had the highest percent biomass relative to other functional groups at 19 of the 20 sites. Graminoids, primarily *A. beyrichiana*, had the second highest mean percent biomass of 18.4 percent (range: 0.08–2.33 Mg ha$^{-1}$). Graminoids had the highest relative biomass at one of the 20 sites. Percent biomass for the remaining plant functional groups was 13.3 percent (range: 0.10–0.99 Mg ha$^{-1}$).

This includes 4.0 percent for forbs (range: 0.01–0.49 Mg ha$^{-1}$), 2.7 percent for vines (range: 0.00–0.39 Mg ha$^{-1}$), and 0.9 percent for understory trees (range: 0.00–0.23 Mg ha$^{-1}$).

### 4.4.1 *Constrained analysis – genera*

Principal Components Analysis of the understory data grouped by genera showed relatively even (i.e., not clumped) dispersion along the first two axes (Figure 4-5). Broken stick analysis suggested that the first two axes explained more variation than would be expected with the broken stick distribution and should be retained. Together, these axes explained 55.1 percent of the observed variation. There also appeared to be an arch effect (Palmer, 2002) on the biplot (Figure 4-5). This was evident in the curved shape of the points along the first axis and suggested

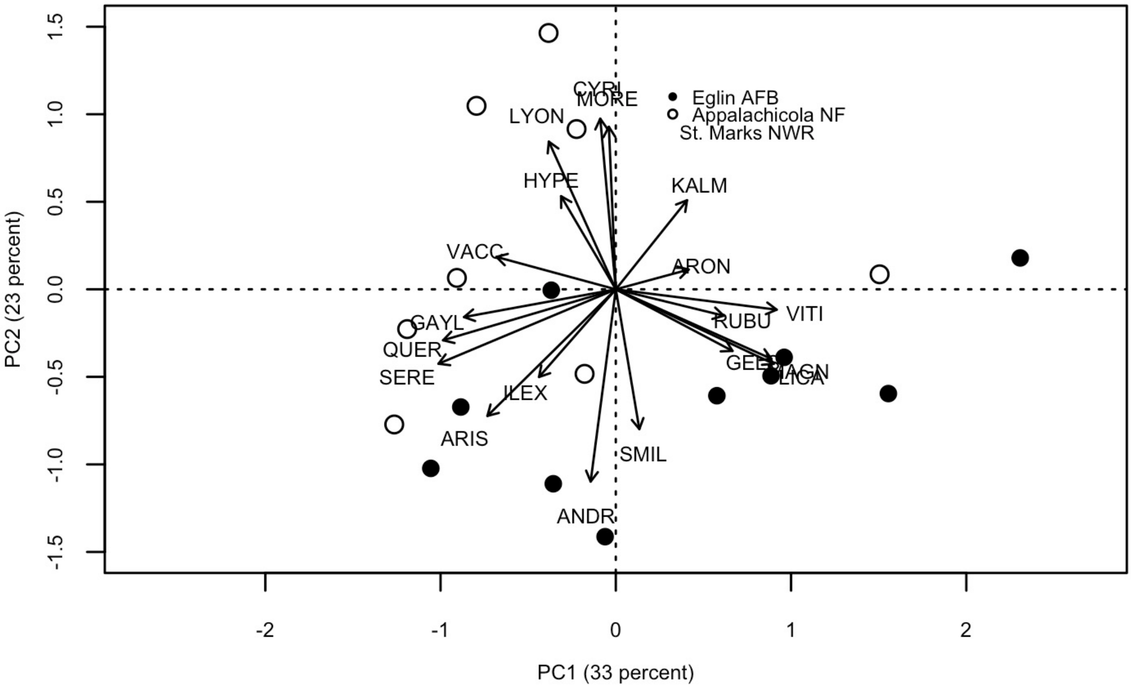


**Figure 4-5.** Sites and understory genera biplot of the first (horizonatal) and second (vertical) axes of the Principal Components Analysis of understory biomass data. Sites are grouped by region with the western sites (Eglin Air Force Base) shaded black and the eastern sites (Appalachicola National Forest and St. Marks National Wildlife Refuge) represented by open circles. Refer to Table 2 to translate species codes to species names.

a longer environmental gradient than was detected in the DCA. The first axis explained 32.5 percent of the variation and showed a gradient of understory composition defined by *Serenoa*, *Quercus*, and *Vaccinium* at one end and by *Vitis*, *Gelsemium*, *Magnolia*, and *Licania* at the other. Sites were equally dispersed along the first axis. This suggested that sites were arranged along a compositional gradient rather than clustered in distinct understory plant communities. Sites were broadly divided by region on the second axis. This suggested that most variation in plant composition when viewed at the genus level was not explained by the two regional sampling blocks. The second axis explained 22.5 percent of the variation. Sites in the western region were similar in that they had a higher biomass of *Andropogon*, *Aristida*, and *Smilax* while those in the eastern region were typified by *Cyrilla*, *Lyonia*, and *Morella*. Redundancy Analysis indicated that cDWD loading and MFI were significant model terms, but these terms were dropped when the adjusted $r^2$ was applied (Table 4-4). The adjusted $r^2$ values for cDWD loading ($r^2_{adj} = 0.12$) and the 20-year MFI ($r^2_{adj} = 0.06$) did not indicate a significant effect for either variable and the null model was accepted. The Pearson's correlation for the 20-year MFI ($r = 0.32$) and cDWD loading ($r = 0.45$) were both weakly positive with the first axis, suggesting that, to some extent, higher fire frequency and lower cDWD loading promoted greater abundance of *Aristida* and several woody genera, including *Serenoa*, *Quercus*, *Ilex*, *Gaylussacia* and *Vaccinium*. Lower fire frequency and high cDWD loading were associated with genera classified as vines and hardwoods, including *Vitus*, *Gelsemium*, *Rubus*, and *Magnolia*, and *Licania*, a genus that included a single species in my samples, *Licania michauxii* (Prance). This plant is a sub-shrub typical of drier sites where fire is less frequent.

### 4.4.2 *Constrained analysis – plant functional groups*

Principal Components Analysis of biomass data aggregated by plant functional group showed that sites were broadly arranged by region on the first axis and along a woody to herbaceous gradient on the second axis (Figure 4-6). Broken stick analysis suggested that only the first axis explained more variation than would be expected with the broken stick distribution. The first axis explained 55.9 percent of the observed variation. Nine of the ten western sites had negative PC1 axis scores while eight of the ten eastern sites had positive PC1 axis scores.

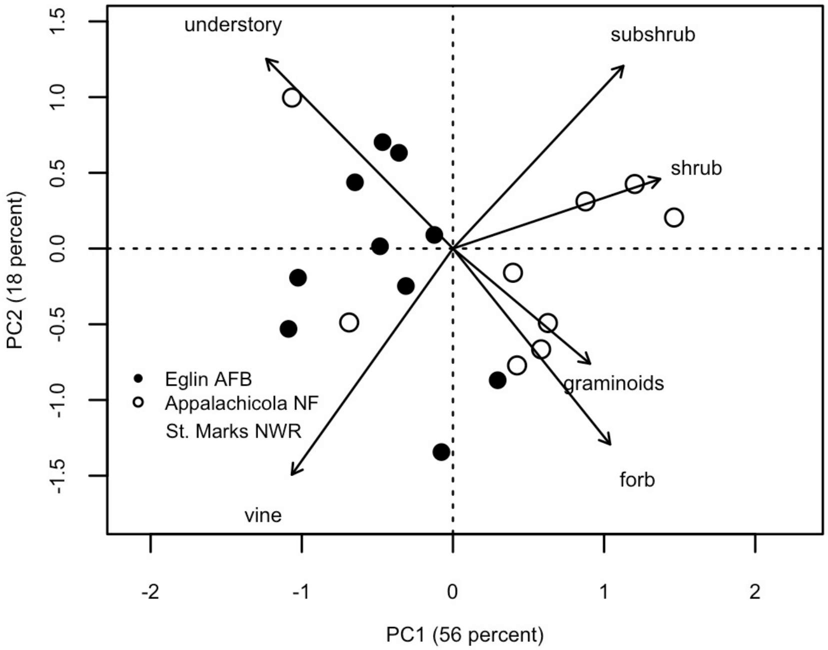


**Figure 4-6.** Sites and plant functional group biplot of the first (horizonatal) and second (vertical) axes of the Principal Components Analysis of understory biomass data. Sites are grouped by region with the western sites (Eglin Air Force Base) shaded black and the eastern sites (Appalachicola National Forest and St. Marks National Wildlife Refuge) represented by open circles. Refer to Table 2 for a list of species in each plant functional group.

Plant functional group scores were all highest along the first axis except for graminoid scores which were highest on the third axis (not shown). Sites along the first axis were arranged along a gradient characterized by declining biomass of understory trees and vines as shrub, sub-shrub, and forb biomass increased. Redundancy Analysis indicated that cDWD loading and MFI were significant model terms, but these terms were dropped when the adjusted $r^2$ was applied (Table 4-4). The two terms with the highest adjusted $r^2$ values were biomass of cDWD ($r^2_{adj}$ = 0.118) and the forest floor ($r^2_{adj}$ = 0.059). The lack of significant explanatory variables suggested that most of the variation encompassed within the first axis (Figure 4-6) was a product of geographic location or that differences in explanatory variables that do explain variance were correlated with the eastern and western sampling blocks. Significance testing between regions showed this was true for many of the managed fire regime variables, but not for any of the forest structure variables (Table 4-5). The 20-year MFI was significantly longer ($P < 0.01$) at sites in the west (4.65 years) compared to the east (3.30 years); standard deviation of MFI was significantly greater ($P < 0.01$) in the west (SD = 2.56) vs. the east (SD = 1.74); and the average length of time units have been under a repeated burning program was significantly longer ($P$ = 0.02) in the west (22.5 years) compared with the east (16.5 years). For the two marginally

**Table 4-4.**
Explanatory variables tested for effect on understory biomass data with the redundancy analysis. Explained variation of all redundancy analysis axes was 28.4 percent for vegetation grouped by genera and 22.4 percent for vegetation grouped by plant functional group.

| Variable | F-value | P-value | Adjusted $r^2$ |
|---|---|---|---|
| *Biomass grouped by genera* | | | |
| Coarse DWD loading | 4.18 | 0.005 | 0.118 |
| 20-year MFI | 2.84 | 0.035 | 0.059 |
| Proportion of growing season burns | 1.58 | 0.135 | -0.021 |
| SD of 20-year MFI | 0.88 | 0.505 | 0.035 |
| Length of fire management | 0.71 | 0.680 | 0.022 |
| Forest floor biomass | 0.70 | 0.695 | 0.014 |
| Canopy coverage | 0.49 | 0.880 | -0.026 |
| *Biomass grouped by plant functional group* | | | |
| Coarse DWD loading | 5.20 | 0.020 | 0.181 |
| 20-year MFI | 2.52 | 0.065 | 0.037 |
| Forest floor biomass | 0.91 | 0.350 | 0.054 |
| Proportion of growing season burns | 0.89 | 0.405 | -0.028 |
| SD of 20-year MFI | 0.82 | 0.480 | 0.003 |
| Length of fire management | 0.63 | 0.580 | 0.015 |
| Canopy coverage | 0.63 | 0.595 | -0.004 |

significant terms, 20-year MFI ($r^2_{adj} = 0.037$) and coarse DWD loading ($r^2_{adj} = 0.181$), there was a weakly negative correlation with the first axis. This suggested that, if not a regional effect, higher fire frequency and lower cDWD loading increased abundance of forbs, graminoids, shrubs, and sub-shrubs while decreasing the biomass of vines and understory hardwood trees. The distribution of understory plants and relationships with the two marginally significant explanatory variables for plant functional groups were similar to those seen in the analysis of plant genera.

**Table 4-5.** Results of Student's *t*-test significance testing of explanatory variables for each regional block.

| Variable | Mean (west) | Mean (east) | *t* | df | *p*-value |
|---|---|---|---|---|---|
| Coarse DWD loading (Mg ha$^{-1}$) | 3.34 | 2.42 | 1.95 | 14.33 | 0.072 |
| 20-year MFI (Years) | 4.65 | 3.30 | 3.47 | 15.20 | 0.003 |
| Forest floor biomass (Mg ha$^{-1}$) | 4.60 | 3.83 | 1.52 | 14.90 | 0.150 |
| Growing season burns (Percent) | 37.50 | 29.80 | 0.19 | 15.84 | 0.854 |
| SD of 20-year MFI | 2.56 | 1.74 | 3.06 | 16.91 | 0.007 |
| Length of fire management (Years) | 22.49 | 16.50 | 2.82 | 9.91 | 0.018 |
| Canopy coverage (Percent) | 38.09 | 43.08 | -1.08 | 15.94 | 0.297 |

### 4.4.3 *Boundary line regression – species*

The boundary line regression showed no significant relationships between species biomass and MFI for 10 common species (Figure 4-7), including *A. beyrichiana* ($r^2 = 0.14$; $P = 0.53$), purple bluestem (*Andropogon glaucopsis* Elliott; $r^2 = 0.17$; $P = 0.50$), *I. glabra* ($r^2 = 0.04$; $P = 0.74$), *L. ferruginea* ($r^2 = 0.04$; $P = 0.74$), *Q. minima* ($r^2 = 0.01$; $P = 0.86$), *S. repens* ($r^2 = 0.10$; $P = 0.60$), dwarf huckleberry (*Gaylussacia dumosa* (Andrews) Torr. & A. Gray; $r^2 = 0.22$; $P = 0.43$), Darrow's blueberry (*Vaccinium darrowii* Camp; $r^2 = 0.08$; $P = 0.65$), yellow jessamine (*Gelsemium sempervirens* (L.) W.T. Aiton; $r^2 = 0.04$; $P = 0.75$), and greenbriar (*Smilax auriculata* Walter; $r^2 = 0.06$; $P = 0.68$).

Boundary line regression of these species tested against percentage of growing-season burns did not produce any significant relationships (Figure 4-8). Although *V. darrowii* ($r^2 = 0.45$;

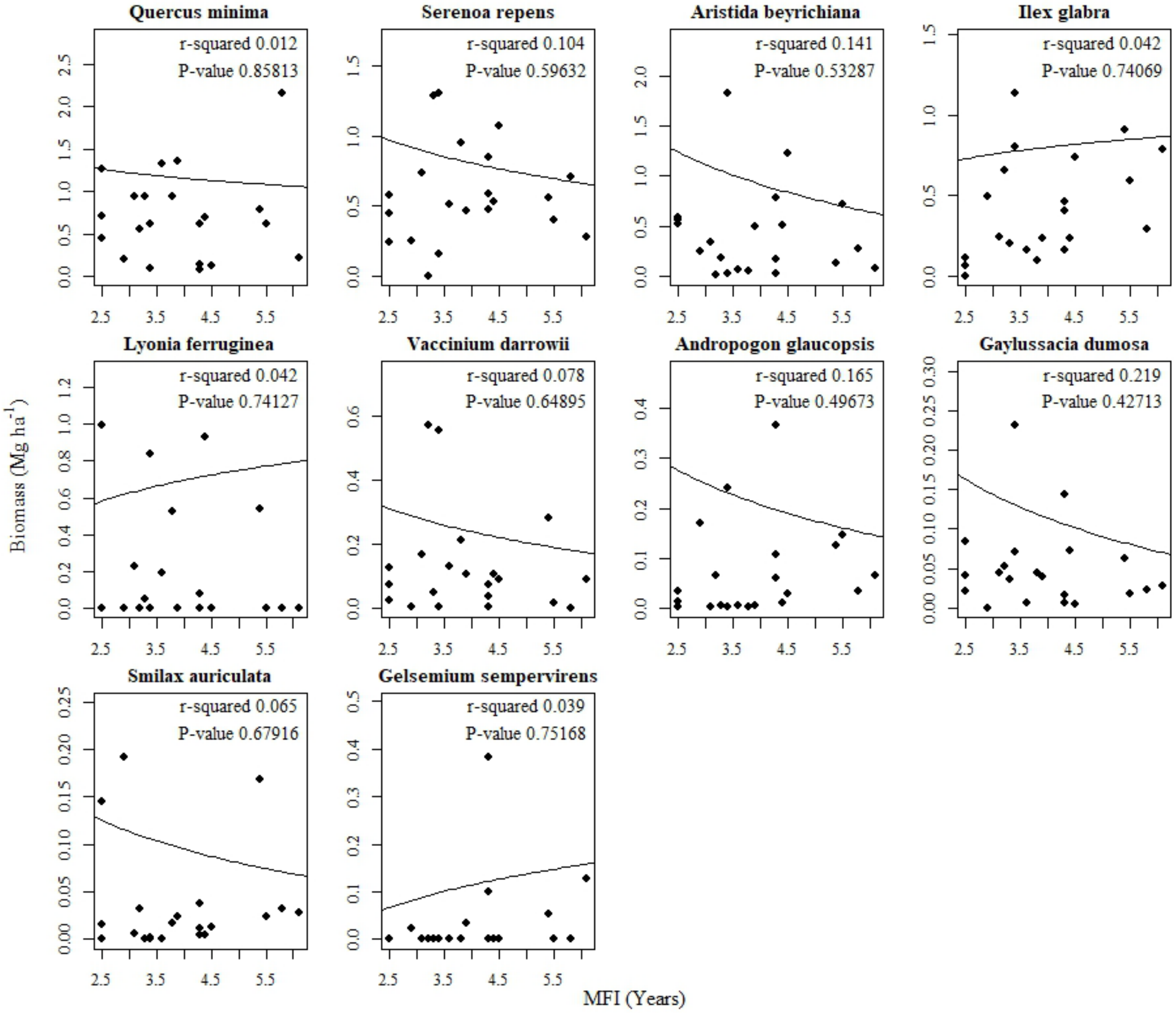


**Figure 4-7.** Boundary line regressions for the 10 species with the highest average biomass (arranged in order from most to least abundant from left to right with most abundant in top left corner and least abundant in bottom right corner) and 20-year mean fire return interval. Solid black circles are maximum points in each bin used for regression.

$P$ = 0.22) and *S. auriculata* ($r^2$ = 0.44; $P$ = 0.22) had the highest $r^2$ values, it was unlikely these represent a relationship between the two variables because biomass was generally flat across the range of MFI values, and the trends were influenced by a few outlier values. Moreover, these relationships did not extend to other species in the same functional groups.

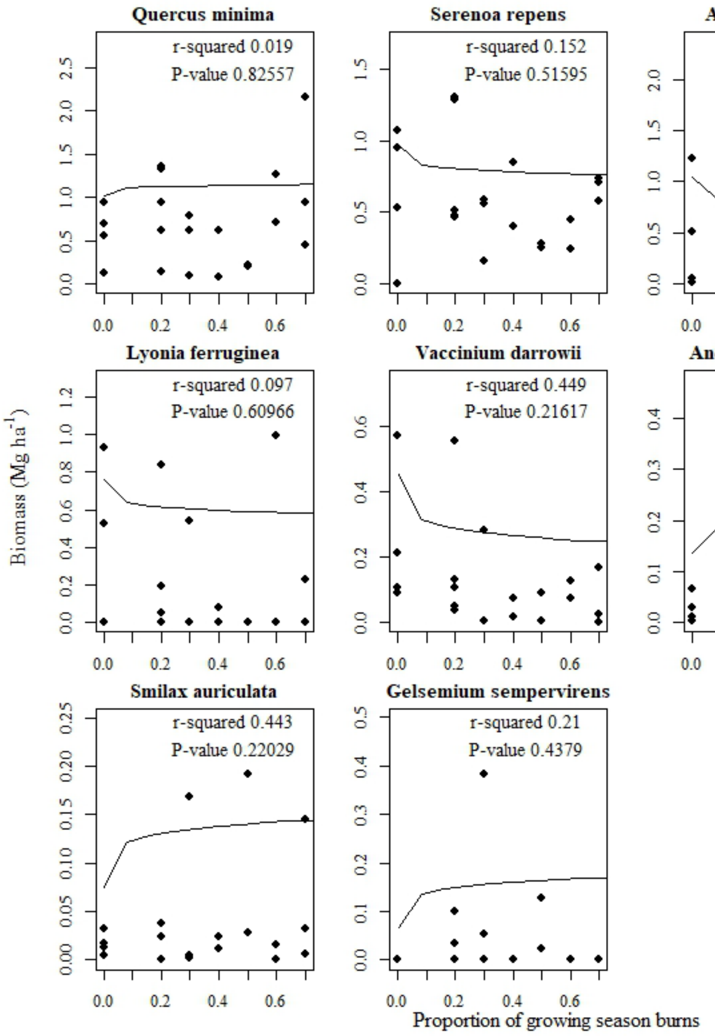


**Figure 4-8.** Boundary line regressions for the 10 species with the highest average biomass (arranged in order from most to least abundant from left to right with most abundant in top left corner and least abundant in bottom right corner) and 20-year proportion of growing season burns. Solid black circles are maximum points in each bin used for regression.

### 4.4.4 *Boundary line regression – plant functional groups*

Trends for plant functional groups mostly reflected the non-significant results of boundary line regressions on the species-level data (Figure 4-9). The effect of MFI was only significant for forbs ($r^2 > 0.99$; $P < 0.01$). Biomass ranged from 0.13–0.49 Mg ha$^{-1}$ when MFI

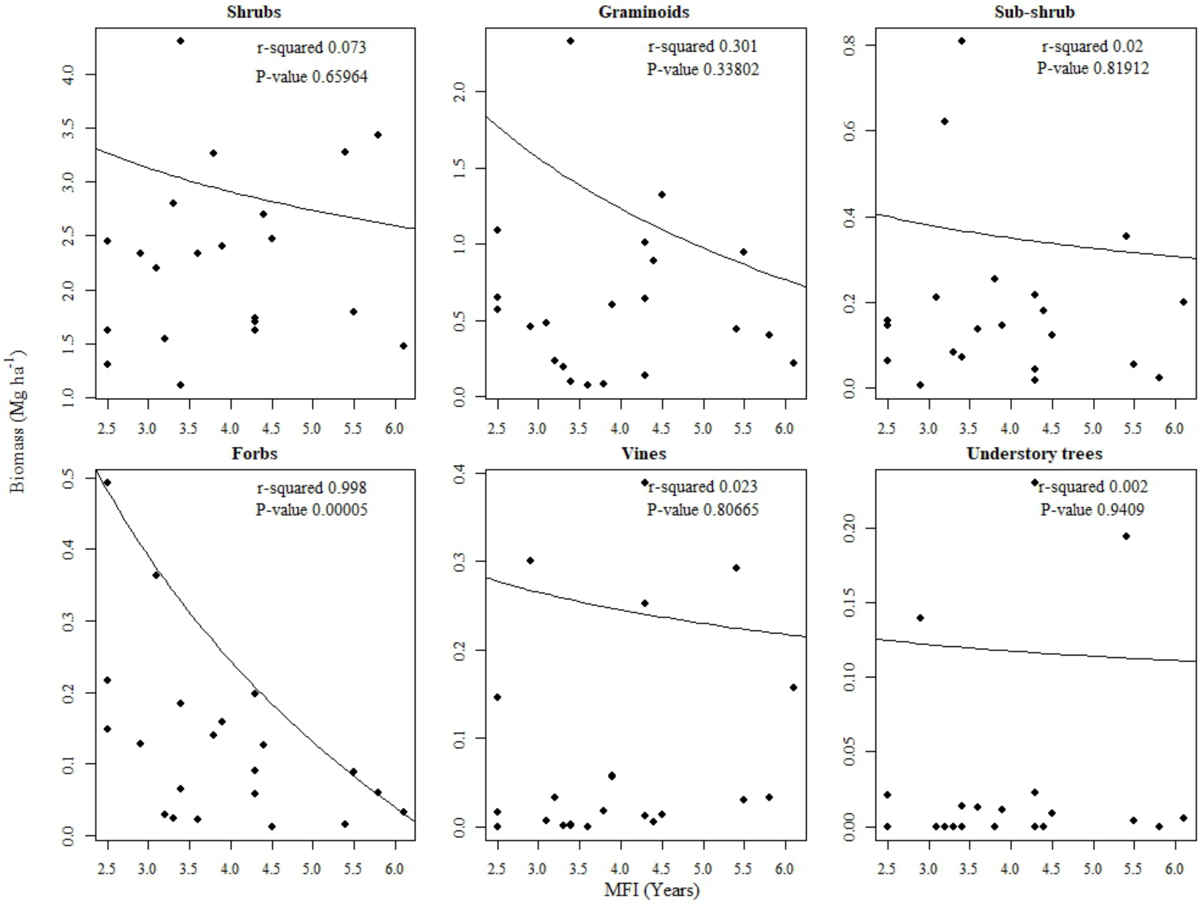


**Figure 4-9.** Boundary line regressions for plant functional groups (arranged in order from most to least abundant from left to right with most abundant in top left corner and least abundant in bottom right corner) and 20-year mean fire interval. Solid black circles are maximum points in each bin used for regression.

was less than three years and 0.01–0.09 Mg ha$^{-1}$ when MFI was between five and six years. There was not a corresponding significant effect of fire frequency on graminoids ($r^2$ = 0.30; $P$ = 0.34). While there was a slight downward curve of graminoid biomass as fire frequency declined, it was primarily driven by a single outlier site in the 3–4 year MFI window with a biomass of 2.33 Mg ha$^{-1}$: nearly double the site with the next highest biomass. Curves associated with the four woody plant groups were flat with $r^2$ values less than 0.1. Biomass was not significantly affected by percentage of growing-season burns for any plant functional group (Figure 4-10) and the result was similar to findings of the species-level boundary line regression.

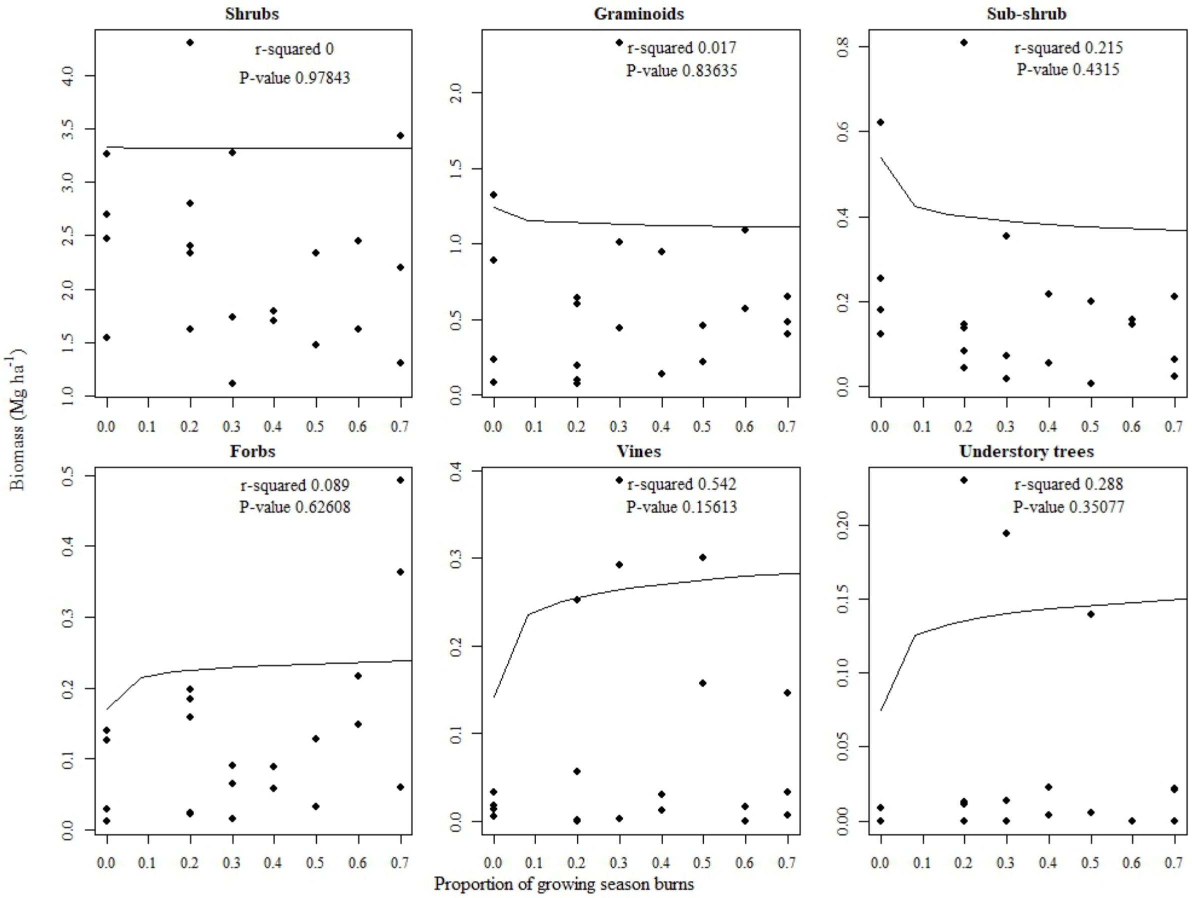


**Figure 4-10.** Boundary line regressions for plant functional groups (arranged in order from most to least abundant from left to right with most abundant in top left corner and least abundant in bottom right corner) and 20-year proportion of growing season burns. Solid black circles are maximum points in each bin used for regression.

## 4.5 Discussion

This study showed that understory composition of longleaf pine flatwoods did not respond to the range of managed fire regime characteristics to the same extent as seen in some controlled studies. While I hypothesized that the ratio of herbaceous-to-woody plants would respond positively to higher fire frequency and percentage of growing-season burns to a lesser extent than observed controlled studies, I did not expect the broad lack of response shown in the results of this study. Although I observed a significant, positive relationship between forb biomass and fire frequency, fire frequency had no significant effect on other plant functional groups. Principal Components Analysis indicated that woody genera and plant functional groups were weakly arranged along a gradient from high to low fire frequency. I did not detect an effect of season-of-burn on understory vegetation composition, as measured by biomass. The lack of response observed in this study can likely be attributed to three factors. First, the range of fire regime characteristics generated by 20 years of prescribed burning was not large enough to have a measurable effect on understory composition. Second, the range of understory conditions I observed was the product of other environmental factors or the legacy of fire regimes that preceded the 20-year record used in this analysis. Third, elements of this study design such as inconsistent classification of taxa, the presence of a blocking factor, and the relatively small sample size may have precluded the detection of more subtle responses of the understory community to variation in the prescribed fire regime.

### 4.5.1 *Fire regime characteristics*

The positive response of forbs to more frequent fire and the equivocal response of woody species reflect current knowledge of how fire affects the understory of longleaf pine flatwoods. This study did not include sites that were burned annually or biennially as is common in many long-term experiments studying the effects of prescribed fire frequency and season-of-burn and may have missed the threshold where fire regime variables have the strongest relationship with understory composition. The largest responses of understory vegetation to repeated low-intensity fire has been observed when the MFI is less than three years (Glitzenstein et al., 2003; Waldrop et al., 1987), whereas the range of MFIs for this study was 2.5 to 6.1 years; a range of MFIs where changes to understory composition, if present, would be more subtle. In addition, season-of-burn generally only has an impact when paired with repeated annual and biennial fire rotations, a condition that was not present among the sites selected for this study.

The cumulative effect of repeated frequent burning is the likely reason many short-term (< 5 years) studies fail to detect an effect of burn season on measures of understory abundance (e.g., Willcox and Giuliano, 2010). In addition to fire frequency and burn season, numerous other environmental factors are known to affect understory composition, including soil texture (Addington et al., 2015b; Glitzenstein et al., 2003; Hannon et al., 2020), soil moisture (Abrahamson, 1984; Kirkman et al., 2001; Walker and Peet, 1984), forest structure (Addington et al., 2015b; Grelen and Lohrey, 1978), surface fuel loading (Gagnon et al., 2012; Thaxton and Platt, 2006), and the legacy of past disturbances (Fill et al., 2017; Olson and Platt, 1995).

### 4.5.2 *Herbaceous vegetation*

The strong link between high forb abundance and frequent burning has been long established (Lemon, 1949) and, to a limited extent, is reflected in the result from this study that observed a significant increase in forb abundance with shorter MFI. An increase in forb abundance has been observed within two years after fire is re-introduced into southeastern pine forests, even after a long absence (Moore et al., 1982) and measures of absolute abundance are typically highest with a 2-year fire return interval (Brockway and Lewis, 1997; Glitzenstein et al., 2012; Waldrop et al., 1987). Absolute abundance typically peaks under biennial burning because annual burns can limit the size and cover of perennial forbs while promoting smaller annual plants. The relative abundance of forbs under an annual burning regime will generally continue to increase because the decline of absolute woody plant abundance is greater.

The relationship between forb biomass and MFI shown by boundary line regression was similar to, but slightly weaker than published values for controlled experiments indicating that these relationships were detectable under more heterogenous conditions as well. Brockway and Lewis (1997) and Robertson et al. (2021) found a 2-3 fold increase in forb biomass from triennially to biennially burned plots. Boundary line regression analysis showed a maximum increase of 20 percent (Figure 4-9), which was closer to the 36 percent increase in biomass of herbs from triennially to biennially burned plots for long-term experiments in longleaf pine flatwoods in South Carolina (Glitzenstein et al., 2003). However, Glitzenstein et al. (2003) grouped graminoids and forbs together; doing so with the data from this study would have substantially diminished this relationship because graminoid biomass was substantially higher than that of forbs. The longer fire rotations for some of my study sites are more difficult to compare with similar studies because few study designs examined sites where the MFI was greater than three years. Brockway and Lewis (1997) reported a doubling of forb biomass from unburned control plots to triennially burned plots while Robertson et al. (2021) observed similar measures of forb biomass between these treatment types. Glitzenstein et al. (2003) found that herb biomass increased 1.6 times for plots burned quadrennially to triennially. The maximum increase observed at my sites was 80 percent and fell within the published range (Figure 4-9). The increase reported by Glitzenstein et al. (2003) more closely resembles the results reported here relative to Robertson et al. (2021), but biomass was grouped for all herbaceous vegetation (i.e., forbs + graminoids) and not reported for forbs alone making a direct comparison difficult.

Research measuring other forms of abundance showed similar response of forbs to changes in MFI. Forb cover on long-term research plots located in longleaf pine flatwoods in Florida increased consistently from 4-yr to 1-yr fire rotations (Glitzenstein et al., 2003) as did forb density at long-term research plots in second growth loblolly pine (*Pinus taeda* L.) forests in South Carolina (Waldrop et al., 1992).

I did not find a significant relationship between graminoid biomass and fire frequency, a result that was unexpected given results from controlled experiments and the positive effect that fire frequency had on forb biomass at my sites. Most research reports a large positive effect of higher fire frequency on measures of graminoid abundance. Graminoid biomass increased by 100 to 200 percent from triennially to biennially burned plots in mesic southern pine forest throughout the coastal plain (Brockway and Lewis, 1997; Glitzenstein et al., 2003; Robertson et al., 2021). Glitzenstein et al., (2003), however, observed a dichotomy in graminoid response to fire frequency between their two study locations in South Carolina and northern Florida. This was attributed to differences in shrub response to fire mediated by soil texture which led to differences in available growing space for graminoids. Specifically, they found that woody plant vigor on fine-textured Ultisols in South Carolina was more sensitive to frequent burns than those on the coarser textured Spodosols in northern Florida. My sites were located on Spodosols or even more coarsely textured Entisols and may have exhibited the same lack of graminoid response to fire frequency observed by Glitzenstein et al. (2003) at their sites in northern Florida. Research that measured different abundance metrics reported a range of strong to weak effects of fire frequency on graminoids. Waldrop et al. (1992) noted 3–5 fold increases in graminoid density when comparing periodic (3–7 year fire rotation) and annually burned plots suggesting that measures of graminoid abundance would increase with more frequent burning. Similarly, Brockway and Lewis (1997) measured a 467 percent increase in *Andropogon* biomass from triennial to biennial burning, but only a 29 percent increase in *Aristida* biomass.

Growing-season burns are generally understood to favor herbaceous vegetation in frequently burned southeastern pine forests by stimulating flowering and seed production of fire-adapted grasses and forbs (Brewer, 2006; Main and Barry, 2002; Platt et al., 1988; Shepherd et al., 2012), but the effects on abundance are more subtle and are sometimes absolute while at others relative. For example, Waldrop et al. (1987) reported that the ratio of herbaceous to woody vegetation was much higher on plots burned annually in the summer relative to plots burned annually in the winter, but that measures of absolute herbaceous plant abundance were higher on winter-burned plots. In contrast, a comparison of summer and winter burning at sites burned three times over a 7-year period found higher absolute measures of herb abundance in growing-season burns, but these were not correlated with changes in abundance of woody understory plants (Addington et al., 2015a). In this case the effect was absolute but not relative.

### 4.5.3 *Woody vegetation*

Fire frequency and season-of-burn did not affect woody plant biomass in my study. There are a host of possible reasons for this that are mostly the result of using data from a management setting rather than a controlled experiment. They include variable application of growing-season burns, other environmental factors, the narrow range of MFIs, and a relatively small sample size. Among environmental factors, soil texture, overstory characteristics, topography, fire behavior, pre-fire fuel structure, and legacy effects of past disturbance regimes have all been found to have interacting effects with fire frequency and season-of-burn regarding their effects on woody plant abundance. These confounding variables and their lack of inclusion in some studies are a likely reason that fire effects research often contains mixed conclusions on the effect of season-of-burn and fire frequency on understory composition.

My expectation that woody plant biomass would be lower on more frequently burned sites with a larger fraction of growing-season burns was based largely on controlled long-term experiments. The most dramatic examples of this are provided by multi-decade studies on understory plant dynamics in mesic pine flatwoods at two sites in South Carolina (Glitzenstein et al., 2003; Waldrop et al., 1992), where significant reductions in shrub abundance were noted on plots burned annually during the growing season with lesser reductions on biennially burned plots and those burned in the dormant season. Similar studies have found little to no significant effects on increases in frequency or number of growing season burns on woody plant abundance. This suggests that even under controlled conditions there is geographic variability in the response of woody understory vegetation to changes in fire frequency and season-of-burn despite the similarity in species composition in mesic pine flatwoods across the region. Season-of-burn alone has been tested for effects on woody plant abundance and most results show little to no effect for shrub species that were abundant at my sites, including *I. glabra* (Hughes and Knox, 1964) and *S. repens* (Willcox and Giuliano, 2010), or for the woody plant functional groups I evaluated (Addington et al., 2015a; Kush et al., 1999). In contrast, some studies do show a significant relationship between season-of-burn and woody understory species but many of the species evaluated were uncommon at my sites. For example, a long-term study on the effect of winter, spring, and summer burning on understory hardwood stem density, primarily oaks (*Quercus* spp.; 86 percent) and flowering dogwood (*Cornus florida* L.; 11 percent), in a young longleaf pine stand in Alabama found that spring and summer burns caused a decline in density over time, whereas density increased over time on plots burned during the winter (Boyer, 1993). Growing-season burns have also been shown to reduce growth rates of shrubs (Robertson and Hmielowski, 2014), although the ultimate effect on shrub abundance is unclear.

High-frequency, growing-season burning is hypothesized to reduce measures of woody plant abundance because belowground carbohydrate stores are lowest as leaves emerge in the spring (Ferguson, 1957; Hough, 1968; Wenger, 1953; Woods et al., 1959). Thus, it is hypothesized that burning in the spring and early summer causes woody plants to draw from diminished reserves after they are top-killed and resprout. Thus, when combined with annual or biennial burning, woody plants draw from carbohydrate reserves faster than they can be replenished, ultimately leading to mortality. Mortality through carbohydrate exhaustion has been difficult to prove broadly across the longleaf pine ecosystem and it is possible that this physiological effect can only be achieved with repeated, annual spring and summer burns over extended time periods (i.e., decades), or with additional woody vegetation control measures (Olson, 1992). My study did include sites with a wide range of values for percentage of growing season burns but none were burned consistently (i.e., 100 percent of the time) during the growing season. Furthermore, my sites did not include annual or biennial burns which is when growing-season fires have been shown to cause the largest reductions of woody understory vegetation.

### 4.5.4 *Confounding variables*

The results of this study, taken in context with current knowledge about the disturbance dynamics of understory vegetation in longleaf pine flatwoods show that a complex web of interactions drives understory composition. Fire frequency is a primary contributor, but only when MFI falls below four years for a sustained period. Sites in this study were not burned frequently enough (MFI: mean = 3.9 years; range = 2.5 to 6.1 years) to affect understory vegetation composition as measured by biomass. When compared to the long list of controlled experiments (Brockway and Lewis, 1997; Glitzenstein et al., 2003; Robertson et al., 2021;

Waldrop et al., 1992), my sites missed the biennial burning threshold where repeated burning and growing-season burns tend to produce the greatest reductions in measures of woody plant abundance. Addington et al. (2015b) found that 2.7 years was the cutoff where shorter MFIs began to negatively impact woody plant cover. Likewise, Robertson et al. (2021) noted that MFI greater than 2 years did not negatively affect understory hardwood abundance in old field loblolly pine forests.

A number of other environmental factors play a role in understory composition as well, often interacting with fire frequency and season-of-burn. Several studies have shown that prescribed fire reduces woody plant abundance in mesic pine flatwood sites with medium-textured Ultisols, but these reductions only occurred when either implemented annually during the dormant season or every two years or less in the growing season (Drewa et al., 2002b; Glitzenstein et al., 2003; Waldrop et al., 1987). Furthermore, this relationship appears to weaken when soil texture becomes either coarser or finer (Addington et al., 2015b; Drewa et al., 2002b; Glitzenstein et al., 2003). Longleaf pine density has a negative relationship with measures of fire tolerant oaks and fire-sensitive hardwood abundance (Hannon et al., 2020). Cover of woody plants has been found to be greater on lower angle slopes (Addington et al., 2015b). Fire behavior can have a significant effect on woody plants if burn intensity is high enough (Hierro and Menges, 2002). In the southeastern US, however, where managed fires are prescribed to fall within a relatively narrow range of lower intensities, fire effects based on higher fire intensity are more likely negligible. This is likely the case for the sites in this study because surface fuel loads were relatively low, falling within a narrow range typical of regularly burned longleaf pine flatwoods (Ottmar and Vihnanek, 2000), and would be more likely to support uniformly low intensity fire behavior. This result is seen in other studies as well. For example, higher fire temperatures did not promote oak mortality on longleaf pine sandhills in Florida (Glitzenstein et al., 1995), nor was there an effect on shrub density in longleaf pine savannas in Louisiana and Florida (Drewa et al., 2002a). In contrast, increases in fire behavior at small spatial scales caused by areas of high fuel loading have been found to increase shrub mortality in frequently burned longleaf pine savannas (Thaxton and Platt, 2006). The prevalence of coarse-textured soils, relatively low fire intensity, and the lack of topography at sites in this study could have all contributed to mute the effects of fire frequency and season-of-burn on understory vegetation dynamics.

The legacy effects of past disturbance regimes could explain the higher abundances of herbaceous plants seen at some of the sites in this study. Herbaceous plant communities in wet pine savannas were found to maintain enough abundance to quickly rebound after a 15-year period of fire exclusion (Hinman and Brewer, 2007) and established *A. beyrichiana* plants have been found to inhibit woody plant invasion during extended periods without fire (Fill et al., 2017). This persistence has also been noted in established woody plants when fire frequency and/or growing-season burns are introduced. The period of fire exclusion during the first half of the 1900s that allowed widespread shrub establishment in longleaf pine forest understories led to a high level of shrub resilience because plants established extensive root systems from which to resprout, large seedbanks, and less competition from extirpated perennial herbs. The resilience of the woody plant component, in turn, means that a resumption of historic fire regimes is often not enough to reduce their abundance, a fact that has been frequently highlighted (Drewa et al., 2002b; Glitzenstein et al., 2003; Olson, 1992). One explanation for how lagged effects of past disturbance regimes could have affected understory vegetation at my sites was if locations with historically high *A. beyrichiana* abundance were subject to a shorter period of fire exclusion.

This could have extended the resistance to woody plant invasion noted by a Fill et al. (2017) into the period where prescribed fires were applied more frequently. In this case, the high level of resilience of herbaceous plants to extended periods without fire noted by Hinman and Brewer (2007) would permit the regeneration of the herbaceous layer over the establishment of woody vegetation.

My sample size (*n* =20) was smaller than other studies that attempt to retrospectively evaluate the effects of the managed fire regime and other environmental constraints on understory plant dynamics in longleaf pine flatwoods. Similar research where results produced significant relationships between understory composition and the managed fire regime included 307 plots at Fort Bragg in North Carolina (Hannon et al., 2020), 189 plots at Fort Benning in Georgia (Addington et al., 2015b), and 49 plots in the Southlands Experimental Forest in Georgia (Hedman et al., 2000). This may have led us to miss some of the more subtle responses of understory vegetation to variation in the managed fire regime.

## 4.6 **Conclusions and management recommendations**

Prescribed burning and other restoration treatments have been utilized widely across longleaf pine-dominated ecosystems by land management agencies for decades. The objectives of these treatments have been to restore the structure and composition of the forest canopy, to provide habitat for rare species dependent on this habitat, to manage for high levels of biodiversity and endemism found in the understory vegetation, and to manage wildfire risk. Managing to restore historical reference conditions, which includes herb dominance in the understory, is an oft-cited objective yet many stands, including those measured in this study, remain shrub dominated. My results, as well as the results of other research, suggest that the current frequency of burning as implemented operationally (i.e., MFI > 3 years) does not have a strong effect on understory composition for herbs or woody plants. Controlled experiments that have implemented annual or biennial burning and regularly apply prescribed fires during the growing season can sometimes shift understory composition from woody to herbaceous plant dominance.

Managers using prescribed fire to maintain ecological characteristics of longleaf pine flatwoods should foremost have a clear idea of the desired understory conditions. If the abundance of herbaceous species is unimportant then the MFI or percentage of growing season burns has less bearing on management objectives so long as burns occur frequently enough to maintain an open understory. If, on the other hand, the herbaceous component is important then changes in MFI and application of growing-season burns should be carefully managed, and attention should be paid to environmental factors and legacy disturbance regimes that are known to affect the extent that prescribed fire can drive understory composition. Based on the results of this and other studies in longleaf pine flatwoods,  annual burns conducted during the growing season for several years are likely necessary to generate reductions in woody species and increases in herbaceous species. However, there are caveats to this recommendation. Most importantly, these recommendations are limited to longleaf pine flatwoods that have been managed with frequent prescribed fire for extended periods of time and have not been subject to major anthropogenic soil disturbance such as agriculture (e.g., Matusick et al., 2020; Robertson et al., 2021). Applying annual burns to longleaf pine stands where fire has been excluded or only applied infrequently could cause widespread overstory mortality (e.g., Slack et al., 2016; Varner et al., 2007) and stands with a history of soil disturbance often have an entirely different community of species in the understory that have different management guidelines (Robertson et al., 2021). In addition, and as noted in the discussion section, several studies show that soil texture can affect the ability of prescribed fire to shift understory composition from woody to herbaceous species dominance. Stands on medium-textured Ultisols appear to have the best response to annual or biennial burns. Finally, the ability to conduct burns with higher fire intensity also appears to improve the likelihood of reducing woody plant abundance. Thus, if prescribed burns can only be accomplished under marginal burning conditions that generate low measures of fire behavior there may be a reduced response.

In any case, managers should monitor efforts to shift understory composition closely as they may not always achieve desired effects. Because burning annually or biennially requires a significant investment of time and resources, new burning regimes should be trialed on small areas to ensure the outcomes are those desired. Coordination among adjacent land management units by sharing data and experimenting with different methods and treatments (e.g., mechanical removal and herbicides) can further reduce the burden of implementing new burning regimes. Once a desired understory composition has been achieved, it may not be necessary to burn at the same frequency or with the same number of growing season burns to maintain the understory in its desired state as it took to restore it.

## 4.7 **References**

Abrahamson, W.G., 1984. Post-fire recovery of Florida Lake Wales Ridge vegetation. Am. J. Bot. 71, 9–21. https://doi.org/https://doi.org/10.1002/j.1537-2197.1984.tb12479.x

Abrahamson, W.G., Abrahamson, C.R., Keller, M.A., 2021. Lessons from four decades of monitoring vegetation and fire: maintaining diversity and resilience in Florida’s uplands. Ecol. Monogr. 91, 1–20. https://doi.org/10.1002/ecm.1444

Addington, R.N., Greene, T.A., Harrison, W.C., Sorrell, G.G., Elmore, M.L., Hermann, S.M., 2015a. Restoring longleaf pine: effects of seasonal prescribed fire and overstory density on vegetation structure of a young longleaf pine plantation. For. Sci. 61, 135–143. https://doi.org/https://doi.org/10.5849/forsci.13-618

Addington, R.N., Knapp, B.O., Sorrell, G.G., Elmore, M.L., Wang, G.G., Walker, J.L., 2015b. Factors affecting broadleaf woody vegetation in upland pine forests managed for longleaf pine restoration. For. Ecol. Manage. 354, 130–138. https://doi.org/10.1016/j.foreco.2015.06.028

Allen, W.J., 1991. Soil survey of Wakulla County, Florida. USDA Soil Conservation Service, Washington, DC.

Alstad, A.O., Damschen, E.I., Givnish, T.J., Harrington, J.A., Leach, M.K., Rogers, D.A., Waller, D.M., 2016. Plant ecology: the pace of plant community change is accelerating in remnant prairies. Sci. Adv. 2. https://doi.org/10.1126/sciadv.1500975

Archer, S.R., Andersen, E.M., Predick, K.I., Schwinning, S., Steidl, R.J., Woods, S.R., 2017. Woody plant encroachment: causes and consequences, in: Briske, D.D. (Ed.), Rangeland Systems: Processes, Management, and Challenges. Gewerbestrasse, Switzerland, pp. 25–84.

Blanchet, F.G., Legendre, P., Borcard, D., 2008. Forward selection of explanatory variables. Ecology 89, 2623–2632. https://doi.org/10.1890/07-0986.1

Bond, W.J., Keeley, J.E., 2005. Fire as a global “herbivore”: the ecology and evolution of flammable ecosystems. Trends Ecol. Evol. 20, 387–394. https://doi.org/https://doi.org/10.1016/j.tree.2005.04.025

Bond, W.J., Woodward, F.I., Midgley, G.F., 2005. The global distribution of ecosystems in a world without fire. New Phytol. 165, 525–538. https://doi.org/10.1111/j.1469-

8137.2004.01252.x

Bowles, M., Apfelbaum, S., Haney, A., Lehnhardt, S., Post, T., 2011. Canopy cover and groundlayer vegetation dynamics in a fire managed eastern sand savanna. For. Ecol. Manage. 262, 1972–1982. https://doi.org/10.1016/j.foreco.2011.08.036

Bowles, M.L., Jones, M.D., McBride, J.L., 2003. Twenty-year changes in burned and unburned sand prairie remnants in northwestern Illinois and implications for management. Am. Midl. Nat. 149, 35–45. https://doi.org/10.1674/0003-0031(2003)149[0035:tyciba]2.0.co;2

Boyer, W.D., 1993. Season of burn and hardwood development in young longleaf pine stands, in: Brissette, J.C. (Ed.), Proceedings of the Seventh Biennial Southern Silvicultural Research Conference. USDA Forest Service, Gen. Tech. Rep. SO-93, New Orleans, Louisiana, pp. 511–515. https://doi.org/https://doi.org/10.2737/SO-GTR-93

Brewer, J.S., 2023. Mechanisms of fire-maintained plant species diversity in species-rich wet pine savannas. Ecosphere 14, 1–28. https://doi.org/10.1002/ecs2.4387

Brewer, J.S., 2017. Stochastic losses of fire-dependent endemic herbs revealed by a 65-year chronosequence of dispersal-limited woody plant encroachment. Ecol. Evol. 4377–4389. https://doi.org/10.1002/ece3.3020

Brewer, J.S., 2006. Long-term population changes of a fire-adapted plant subjected to different fire seasons. Nat. Areas J. 26, 267–273. https://doi.org/10.3375/0885-8608(2006)26[267:lpcoaf]2.0.co;2

Brockway, D.G., Lewis, C.E., 1997. Long-term effects of dormant-season prescribed fire on plant community diversity, structure and productivity in a longleaf pine wiregrass ecosystem. For. Ecol. Manage. 96, 167–183. https://doi.org/https://doi.org/10.1016/S0378-1127(96)03939-4

Brown, J.K., 1974. Handbook for inventorying downed woody material. USDA Forest Service, Gen. Tech. Rep. INT-16, Ogden, Utah.

Brudvig, L.A., Orrock, J.L., Damschen, E.I., Collins, C.D., Hahn, P.G., Mattingly, W.B., Veldman, J.W., Walker, J.L., 2014. Land-use history and contemporary management inform an ecological reference model for longleaf pine woodland understory plant communities. PLoS One 9. https://doi.org/10.1371/journal.pone.0086604

Burrows, N., Ward, B., Wills, A., Williams, M., Cranfield, R., 2019. Fine-scale temporal turnover of jarrah forest understory vegetation assemblages is independent of fire regime. Fire Ecol. 15. https://doi.org/10.1186/s42408-019-0025-0

Cerling, T.E., Harris, J.M., MacFadden, B.J., Leakey, M.G., Quade, J., Eisenmann, V., Ehieringer, J.R., 1997. Global vegetation change through the Miocene/Pliocene boundary. Nature 389, 153–158. https://doi.org/10.1038/38229

Collins, S.L., Glenn, S.M., Gibson, D.J., 1995. Experimental analysis of intermediate disturbance and initial floristic composition: decoupling cause and effect. Ecology 76, 486–492. https://doi.org/10.2307/1941207

Connell, J.H., 1978. Diversity in tropical rain forests and coral reefs. Science 199, 1302–1310. https://doi.org/10.1126/science.199.4335.1302

Cronan, J.B., Wright, C.S., Petrova, M., 2015. Effects of dormant and growing season burning on surface fuels and potential fire behavior in northern Florida longleaf pine (*Pinus palustris*) flatwoods. For. Ecol. Manage. 354, 318–333. https://doi.org/10.1016/j.foreco.2015.05.018

Custer, G., 2011. Growing season prescribed fire on the Ocala National Forest [Presentation]. Pinelands Alliance, Southampton, New Jersey.

de Souza, G.F., Ferreira, M.C., Munhoz, C.B.R., 2022. Decrease in species richness and diversity, and shrub encroachment in Cerrado grasslands: a 20 years study. Appl. Veg. Sci. 25, 1–16. https://doi.org/10.1111/avsc.12668

Dee, J.R., Menges, E.S., 2014. Gap ecology in the Florida scrubby flatwoods: effects of time-since-fire, gap area, gap aggregation and microhabitat on gap species diversity. J. Veg. Sci. 25, 1235–1246. https://doi.org/10.1111/jvs.12170

Drewa, P.B., Platt, W.J., Moser, E.B., 2002a. Community structure along elevation gradients in headwater regions of longleaf pine savannas. Plant Ecol. 160, 61–78.

Drewa, P.B., Platt, W.J., Moser, E.B., 2002b. Fire effects on resprouting of shrubs in headwaters of southeastern longleaf pine savannas. Ecology 83, 755–767. https://doi.org/Doi 10.2307/3071879

Edwards, E.J., Osborne, C.P., Strömberg, C.A., Smith, S.A., 2010. The origins of C4 grasslands: integrating evolutionary and ecosystem science. Science 328, 587–59. https://doi.org/https://doi.org/10.1126/science.1177216

Ferguson, E.R., 1957. Stem-kill and sprouting following prescribed fires in a pine-hardwood stand in Texas. J. For. 55, 426–429.

Ferguson, J.P., 1998. Prescribed fire on the Apalachicola Ranger District: the shift from dormant season to growing season and effects on wildfire suppression, in: Pruden, T.L., Brennan, L.A. (Eds.), Fire in Ecosystem Management: Shifting the Paradigm from Suppression to Prescription, Tall Timbers Fire Ecology Conference Proceedings No. 20. Tall Timbers Research Station, Tallahassee, Florida, pp. 120–126. https://doi.org/https://doi.org/10.1046/j.1526-100x.2000.80045.x

Fernández-García, V., Alonso-González, E., 2023. Global patterns and dynamics of burned area and burn severity. Remote Sens. 15, 1–24. https://doi.org/https://doi.org/10.3390/rs15133401

Fill, J.M., Glitzenstein, J.S., Streng, D.R., Stowe, J., Mousseau, T.A., 2017. Wiregrass (*Aristida beyrichiana*) may limit woody plant encroachment in longleaf pine (*Pinus palustris*) ecosystems. Am. Midl. Nat. 177, 153–161. https://doi.org/10.1674/0003-0031-177.1.153

Filzmoser, P., Gschwander, M., 2021. mvoutlier: multivariate outlier detection based on robust methods [Computer software]. R package version 2.1.1. https://CRAN.R-project.org/package=mvoutlier.

Freeman, J.E., Kobziar, L.N., Leone, E.H., Williges, K., 2019. Drivers of plant functional group richness and beta diversity in fire-dependent pine savannas. Divers. Distrib. 25, 1024–1044. https://doi.org/10.1111/ddi.12926

Fritz, H., Loison, A., 2006. Large herbivores across biomes, in: Danell, K., Duncan, P., Bergstrom, R., Pastor, J. (Eds.), Large Herbivore Ecology, Ecosystem Dynamics and Conservation. Cambridge University Press, Cambridge, pp. 19–49. https://doi.org/10.1017/cbo9780511617461.003

Frontier, S., 1976. Étude de la décroissance des valeurs propres dans une analyse en composantes principales: comparaison avec le modd́le du bâton brisé. J. Exp. Mar. Bio. Ecol. 25, 67–75. https://doi.org/https://doi.org/10.1016/0022-0981(76)90076-9

Frost, C.C., 2006. History and future of the longleaf pine ecosystem, in: Jose, S., Jokela, E.J., Miller, D.L. (Eds.), The Longleaf Pine Ecosystem. Springer, New York, pp. 9–48. https://doi.org/10.1007/978-0-387-30687-2_2

Frost, P.G.H., Robertson, F., 1987. The ecological effects of fire in savannas, in: Walker, B.H. (Ed.), Determinants of Tropical Savannas. IRL Press, Oxford, pp. 93–140.

https://doi.org/https://doi.org/10.1007/978-3-642-78969-4_2

Gagnon, P.R., Harms, K.E., Platt, W.J., Passmore, H.A., Myers, J.A., 2012. Small-scale variation in fuel loads differentially affects two co-dominant bunchgrasses in a species-rich pine savanna. PLoS One 7. https://doi.org/ARTN e29674DOI 10.1371/journal.pone.0029674

Gilliam, F.S., Platt, W.J., 1999. Effects of long-term fire exclusion on tree species composition and stand structure in an old-growth *Pinus palustris* (longleaf pine) forest. Plant Ecol. 140, 15–26. https://doi.org/Doi 10.1023/A:1009776020438

Glitzenstein, J.S., Platt, W.J., Streng, D.R., 1995. Effects of fire regime and habitat on tree dynamics in north Florida longleaf pine savannas. Ecol. Monogr. 65, 441–476. https://doi.org/https://doi.org/10.2307/2963498

Glitzenstein, J.S., Streng, D.R., Masters, R.E., Robertson, K.M., Hermann, S.M., 2012. Fire-frequency effects on vegetation in north Florida pinelands: another look at the long-term Stoddard Fire Research Plots at Tall Timbers Research Station. For. Ecol. Manage. 264, 197–209. https://doi.org/DOI 10.1016/j.foreco.2011.10.014

Glitzenstein, J.S., Streng, D.R., Wade, D.D., 2003. Fire frequency effects on longleaf pine (*Pinus palustris*, P. Miller) vegetation in South Carolina and northeast Florida, USA. Nat. Areas J. 23, 22–37.

Gold, Z.J., Pellegrini, A.F.A., Refsland, T.K., Andrioli, R.J., Bowles, M.L., Brockway, D.G., Burrows, N., Franco, A.C., Hallgren, S.W., Hobbie, S.E., Hoffmann, W.A., Kirkman, K.P., Reich, P.B., Savadogo, P., Silvério, D., Stephan, K., Strydom, T., Varner, J.M., Wade, D.D., Wills, A., Staver, A.C., 2023. Herbaceous vegetation responses to experimental fire in savannas and forests depend on biome and climate. Ecol. Lett. 26, 1237–1246. https://doi.org/10.1111/ele.14236

Gordijn, P.J., Everson, T.M., O'Connor, T.G., 2018. Resistance of Drakensberg grasslands to compositional change depends on the influence of fire-return interval and grassland structure on richness and spatial turnover. Perspect. Plant Ecol. Evol. Syst. 34, 26–36. https://doi.org/10.1016/j.ppees.2018.07.005

Gordijn, P.J., O'Connor, T.G., 2021. Multidecadal effects of fire in a grassland biodiversity hotspot: Does pyrodiversity enhance plant diversity? Ecol. Appl. 31, 1–19. https://doi.org/10.1002/eap.2391

Grace, J., José, J.S., Meir, P., Miranda, H.S., Montes, R.A., 2006. Productivity and carbon fluxes of tropical savannas. J. Biogeogr. 33, 387–400. https://doi.org/10.1111/j.1365-2699.2005.01448.x

Grelen, H.E., Lohrey, R.E., 1978. Herbage yield related to basal area and rainfall in a thinned longleaf plantation. USDA Forest Service, Res. Note SO-232, New Orleans, Louisiana.

Hannon, D.R., Moorman, C.E., Schultz, A.D., Gray, J.M., DePerno, C.S., 2020. Predictors of fire-tolerant oak and fire-sensitive hardwood distribution in a fire-maintained longleaf pine ecosystem. For. Ecol. Manage. 477, 118468. https://doi.org/10.1016/j.foreco.2020.118468

Hardin, E.D., White, D.L., 1989. Rare vascular plant taxa associated with wiregrass (*Aristida stricta*) in the southeastern United States. Nat. Areas J. 9, 234–245.

Haywood, J.D., Harris, F.L., Grelen, H.E., Pearson, H.A., 2001. Vegetative response to 37 years of seasonal burning on a Louisiana longleaf pine site. South. J. Appl. For. 25, 122–130. https://doi.org/10.1093/sjaf/25.3.122

He, T., Lamont, B.B., Pausas, J.G., 2019. Fire as a key driver of Earth's biodiversity. Biol. Rev. 94, 1983–2010. https://doi.org/10.1111/brv.12544

Hedman, C.W., Grace, S.L., King, S.E., 2000. Vegetation composition and structure of southern coastal plain pine forests: an ecological comparison. For. Ecol. Manage. 134, 233–247. https://doi.org/https://doi.org/10.1016/S0378-1127(99)00259-5

Hierro, J.L., Menges, E.S., 2002. Fire intensity and shrub regeneration in palmetto-dominated flatwoods of central Florida. Florida Sci. 65, 51–61.

Hiers, J.K., O'Brien, J.J., Will, R.E., Mitchell, R.J., 2007. Forest floor depth mediates understory vigor in xeric *Pinus palustris* ecosystems. Ecol. Appl. 17, 806–814. https://doi.org/https://doi.org/10.1890/06-1015

Hinman, S.E., Brewer, J.S., 2007. Responses of two frequently-burned wet pine savannas to an extended period without fire. J. Torrey Bot. Soc. 134, 512–526. https://doi.org/Doi 10.3159/07-Ra-005.1

Hough, W.A., 1968. Carbohydrate reserves of saw-palmetto: seasonal variation and effects of burning. For. Sci. 14, 399–405. https://doi.org/https://doi.org/10.1093/forestscience/14.4.399

Hughes, R.H., Knox, F.E., 1964. Response of gallberry to seasonal burning. USDA Forest Service, Res. Note SE-21, Asheville, North Carolina.

Johansson, T., 1985. Estimating canopy density by the vertical tube method. For. Ecol. Manage. 11, 139–144. https://doi.org/10.1016/0378-1127(85)90063-5

Jose, S., Jokela, E.J., Miller, D.L., 2006. The longleaf pine ecosystem: an overview, in: Jose, S., Jokela, E.J., Miller, D.L. (Eds.), The Longleaf Pine Ecosystem: Ecology, Silviculture, and Restoration. Springer, New York, pp. 3–8. https://doi.org/10.1007/978-0-387-30687-2

Kirkman, L.K., Mitchell, R.J., Helton, R.C., Drew, M.B., 2001. Productivity and species richness across an environmental gradient in a fire-dependent ecosystem. Am. J. Bot. 88, 2119–2128. https://doi.org/Doi 10.2307/3558437

Kush, J., Meldahl, R.S., Boyer, W.D., 1999. Understory plant community response after 23 years of hardwood control treatments in natural longleaf pine (*Pinus palustris*) forests. Can. J. For. Res. 29, 1047–1054. https://doi.org/https://doi.org/10.1139/x99-063

Lavoie, M., Kobziar, L., Long, A., Hainds, M., 2011. Problems and needs for restorationists of longleaf pine ecosystems: a survey. Nat. Areas J. 31, 294–299. https://doi.org/https://doi.org/10.3375/043.031.0312

Leach, M.K., Givnish, T.J., 1996. Ecological determinants of species loss in remnant prairies. Science 273, 1555–1558. https://doi.org/10.1126/science.273.5281.1555

Lehmann, C.E.R., Anderson, T.M., Sankaran, M., Higgins, S.I., Archibald, S., Hoffmann, W.A., Hanan, N.P., Williams, R.J., Fensham, R.J., Felfili, J., Hutley, L.B., Ratnam, J., Jose, J.S., Montes, R., Franklin, D., Russell-Smith, J., Ryan, C.M., Durigan, G., Hiernaux, P., Haidar, R., Bowman, D.M.J.S., Bond, W.J., 2014. Savanna vegetation-fire-climate relationships differ among continents. Science 343, 548–552. https://doi.org/https://doi.org/10.1126/science.1247355

Lemon, P.C., 1949. Successional responses of herbs in the longleaf-slash pine forest after fire. Ecology 30, 135–145. https://doi.org/Doi 10.2307/1931182

Main, M.B., Barry, M.J., 2002. Influence of season of fire on flowering of wet prairie grasses in South Florida, USA. Wetlands 22, 430–434. https://doi.org/Doi 10.1672/0277-5212(2002)022[0430:Iosofo]2.0.Co;2

Makowski, D., Dore, T., Monod, H., 2007. A new method to analyse relationships between yield components with boundary lines. Agron. Sustain. Dev. 27, 119–128. https://doi.org/Doi 10.1051/Agro:2006029

Maliakal, S.K., Menges, E.S., Denslow, J.S., 2000. Community composition and regeneration of

Lake Wales Ridge wiregrass flatwoods in relation to time-since-fire. J. Torrey Bot. Soc. 127, 125–138. https://doi.org/10.2307/3088690

Marchant, R., 1990. Robustness of classification and ordination techniques applied to macroinvertebrate communities from the La Trobe River, Victoria. Mar. Freshw. Res. 41, 493–504. https://doi.org/https://doi.org/10.1071/MF9900493

Matusick, G., Hudson, S.J., Garrett, C.Z., Samuelson, L.J., Kent, J.D., Addington, R.N., Parker, J.M., 2020. Frequently burned loblolly – shortleaf pine forest in the southeastern United States lacks the stability of longleaf pine forest. Ecosphere 11. https://doi.org/10.1002/ecs2.3055

Maurin, O., Davies, T.J., Burrows, J.E., Daru, B.H., Yessoufou, K., Muasya, A.M., van der Bank, M., Bond, W.J., 2014. Savanna fire and the origins of the "underground forests" of Africa. New Phytol. 204, 201–214. https://doi.org/10.1111/nph.12936

McCune, B., Grace, J.B., 2002. Analysis of ecological communities. MjM Software Design, Gleneden Beach, Oregon.

McIntyre, R.K., Guldin, J.M., Ettel, T., Ware, C., Jones, K., 2018. Restoration of longleaf pine in the southern United States: a status report, in: Kirschman, J.E. (Ed.), Proceedings of the 19th Biennial Southern Silvicultural Research Conference. USDA Forest Service, e-Gen. Tech. Rep. SRS-234, Asheville, North Carolina, pp. 297–302. https://doi.org/https://doi.org/10.2737/SRS-GTR-234

McWhite, R.W., Furman, J., Petrick, C.J., 1999. Eglin Air Force Base integrated natural resources transitional plan 1998-2001. US Department of Defense, Air Force, Natural Resources Management Branch, Niceville, Florida.

Meller, P., Frazão, R., Lages, F., Jürgens, N., Finckh, M., 2022. Tipping the scales: how fire controls the balance among functional groups in Angolan grasslands. African J. Range Forage Sci. 39, 56–69. https://doi.org/10.2989/10220119.2021.2012822

Mitchell, R.J., Duncan, S.L., 2009. Range of variability in southern coastal plain forests: its historical, contemporary, and future role in sustaining biodiversity. Ecol. Soc. 14.

Mogashoa, R., Dlamini, P., Gxasheka, M., 2021. Grass species richness decreases along a woody plant encroachment gradient in a semi-arid savanna grassland, South Africa. Landsc. Ecol. 36, 617–636. https://doi.org/10.1007/s10980-020-01150-1

Moore, W.H., Swindel, B.F., Terry, W.S., 1982. Vegetative response to prescribed fire in a north Florida flatwoods forest. J. Range Manag. 35, 386–389. https://doi.org/Doi 10.2307/3898325

Moser, W.K., Wade, D.D., 2005. Fire exclusion as a disturbance in the temperate forests of the USA: examples from longleaf pine forests. Scand. J. For. Res. 20, 17–26. https://doi.org/Doi 10.1080/14004080510041048

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature 403, 853–858. https://doi.org/10.1080/21564574.1998.9650003

Nayak, R.R., Vaidyanathan, S., Krishnaswamy, J., 2014. Fire and grazing modify grass community response to environmental determinants in savannas: implications for sustainable use. Agric. Ecosyst. Environ. 185, 197–207. https://doi.org/10.1016/j.agee.2014.01.002

Noss, R.F., Platt, W.J., Sorrie, B.A., Weakley, A.S., Means, D.B., Costanza, J., Peet, R.K., 2015. How global biodiversity hotspots may go unrecognized: lessons from the North American Coastal Plain. Divers. Distrib. 21, 236–244. https://doi.org/10.1111/ddi.12278

O'Mara, F.P., 2012. The role of grasslands in food security and climate change. Ann. Bot. 110, 1263–1270. https://doi.org/10.1093/aob/mcs209

Oksanen, J., Simpson, G., Blanchet, F., Kindt, R., Legendre, P., Minchin, P., O'Hara, R., Solymos, P., Stevens, M., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Borman, T., Carvalho, G., Chirico, M., De Caceres, M., Durand, S., Evangelista, H.B.A., FitzJohn, R., Friendly, M., Furneaux, B., Hannigan, G., Hill, M., Lahti, L., Martino, C., McGlinn, D., Ouellette, M., Cunha, E.R., Smith, T., Stier, A., Ter Braak, C., Weedon, J., 2022. vegan: community ecology R package, version 2.6-2. https://cran.r-project.org/package=vegan.

Olson, M.S., 1992. Effects of early and late growing season fires on resprouting of shrubs in upland longleaf pine savannas and embedded seepage savannas. Masters Thesis. Louisiana State University, Baton Rouge, Louisiana.

Olson, M.S., Platt, W.J., 1995. Effects of habitat and growing-season fires on resprouting of shrubs in longleaf pine savannas. Vegetatio 119, 101–118. https://doi.org/https://doi.org/10.1007/BF00045593

Omernik, J.M., 1987. Ecoregions of the conterminous United States. Ann. Assoc. Am. Geogr. 77, 118–125. https://doi.org/https://doi.org/10.1111/j.1467-8306.1987.tb00149.x

Ottmar, R.D., Vihnanek, R.E., 2000. Stereo photo series for quantifying fuels. Volume VI: longleaf pine, pocosin, and marshgrass types in the southeast United States. National Wildfire Coordinating Group, National Interagency Fire Center, PMS 835, Boise, Idaho.

Overing, J.D., Watts, F.C., 1989. Soil survey of Walton County, Florida. USDA Soil Conservation Service, Washington, DC.

Overing, J.D., Weeks, H.H., Wilson Jr., J.P., Sullivan, J., Ford, R.D., 1995. Soil survey of

Okaloosa County, Florida. USDA Soil Conservation Service, Washington, DC.

Palmer, M., 2002. A glossary of ordination-related terms. https://ordination.okstate.edu/glossary.htm.

Palmquist, K.A., Peet, R.K., Weakley, A.S., 2014. Changes in plant species richness following reduced fire frequency and drought in one of the most species-rich savannas in North America. J. Veg. Sci. 25, 1426–1437. https://doi.org/10.1111/jvs.12186

Pausas, J.G., Ribeiro, E., 2017. Fire and plant diversity at the global scale. Glob. Ecol. Biogeogr. 26, 889–897. https://doi.org/10.1111/geb.12596

Peet, R.K., 2006. Ecological classification of longleaf pine woodlands, in: Jose, S., Jokela, E.J., Miller, D.L. (Eds.), The Longleaf Pine Ecosystem: Ecology, Silviculture, and Restoration. Springer, New York, pp. 51–93. https://doi.org/10.1007/978-0-387-30687-2

Peet, R.K., Allard, D.J., 1993. Longleaf pine vegetation of the southern Atlantic and eastern Gulf coast regions: a preliminary classification, in: Hermann, S.M. (Ed.), Tall Timbers Fire Ecology Conference Proceedings No. 18. Tall Timbers Research Station, Tallahassee, Florida, pp. 45–81. https://doi.org/10.1086/284833

Platt, W.J., Evans, G.W., Davis, M.M., 1988. Effects of fire season on flowering of forbs and shrubs in longleaf pine forests. Oecologia 76, 353–363. https://doi.org/https://doi.org/10.1007/BF00377029

Prichard, S.J., Andreu, A.G., Eagle, P., Swedin, K., Sandberg, D.V., Ottmar, R.D., Eberhardt, E., 2013. Fuel Characteristic Classification System version 3.0: technical documentation. USDA Forest Service, Gen. Tech. Rep. PNW-GTR-887, Portland, Oregon. https://doi.org/https://doi.org/10.2737/PNW-GTR-887

Provencher, L., Herring, B.J., Gordon, D.R., Rodgers, H.L., Galley, K.E.M., Tanner, G.W., Hardesty, J.L., Brennan, L.A., 2001. Effects of hardwood reduction techniques on longleaf pine sandhill vegetation in northwest Florida. Restor. Ecol. 9, 13–27. https://doi.org/DOI 10.1046/j.1526-100x.2001.009001013.x

R Development Core Team, 2022. R: A language and environment for statistical computing [Computer software]. Foundation for Statistical Computing, Vienna. https://www.r-project.org/.

Rao, C.R., 1964. The use and interpretation of principal component analysis in applied research. Sankhyā Indian J. Stat. 26, 329–358.

Ratajczak, Z., Nippert, J.B., Collins, S.L., 2012. Woody encroachment decreases diversity across North American grasslands and savannas. Ecology 93, 697–703. https://doi.org/https://doi.org/10.1890/11-1199.1

Robertson, K.M., Hermann, S.M., Staller, E.L., 2021. Frequent prescribed fire sustains old field loblolly pine-shortleaf pine woodland communities: results of a 53-year study. J. For. 119, 549–556. https://doi.org/10.1093/jofore/fvab035

Robertson, K.M., Hmielowski, T.L., 2014. Effects of fire frequency and season on resprouting of woody plants in southeastern US pine-grassland communities. Oecologia 174, 765–776. https://doi.org/DOI 10.1007/s00442-013-2823-4

Roleček, J., Dřevojan, P., Hájková, P., Hájek, M., 2019. Report of new maxima of fine-scale vascular plant species richness recorded in East-Central European semi-dry grasslands. Tuexenia 39, 423–431. https://doi.org/10.14471/2019.39.008

Sanders, T.E., 1981. Soil survey of Leon County, Florida. USDA Soil Conservation Service, Washington, DC.

Scheiter, S., Higgins, S.I., Osborne, C.P., Bradshaw, C., Lunt, D., Ripley, B.S., Taylor, L.L., Beerling, D.J., 2012. Fire and fire-adapted vegetation promoted C4 expansion in the late Miocene. New Phytol. 195, 653–666. https://doi.org/DOI 10.1111/j.1469-8137.2012.04202.x

Shatar, T.M., McBratney, A.B., 2004. Boundary-line analysis of field-scale yield response to soil properties. J. Agric. Sci. 142, 553–560. https://doi.org/Doi 10.1017/S0021859604004642

Shepherd, B.J., Miller, D.L., Thetford, M., 2012. Fire season effects on flowering characteristics and germination of longleaf pine (*Pinus palustris*) savanna grasses. Restor. Ecol. 20, 268–276. https://doi.org/10.1111/j.1526-100X.2010.00759.x

Simon, M.F., Pennington, T., 2012. Evidence for adaptation to fire regimes in the tropical savannas of the Brazilian Cerrado. Int. J. Plant Sci. 173, 711–723. https://doi.org/10.1086/665973

Slack, A.W., Zeibig-Kichas, N.E., Kane, J.M., Varner, J.M., 2016. Contingent resistance in longleaf pine (*Pinus palustris*) growth and defense 10 years following smoldering fires. For. Ecol. Manage. 364, 130–138. https://doi.org/10.1016/j.foreco.2016.01.014

Stanturf, J.A., Wade, D.D., Waldrop, T.A., Kennard, D.K., Achtemeier, G.L., 2002. Background paper: fire in southern forest landscapes, in: Wear, D.N., Greis, J.G. (Eds.), Southern Forest Resource Assessment. USDA Forest Service, Gen. Tech. Rep. SRS-53, Asheville, North Carolina, pp. 607–630. https://doi.org/https://doi.org/10.2737/SRS-GTR-53

Suttie, J.M., Reynolds, S.G., Batello, C. (Eds.), 2005. Grasslands of the World. United Nations, Food and Agriculture Organization, Rome.

Sydes, C., Grime, J.P., 1981. Effects of tree leaf litter on herbaceous vegetation in deciduous woodland. J. Ecol. 69, 237–248. https://doi.org/Doi 10.2307/2259828

Teixeira, J., Souza, L., Le Stradic, S., Fidelis, A., 2022. Fire promotes functional plant diversity and modifies soil carbon dynamics in tropical savanna. Sci. Total Environ. 812, 152317. https://doi.org/10.1016/j.scitotenv.2021.152317

Ter Braak, C.J.F., Prentice, I.C., 1988. A theory of gradient analysis. Adv. Ecol. Res. 18, 271–317. https://doi.org/https://doi.org/10.1016/S0065-2504(08)60183-X

Thaxton, J.M., Platt, W.J., 2006. Small-scale fuel variation alters fire intensity and shrub abundance in a pine savanna. Ecology 87, 1331–1337. https://doi.org/10.1890/0012-9658(2006)87[1331:sfvafi]2.0.co;2

Titshall, L.W., O'Connor, T.G., Morris, C.D., 2000. Effect of long-term exclusion of fire and herbivory on the soils and vegetation of sour grassland. African J. Range Forage Sci. 17, 70–80. https://doi.org/10.2989/10220110009485742

Toribio-Diaz, M.H., Carr, S., Putz, F.E., 2019. Pine savanna plant community disassembly after fire suppression. J. Veg. Sci. 0–3. https://doi.org/10.1111/jvs.12843

van der Werf, G.R., Randerson, J.T., Giglio, L., van Leeuwen, T.T., Chen, Y., Rogers, B.M., Mu, M., van Marle, M.J.E., Morton, D.C., Collatz, G.J., Yokelson, R.J., Kasibhatla, P.S., 2017. Global fire emissions estimates during 1997-2016. Earth Syst. Sci. Data 9, 697–720. https://doi.org/10.5194/essd-9-697-2017

Varner, J.M., Hiers, J.K., Ottmar, R.D., Gordon, D.R., Putz, F.E., Wade, D.D., 2007. Overstory tree mortality resulting from reintroducing fire to long-unburned longleaf pine forests: the importance of duff moisture. Can. J. For. Res. 37, 1349–1358. https://doi.org/10.1139/xo6-315

Veldman, J.W., Buisson, E., Durigan, G., Fernandes, G.W., Le Stradic, S., Mahy, G., Negreiros, D., Overbeck, G.E., Veldman, R.G., Zaloumis, N.P., Putz, F.E., Bond, W.J., 2015. Toward an old-growth concept for grasslands, savannas, and woodlands. Front. Ecol. Environ. 13, 154–162. https://doi.org/10.1890/140270

Vynne, C., Gosling, J., Maney, C., Dinerstein, E., Lee, A.T.L., Burgess, N.D., Fernández, N., Fernando, S., Jhala, H., Jhala, Y., Noss, R.F., Proctor, M.F., Schipper, J., González-Maya, J.F., Joshi, A.R., Olson, D., Ripple, W.J., Svenning, J.C., 2022. An ecoregion-based approach to restoring the world's intact large mammal assemblages. Ecography (Cop.). 2022, 1–12. https://doi.org/10.1111/ecog.06098

Wahlenberg, W.G., 1946. Longleaf Pine: Its Use, Ecology, Regeneration, Protection, Growth, and Management, 1st ed. Charles Lathrop Pack Forestry Foundation, Washington, DC.

Waldrop, T.A., Van Lear, D.H., Lloyd, F.T., Harms, W.R., 1987. Long-term studies of prescribed burning in loblolly pine forests of the Southeastern Coastal Plain. USDA Forest Service, Gen. Tech. Rep. SE-45, Asheville, North Carolina. https://doi.org/https://doi.org/10.2737/SE-GTR-45

Waldrop, T.A., White, D.L., Jones, S.M., 1992. Fire regimes for pine grassland communities in the southeastern United States. For. Ecol. Manage. 47, 195–210. https://doi.org/https://doi.org/10.1016/0378-1127(92)90274-D

Walker, J., Peet, R.K., 1984. Composition and species diversity of pine-wiregrass savannas of the Green Swamp, North Carolina. Vegetatio 55, 163–179. https://doi.org/https://doi.org/10.1007/978-94-009-5526-4_20

Webb, R.A., 1972. Use of boundary line in analysis of biological data. J. Hortic. Sci. Biotechnol. 47, 309–319. https://doi.org/https://doi.org/10.1080/00221589.1972.11514472

Wenger, K.F., 1953. The sprouting of sweetgum in relation to season of cutting and carbohydrate content. Plant Physiol. 28, 35–49. https://doi.org/https://doi.org/10.1104/pp.28.1.35

White, D.L., Waldrop, T.A., Jones, S.M., 1991. Forty years of prescribed burning on the Santee

Fire Plots: effects on understory vegetation. USDA Forest Service, Gen. Tech. Rep. SE-69, Asheville, North Carolina.

Willcox, E.V., Giuliano, W.M., 2010. Seasonal effects of prescribed burning and roller chopping on saw palmetto in flatwoods. For. Ecol. Manage. 259, 1580–1585. https://doi.org/10.1016/j.foreco.2010.01.034

Wilson, J.B., Peet, R.K., Dengler, J., Pärtel, M., 2012. Plant species richness: the world records. J. Veg. Sci. 23, 796–802. https://doi.org/10.1111/j.1654-1103.2012.01400.x

Woods, F.W., Harris, H.C., Caldwell, R.E., 1959. Monthly variations of carbohydrates and nitrogen in roots of sandhill oaks and wiregrass. Ecology 40, 292–295. https://doi.org/Doi 10.2307/1930040

Wright, C.S., 2013. Fuel consumption models for pine flatwoods fuel types in the southeastern United States. South. J. Appl. For. 37, 148–159. https://doi.org/Doi 10.5849/Sjaf.12-006

Zohary, D., Hopf, M., Weiss, E., 2000. Domestication of Plants in the Old World, 4th ed. Oxford University Press, New York.

# 5. Simulated changes in fuels and fire hazard in a longleaf pine (*Pinus palustris*) ecosystem under multiple prescribed fire scenarios

## 5.1 Abstract

Land management agencies are often confronted with the dilemma of aggressively using prescribed fire to meet management objectives or scaling them back in response to opposition to concerns such as escaped fires and smoke impacts. Simulation model exercises can be useful tools for quantifying the trade-offs associated with different rates of prescribed fire application. I developed and used the Fuelbed Dynamics Model (FDM), a landscape-succession model that incorporates fire and other disturbances, to simulate changes in fuels at Eglin Air Force Base (hereafter "Eglin") in northwestern Florida, US for 50-year time periods under four scenarios representing different amounts of prescribed burning. The purpose of this modeling experiment was to quantify the effect that prescribed burning would have on fuel dynamics and potential fire behavior. The longleaf pine ecosystem is adapted to frequent, low intensity fires; in their absence, flammable understory fuels accumulate rapidly, which can support high intensity wildfires that may be difficult and costly to control. Eglin mitigates fire hazard and manages threatened and endangered species through widespread application of prescribed fire, averaging 36,000 ha yr$^{-1}$. Despite these benefits, smoke from prescribed burning can negatively affect base operations and adjoining communities. Consequently, Eglin faces pressure to reduce the rate of burning. Simulations conducted for this modeling experiment indicate that hazardous surface fuelbeds would increase by up to 13.6 percent of Eglin's area while fuelbeds with high crown fire hazard would temporarily increase by up to 17.5 percent of Eglin under reduced prescribed fire scenarios (20k and 30k ha yr$^{-1}$), remain relatively unchanged (less than five percent of land

area) at the current levels (40k ha $yr^{-1}$), and decline up to 1.5 percent and 9.6 percent, respectively for surface and crown fire metrics, if prescribed burning increased (50k ha $yr^{-1}$). There would be a corresponding decrease in stands with low mean fire intervals (MFI) of up to 13.6 percent of Eglin and longleaf pine cover of up to 32.7 percent of Eglin with reduced application of prescribed fire. Simulated landscape composition indicates that lower rates of prescribed burning are insufficient to maintain current levels of low fire hazard and that higher rates of burning would generate modest improvements. Potential consequences of reduced levels of prescribed fire include larger, higher intensity fires with higher burn severity over a 20- to 30-year period and a transition to mesophytic forests with lower flammability (except during abnormally dry periods) towards the end of the 50-year simulation. This could increase suppression costs, pose a greater risk to on- and off-base property, cause long-duration, high impact smoke events, and degrade wildlife habitat for threatened and endangered species. Conversely, continuation of current or increased rates of prescribed fire could yield more frequent, albeit less impactful smoke events while maintaining current levels of fire hazard.

## 5.2 Introduction

Prescribed fire and other fuel treatments are implemented on millions of hectares of public land annually in the United States (US; USDA & USDI, 2021) to reduce accumulations of flammable vegetation (Agee and Skinner, 2005; Reinhardt et al., 2008) attributed to historic land use and fire suppression (Agee, 1993; Arno and Allison-Bunnell, 2002; Baker, 2009; Nowacki and Abrams, 2008). Their use in low- to mixed-severity fire regimes has been shown to reduce fire behavior (Piqué and Domènech, 2018; Wu et al., 2023), firefighting costs (Strabo and Reimer, 2024), and burn severity (Brodie et al., 2024; Vorster et al., 2024) associated with wildfires. Hazardous fuels, along with climate change, are major drivers of greater area burned (Abatzoglou and Williams, 2016; Salguero et al., 2020; Westerling et al., 2006) and higher burn severity (Parks and Abatzoglou, 2020) over recent decades. These larger, higher severity fires can, in some instances (Keane et al., 2008) increase the magnitude of ecological damage (Davis et al., 2019; Halofsky et al., 2020) and reduce ecosystem benefits (Lee et al., 2015). The wildland urban interface (WUI) has expanded (Radeloff et al., 2018) in tandem with increasingly severe fire seasons. Together these factors have compounded the economic cost of wildfires in the US (Dale, 2010; Thomas et al., 2017) – costs that are expected to rise over the coming decades due to the effects of climate change (An et al., 2015; Flannigan et al., 2013) and an expanding WUI (Gude et al., 2008; Theobald and Romme, 2007).

Prescribed fire is a viable method for mitigating the ecological and socioeconomic risks associated with more active fire regimes (Aponte et al., 2016). When applied correctly (Bar Massada et al., 2011; Brown et al., 2004), it mitigates resource risks by limiting the frequency, severity, and extent of wildfires (Fernandes, 2015). These benefits are not without costs, however, as the tradeoffs between smoke from prescribed fires and wildfires they likely mitigate is unclear (Jones et al., 2022). As discrete events prescribed fires contribute to air pollution (Liu and Achtemeier, 2003; Reisen et al., 2011) that can negatively impact human health, public safety, and visibility (Achtemeir et al., 1998; Afrin & Garcia-Menendez, 2021; Huang et al., 2019; Jones & Berrens, 2020; Liu & Achtemeier, 2003; Weinhold, 2011). Prescribed fires can reduce smoke exposure if they supplant wildfires because smoke from prescribed fires is more localized and contains fewer pollutants (Navarro et al., 2018). They are also planned and executed during weather conditions that will transport smoke away from population centers (Jaffe et al., 2020). Air quality concerns can substantially reduce the area treated with prescribed fire (Goodrick et al., 2010; Quinn-Davidson and Varner, 2012), hampering the ability to manage hazardous fuels and potentially causing larger cumulative emissions from future wildfires (Hurteau and North, 2009; Stephens et al., 2009). Balancing the trade-offs of prescribed fire programs is a complex exercise and landscape models are an important tool that can be used to quantify the costs and benefits of different management scenarios (Hunter and Robles, 2020).

Prescribed fire is widely implemented across the southeastern US (Johnson and Hale, 2002). It accomplishes several resource objectives with habitat management and hazardous fuels reduction usually ranking among the highest (Haines et al., 2001; Kobziar et al., 2015; Kupfer et al., 2022). Annual area burned with prescribed fire in the region is consistently higher than any other in the US with at least 1.6 million ha treated annually since the 1980s (Melvin, 2020; Wade and Lunsford, 1989). Historically, fire was used throughout the region for thousands of years by Native Americans and subsequently adopted by European settlers (Lafon, 2010). Currently, conservation areas are sufficiently small, fragmented, and surrounded by the WUI (Oswalt et al., 2012) that lightning-ignited fires, therefore, often cannot be allowed to burn freely and prescribed fire must be substituted in order to maintain a semblance of historic fire regimes. The importance of fire as an ecosystem process has long been documented (Heyward, 1939) and public land managers have been using prescribed fire since the 1950s (Riebold, 1971). Despite this awareness and the long history of use as a land management tool, the scale of prescribed burning in the southeastern US remains insufficient to maintain historic fire regimes across remaining natural areas (Ware et al., 1993).

Longleaf pine (*Pinus palustris* Mill.) forests, woodlands, and savannas were historically prevalent throughout the southeastern US (Frost, 1993; Oswalt et al., 2012) and are currently the major vegetation types managed with prescribed fire. Managing fire hazard in longleaf pine-dominated ecosystems is important because human and lightning-caused wildfires are common (Duncan et al., 2010; Mitchener and Parker, 2005), there is an extensive WUI (Zhang et al., 2008), and large destructive wildfires occur during dry periods (Butry et al., 2001; Reilly et al., 2022). Accumulated needlecast (Hiers et al., 2009) and, to a lesser extent, the herbaceous and shrub layers (Andreu et al., 2012; Hough and Albini, 1978), are the primary drivers of surface fire behavior in southeastern pine forests.

Longleaf pine is a pyrophytic species and among its many adaptions to fire, are highly flammable needles (Fonda, 2001; Varner et al., 2021) and that accumulate in such a way structure that promotes rapid drying and active fire behavior (Hendricks et al., 2002). A host of understory associates also contribute to the flammability of this ecosystem. The leaf litter produced by some species of understory oaks such as turkey oak (*Quercus laevis* Walter) and post oak (*Quercus margarettae* (Ashe) Small) has high measures of flammability (Kane et al., 2008). Common shrubs, including gallberry (*Ilex glabra* (L.) A. Gray) and saw palmetto (*Serenoa repens* (W. Bartram) Small), have high biomass and foliar energy content that further increase flammability relative to other southeastern forest types (Behm et al., 2004). Abundant species in the herbaceous layer, including wiregrass (*Aristida beyrichiana* Trin. & Rupr.), purple bluestem (*Andropogon glaucopsis* Elliot), and bracken fern (*Pteridium aquilinum* (L.) Kuhn var. *pseudoclaudatum* (Clute) A. Heller), have flammable foliage that produces greater flame heights than longleaf pine needles in laboratory experiments (Emery and Hart, 2020).

Fuels accumulate rapidly in southeastern US pine forests following treatment. The accumulation of fine dead fuels and live shrub fuels in the absence of what were historically frequent fires, can generate high-intensity surface fires that are difficult to control (Hough and Albini, 1978) and may ultimately support crown fires in an ecosystem in which they were historically very rare (Andreu et al., 2018). Prescribed fire effectively reduces surface fuels (Haywood, 2010; Ottmar and Prichard, 2012), but both forest floor and shrub fuels re-accumulate quickly between treatments (McNab et al., 1978), with shrub fuels reaching pre-treatment loading in five years (Davis & Cooper, 1963). Modeled fire behavior for the southeastern pine forests treated with regular prescribed fire suggest that prescribed fire treatment longevity is 3-5 years (Brose and Wade, 2002). These findings are echoed by fire use practitioners, 90 percent of whom believed that prescribed fire effectively mitigated hazardous fuels for five years or less (Kobziar et al., 2015). Thus, for a prescribed fire program to be effective, frequent application is necessary.

Mechanical and chemical fuel treatments can also be effective tools for reducing fire hazard in longleaf pine forests (Brose and Wade, 2002; Kreye et al., 2014), but they are best utilized in conjunction with re-introducing fire in fire-excluded stands (Provencher et al., 2001, 2000). Mechanical and chemical fuel treatments do not generate the same ecological benefits as prescribed fire (Menges and Gordon, 2010); do not have a lasting effect on fire hazard (O’Brien et al., 2013); and, when used as a stand-alone treatment, may reduce biological diversity and increase the susceptibility of the overstory to mortality during wildfires due to long-duration smoldering combustion associated with the build-up of the duff layer (O’Brien et al., 2010; Varner et al., 2007).

## 5.3 Objectives and questions

Eglin Air Force Base (hereafter Eglin) provides an example of the national-scale problem of balancing the costs and benefits of prescribed burning. The challenge of balancing aggressive use of prescribed fire (Ferguson, 2005; New York Times, 2010) with smoke management at

Eglin (Science Applications International Corporation, 2010) is reflective of conditions throughout the southeastern US where prescribed burning is widely used to manage hazardous fuels (Haines et al., 2001; Kobziar et al., 2015), but meeting air quality standards can be difficult (Goodrick et al., 2010; Liu & Achtemeier, 2003). Fire managers across the southeastern US believe it will become increasingly difficult to maintain the levels of prescribed fire necessary to achieve management goals over the coming decades due to a combination of climate change, expanding WUI, and more stringent air quality regulations (Kupfer et al., 2022).

The goal of this research was to project long-term changes in fuels and fire hazard at Eglin under a range of prescribed fire scenarios. Eglin was chosen as the study area because fire managers identified reductions in prescribed burning as a future concern (B. Williams – personal communication) and prescribed fire, along with other fuel treatments, are essential to managing hazardous fuels on fire-prone forests across the entire base. A spatially explicit landscape succession model, the Fuelbed Dynamics Model (FDM; Wright, 2010), coupled with the Fuelbed Characteristic Classification System (FCCS; Ottmar et al., 2007) was used to simulate impacts of four prescribed fire scenarios on the fuel dynamics across Eglin. FDM is a landscape-scale fuelbed simulation model that incorporates prescribed fire, non-fire forest management practices, and wildfire. FCCS provides detailed descriptions of fuels, vegetation, and the manner in which they transition among states over time coupled with estimates of fire behavior potential. Two broad research questions were addressed by this modeling experiment:

1) Does the amount of prescribed fire applied to the landscape affect the quantity, type, and distribution of fuels?
2) If there are effects on fuels, what are the implications for potential fire behavior?

These results will help Eglin evaluate and communicate how different levels of prescribed fire will impact the distribution of vegetation as it relates to ecological and fuels management goals. More broadly, these results will quantify the trade-offs associated with reductions in prescribed fire to reduce impacts on air quality will have on fire hazard, as well as habitat for fire-dependent species, for organizations managing southeastern pine forests.

## 5.4 **Methods**

### 5.4.1 *Study area*

Eglin occupies the southern half of Okaloosa and Walton Counties and the southeastern corner of Santa Rosa County on the Florida panhandle (Figure 5-1). At 187,555 ha, Eglin is the largest forested military installation in the United States with over 80 percent longleaf pine cover. The base was established in 1935 and expanded in 1940 with the acquisition of the Choctawhatchee National Forest. Prior to federal ownership, the area was actively managed for turpentine extraction for the naval stores industry and the fire regime was characterized by frequent, low-intensity fires typical of the longleaf pine ecosystem (Henderson, 2006). Fire was largely excluded by suppression policies implemented by the U.S. Forest Service and Air Force until 1989. Today, Eglin manages fire-dependent community types across the base with several types of treatment, the most common of which is prescribed fire. Their prescribed fire program has an annual burn area goal of 36k ha and 3k ha of land are treated annually with restoration activities, including pre-commercial thinning (PCT) and herbicide (US Air Force, 2017).

The base lies within the East Gulf Coastal Plain physiographic province (Fenneman and Johnson, 1946) with the northern half characterized by landforms in the Western Highlands and southern half within the Coastal Lowlands divisions (Cook, 1939). Soils of the Western

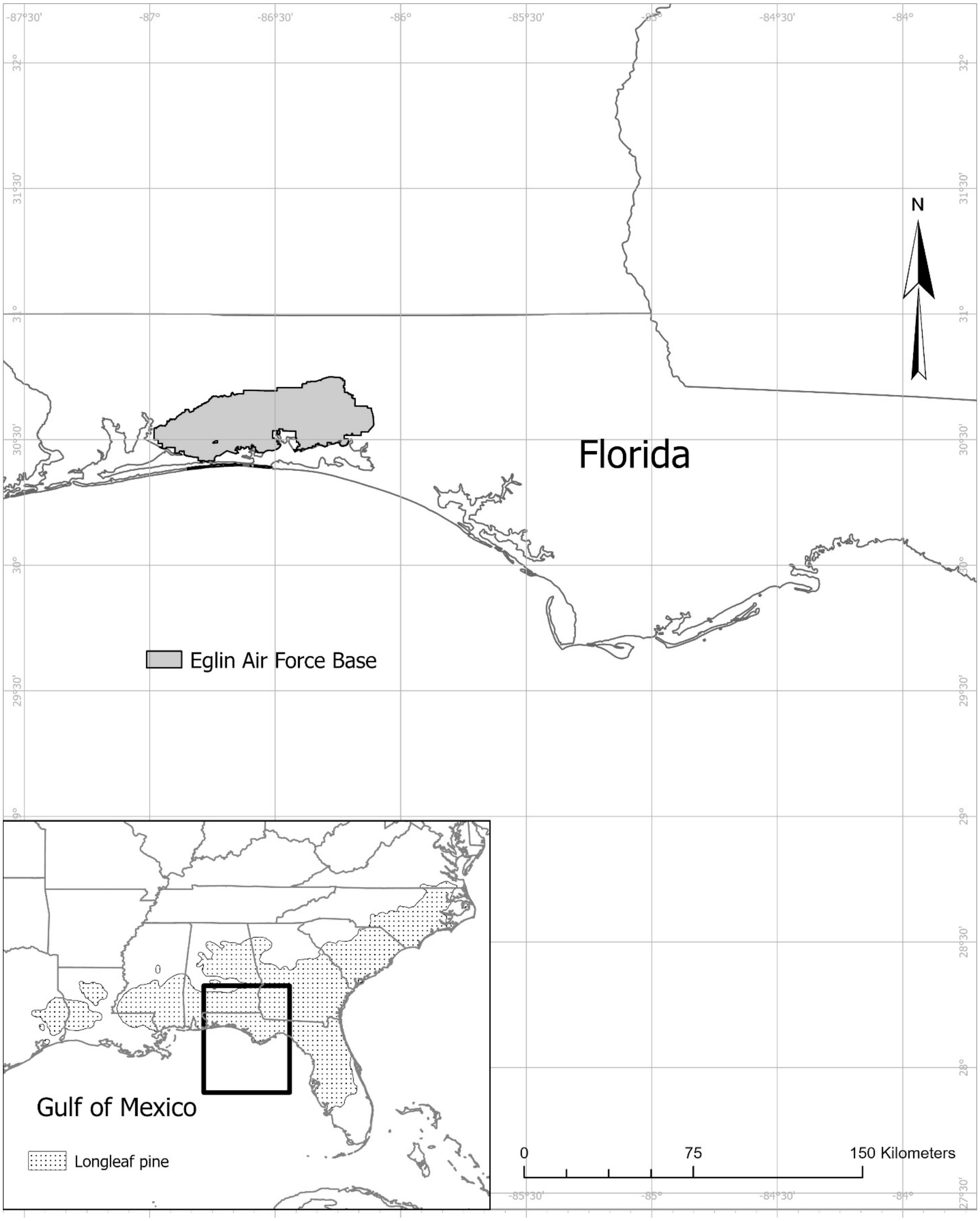


**Figure 5-1.** Location of Eglin Air Force Base relative to the historic distribution of longleaf pine.

Highlands are primarily sands while soils in the Coastal Lowlands are primarily composed of medium-grained quartz sands (Overing and Watts, 1989). Northern Florida has a humid-subtropical climate (Kottek et al., 2006) and temperatures range from an average minimum of 5°C in January to an average maximum of 33°C in July. Average annual precipitation is 1525-1650 mm. Longleaf pine forests are the prevalent natural community on Eglin. The growing season (frost-free period) runs from late February through early December. Sandhill vegetation is the largest vegetation type on Eglin and occupies 78 percent of the base (Science Applications International Corporation, 2008). Sandhills are characterized by open, xeric longleaf pine and turkey oak forests with an understory of grasses and shrubs. Longleaf pine flatwoods account for an additional three percent of longleaf pine forests at Eglin (Science Applications International Corporation, 2008). Flatwoods are wet to mesic and as a result support taller, more densely spaced trees than sandhills. As with sandhills, the understory is open and dominated by a range of grasses, forbs, and shrubs. Approximately 14 percent of Eglin is classified as wetlands, of which there are 25 different types. The remaining five percent of the base is comprised primarily of developed and semi-improved (i.e., open military ranges) lands.

### 5.4.2 *Model description and parameterization*

The Fuelbed Dynamics Model was developed used to simulate fuelbed change and corresponding measures of potential fire behavior. This model simulates the effects of fire, management treatments, and succession on fuel composition over decadal to centennial time periods at landscape scales. Spatial data are represented by layered 30 x 30 m raster datasets. Succession is simulated through deterministic, multi-path, state-and-transition models (STMs). Disturbance patterns are simulated with a simple cellular automata model (Karafyllidis and

Thanailakis, 1997) across the raster grid. The simulated landscape includes Eglin and a 10-km buffer (total area: 424,000 ha). Replicate simulations ($n$ = 10) were run for each of four prescribed fire management scenarios (20k, 30k, 40k [*status quo*], and 50k ha $yr^{-1}$) for 50 years. Other disturbances incorporated into simulations included precommercial thinning (PCT), herbicide applications, and wildfire. Simulated PCT and herbicide treatment rates were based on Eglin's forest management activities from 2004 to 2014, and each had a target area of 2025 ha $yr^{-1}$. Simulated wildfire was parameterized with historic data from Eglin for the lands within the base and the State of Florida for lands in the buffer zone. Eglin's historic fire rotation (excluding prescribed fires) was 54.4 years (annual area burned: 3475 ha) and the average fire size was 42.0 ha (standard deviation ± 146.1). For the buffer zone, the historic fire rotation was 457.4 years (annual area burned: 517 ha) and the average fire size was 2.1 ha (standard deviation ± 5.7). FDM operates in the R programming environment (R Development Core Team, 2008).

FDM tracked two measures of area treated for prescribed fire, PCT, and herbicide: the area of the management unit the treatment was applied to and the suitable area treated within the unit. For instance, if a 250-ha management unit scheduled for herbicide application to reduce oak cover had 50 ha of sand pine and 200 ha of oak then the two treatment areas were the 250-ha management unit and the 200 ha of oak within the unit. Similarly, prescribed fires can be patchy if fuels within the unit are not receptive to fire. The former measure is typically how land management organizations report area burned or treated because detailed post-burn mapping of each prescribed fire is too costly and time consuming. This measure was reported in the results and used to track scenario progress towards annual treatment quotas to maintain consistency with reporting procedures used by land management agencies. The latter measure was utilized by FDM to simulate vegetation patterns. Dividing the latter by the former produces percent area treated. This value was typically less than 100 percent because natural variation in vegetation leads to some areas are not receptive to fire (Kennard and Outcalt, 1996) or appropriate for restoration treatments.

FDM was initialized with a rasterized FCCS fuelbed map of baseline conditions. This map was generated with land cover data used to make fuelbed assignments at 30-m resolution for Eglin and a buffer area extending 10-km from the base's perimeter (Figure 5-2). The buffer area accounted for impacts of wildfires originating outside of Eglin and reduced boundary effects (Keane et al., 2006, 2002). FCCS fuelbeds were assigned to unique combinations of five landscape metrics: topographic position, canopy cover type, silvicultural history, mean fire

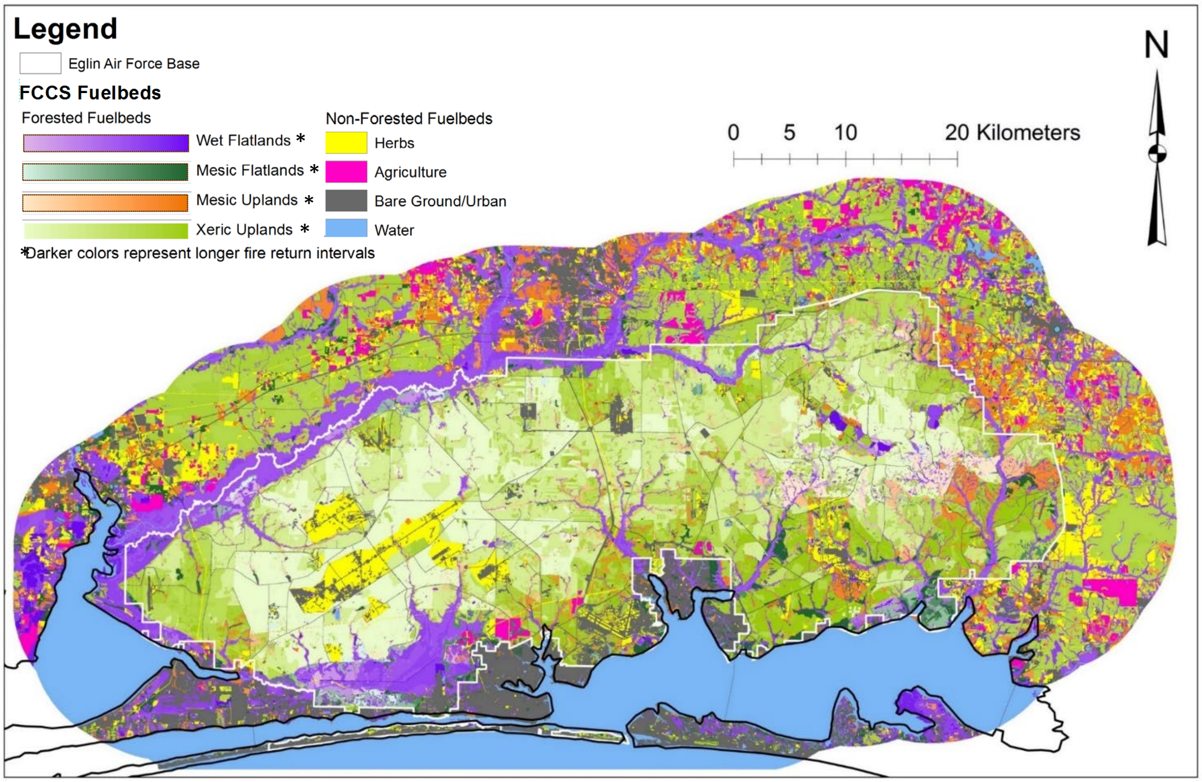


**Figure 5-2.** FCCS fuelbed map for Eglin Air Force Base and 10-km buffer zone. EAFB's perimeter is delineated in white.

interval (MFI), and stand age (Figure 5-3). Fuelbeds were initially cross-walked with land cover types from the 2012 Florida Cooperative Land Cover Map (v. 2.3; Florida Natural Areas Inventory, 2012). This map was used to assign topographic position and initial canopy cover designations. A vegetation map developed using non-differenced vegetation index (NDVI; Chafin et al., 1997; Knight et al., 2010) was used to improve the initial canopy cover designations and delineate natural stands from timber plantations. Fire history records were used to characterize MFI-derived understory fuels in pine-dominated fuelbeds. Records of recent silvicultural treatments were used to assign stand age and post-disturbance fuelbeds. To assess the accuracy of the fuelbed map, fuel characteristics were compared with observations at points randomly located across the study area ($n$ = 120) and long-term monitoring plots at Eglin ($n$ = 204). Classification accuracy was 73.5 percent and 85.1 percent, respectively, suggesting that fuelbed assignments adequately characterized the distribution of fuels.

FCCS fuelbeds were developed using a multi-step process. Variables were initially populated with data from existing fuelbeds for the southeastern US that closely resembled vegetation types at Eglin (Andreu et al., 2012; Ryan and Opperman, 2013) and then refined with locally collected field measurements (Cronan et al., 2015; Hiers et al., 2007; Ottmar et al., 2003; Ottmar and Vihnanek, 2000; Prichard et al., 2014); 1437 fuelbeds were developed to account for expected differences in fuels, fire hazard, and vegetation. Feedback from staff at Eglin was solicited to evaluate the accuracy of fuelbed characteristics and potential fire behavior. This feedback was used to make necessary adjustments to fuelbed variables. A modular naming scheme was used to label fuelbeds where each component represents a major driver of fuel characteristics and informs STM successional stages (Table 5-1).

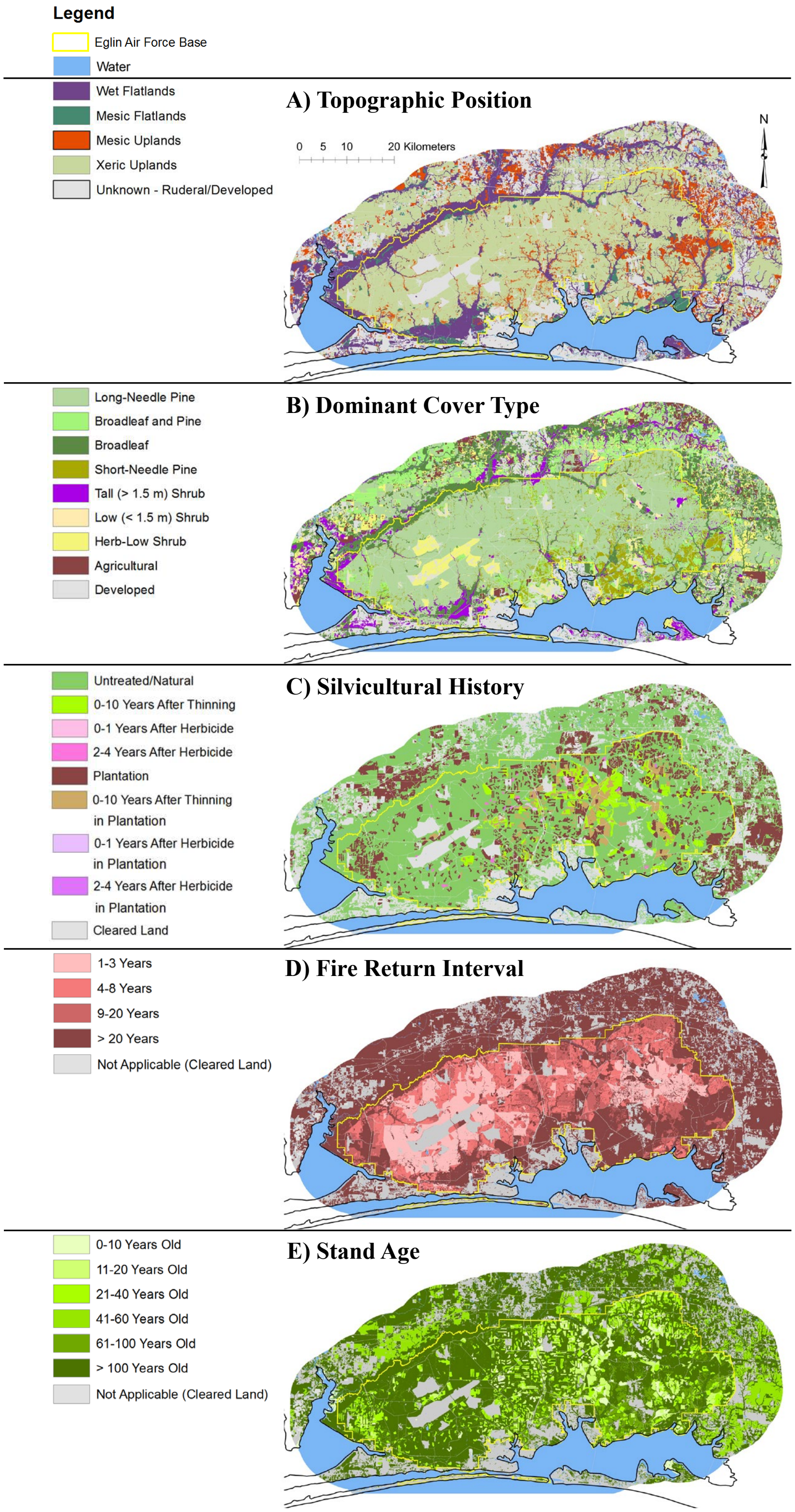


**Figure. 5-3.** FCCS fuelbeds were assigned to unique combinations of categories from five environmental datasets for Eglin AFB and the surrounding 10-km buffer zone. They include A) topographic position, B) dominant cover type, C) silvicultural history, D) mean fire return interval, and E) stand age.

The fuelbed map was overlain with a raster layer of Eglin's burn units. There are 1016 units that cover 82 percent of Eglin's area. The remaining area included developed infrastructure, cleared areas, and water. The median burn unit area was 107 ha with a range of 19 to 1428 ha. Simulated prescribed burns and restoration treatments were confined by burn unit perimeters. Simulated suppression actions on wildfires were also implemented along burn unit boundaries.

**Table 5-1.** Factors representing each digit in the FCCS fuelbed numbers. Each factor is a major driver of fuels and fire behavior in the southeastern US.

| **1st Digit** Topographic Position | | **2nd Digit** Dominant Overstory Species | | **3rd Digit** Management History | | **4th Digit** Mean Fire Interval | | **5th Digit** Stand Age | |
|---|---|---|---|---|---|---|---|---|---|
| Value | Description | Value | Description | Value | Description | Value | Description | Value | Description |
| 1 | Wet Flatlands | 1 | Longleaf Pine | 1 | Natural | 1 | 1-3 years | 1 | 0-10 years |
| 2 | Mesic Flatlands | 2 | Mixed Broadleaf-Pine | 2 | Sand pine removal (0-10 years post-treatment) | 2 | 4-8 years | 2 | 11-20 years |
| 3 | Mesic Uplands | 3 | Broadleaf | 3 | Herbicide (no understory; 0-1 years post-treatment) | 3 | 8-20 years | 3 | 21-40 years |
| 4 | Xeric Uplands | 4 | Sand Pine | 4 | Herbicide (grass understory; 2-4 years post-treatment) | 4 | > 20 years | 4 | 41-60 years |
| 5 | Modified | 5 | Tall shrub | 5 | Plantation | | | 5 | 60-100 years |
| | | 6 | Short shrub | 6 | Plantation + sand pine removal | | | 6 | > 100 years |
| | | 7 | Mixed shrub/herb | 7 | Plantation + herbicide (no no understory) | | | | |
| | | 8 | Herbaceous | 8 | Plantation + herbicide (grass understory) | | | | |
| | | 9 | Non-vegetated | 9 | Vegetation cleared | | | | |

One of four management options was assigned to each burn unit. These options were based on the same framework used by Eglin to prioritize the selection of burn units and guided unit selection during the simulations. The management options, in order from highest to lowest prescribed burn priority, are: Burned Annually No Suppression Areas (BANSA), Core Conservation Areas (CCA), prescribed fire permitted, and prescribed fire prohibited. BANSA burn units generally surround ordnance ranges. These are burned annually to reduce fire hazard and occupy 1.3 percent of the base's land area. CCA burn units encompass areas of longleaf pine that feature high habitat value for threatened and endangered species. They are burned less frequently than the BANSA burn units, but with a high enough frequency to maintain an open understory. CCA burn units represent the most common management option designation and cover 60.2 percent of Eglin. Burn units where prescribed fire is permitted but fall outside of the BANSA or CCA designations include 22.2 percent of Eglin. These units are generally burned only after burning quotas have been met in the BANSA or CCA burn units. Burn units where prescribed fire is prohibited cover 16.3 percent of Eglin's land area. Burn units in this category are not zoned for burning and typically include restricted military areas.

Vegetation growth and succession is modeled in FDM with Eglin-specific STMs. Each state is represented by a time-limited FCCS fuelbed with shorter limits for early seral and post-treatment fuelbeds that progressively lengthen as vegetation matures. Vegetation in northwest Florida is heavily influenced by soil moisture and texture (Peet, 2006), with productivity, species composition, and succession pathways changing along this physiographic gradient. STMs classify vegetation across this gradient with individual pathways for xeric uplands, mesic uplands, mesic lowlands, and wet lowlands. Understory and overstory vegetation respond independently to disturbance factors, and multiple pathways introduce stochasticity to forest and fuelbed succession. Vegetation, and by extension fuels, remain static except when transitioning to a new fuelbed. Understory vegetation responds incrementally to changes in the mean interval of low-intensity surface fires and immediately to forest management operations or high intensity wildfire. This STM is based on existing models (Maliakal et al., 2000; Menges et al., 1993;

Peterson, 2002; Shaw and Long, 2007) and growth data (McNab et al., 1978) with revisions based on workshops held at Eglin.

### 5.4.3 *Characterizing fire hazard*

Simulated fire hazard was assessed with two metrics to characterize the contribution of fuels to surface and crown fire behavior: surface fine fuel loading and FCCS crown fire potential. Loading of fine surface fuels is a reliable predictor of potential surface fire behavior throughout pine forests in the southeastern US (Brose and Wade, 2002; Hough and Albini, 1978; McNab et al., 1978). Higher loading of fine fuels is correlated with higher fire intensity, greater suppression difficulty, and higher likelihood of crown fire initiation. Fine fuel loading was calculated from FCCS fuelbeds by summing the loading of litter, 1-hr downed woody debris, herbaceous fuels, and shrubs. These fuelbed strata are all known to contribute to surface fire behavior in southeastern fuel types. The FCCS crown fire summary potentials (Sandberg et al., 2007) were used to represent crown fire hazard because the metric incorporates several fuel characteristics represented in crown fire models (Alexander, 1998; Scott and Reinhardt, 2001; Van Wagner, 1977). The crown fire summary potential is a unitless measure scaled from 0 (no potential for crown fire) to 9 (high potential for crown fire) that is a function of FCCS potentials for crown fire initiation, crown-to-crown transmissivity, and crown fire rate of spread (Prichard et al., 2011).

### 5.4.4 *Characterizing landscape condition*

Two landscape condition characteristics, MFI and vegetation cover type provided additional context for the aforementioned fire hazard metrics by describing how vegetation was contributing to simulated changes in fuels. MFI is a strong driver of understory vegetation composition and structure in pine- and oak-dominated forests in the southeastern US (Glitzenstein et al., 2003; Waldrop et al., 1987). There are four MFI categories: high (MFI: 1–3 years), intermediate (MFI: 4–8 years), low (MFI: 9–20 years), and fire-excluded (MFI: greater than 20 years). Frequently burned longleaf pine forests (high MFI) are typically associated with lower fire hazard; as MFI lengthens hazard increases. Vegetation cover type is also a useful measure for assessing fire hazard and habitat quality. There are nine categories, though only the four forested types common at Eglin were included in this analysis. They include longleaf pine, broadleaf, sand pine, and mixed broadleaf-pine. The longleaf pine category includes, loblolly and slash pine, two other long-needled pine species that are a minor component of Eglin's forests. Broadleaf species are a mix of fire-inhibiting and fire-facilitating oaks (Kane et al., 2008) in xeric and mesic uplands (i.e., sandhill communities), while wet and mesic lowlands (i.e., flatwoods) include a large number of fire-inhibiting broadleaf species including oaks, sweetgum (*Liquidambar styraciflua* L.), sweetbay (*Magnolia virginiana* L.), and southern magnolia (*Magnolia grandiflora* L.). Sand pine (*Pinus clausa* (Chapm. ex Engelm.) Vasey ex Sarg. var. *immuginata* Ward) at Eglin is non-serotinous (Parker et al., 2004) and occurs exclusively in sandhill communities. The mixed broadleaf-pine cover type includes areas where the overstory is a mix of the above species. The remaining five categories represent non-forested areas of the base including wetlands, open ranges, and developed locations. Eglin is primarily managed for longleaf pine because this species provides habitat for threatened and endangered wildlife species and, and when frequently burned, presents low fire hazard.

### 5.4.5 *Analysis*

Summary statistics describe composite landscape composition and fire hazard metrics for replicate simulations at each time-step and experimental treatment level. Fire hazard metrics (i.e., fine fuel loading and crown fire potential) and landscape conditions (i.e., MFI and vegetation cover type) are plotted at 5-year intervals. All metrics were tested for significance ($P < 0.05$) among treatment scenarios at 10-year intervals with two-way repeated measures ANOVA and the Tukey's HSD *post-hoc* multiple comparison tests (Tukey, 1949). Homogeneity of variance for the ANOVA was assessed with Levene's test (Levene, 1960). If variables did not meet homogeneity of variance assumptions, *post-hoc* multiple comparison tests were conducted using Aligned Rank Transformation (ART-C) procedure for nonparametric data (Elkin et al. 2021). Normality was assessed with Shapiro-Wilk tests ($P > 0.05$; Shapiro & Wilk, 1965). Sphericity was assessed with Mauchly's test (Mauchly, 1940) and a Greenhouse-Geisser sphericity correction (Greenhouse and Geisser, 1959) was applied where this assumption was violated.

## 5.5 **Results**

Simulated reductions in prescribed fire resulted in several landscape-scale changes to the distribution of vegetation and associated measures of fire hazard (Table 5-2). Lowering the rate of prescribed fire (i.e., 20k and 30k burn scenarios) shifted 20–35 percentage points of the overstory composition from longleaf pine to sand pine and broadleaf cover types and caused a more than five percentage point shift from low to high surface fuel loading categories over the 50-year simulation period. The increase in fuel loading was reflected by the 15–25 percentage point shift to fire-excluded MFI (> 20 years) fuelbeds. A similar, but smaller shift in overstory

**Table 5-2.** Area (ha) of land within Eglin Air Force Base for selected categories under initial conditions and at the end (50 years) of each prescribed fire scenario. Significance levels from one-sided Wilcoxon signed-rank test.

| Scenarios | Initial Conditions | Prescribed Fire Scenarios | | | |
|---|---|---|---|---|---|
| | | 20k-ha yr$^{-1}$ | 30k-ha yr$^{-1}$ | 40k-ha yr$^{-1}$ | 50k-ha yr$^{-1}$ |
| Fine Fuel Loading | | | | | |
| Low (<4.5 Mg ha$^{-1}$) | 90,508 | 62,803** | 74,057** | 84,769** | 92,819** |
| Medium (4.5-9.0 Mg ha$^{-1}$) | 33,889 | 36,938** | 35,988** | 34,610** | 33,136** |
| High (>9.0 Mg ha$^{-1}$) | 50,783 | 75,438* | 65,135** | 55,801** | 49,224** |
| Crown Fire Potential | | | | | |
| Low (1-3) | 98,115 | 81,979** | 94,116** | 104,534** | 113,073** |
| High (4-6) | 66,650 | 80,570** | 69,386** | 59,301** | 50,836** |
| Vegetation Cover | | | | | |
| Longleaf Pine | 111,418 | 50,567** | 68,400** | 82,115** | 89,939** |
| Mixed Pine-oak | 13,216 | 27,049** | 23,345** | 19,819** | 16,892** |
| Broadleaf | 17,145 | 39,256** | 33,031** | 28,917** | 26,916** |
| Sand Pine | 16,357 | 37,687** | 31,076** | 26,530** | 24,589** |
| Shrub | 6,632 | 10,208** | 8,915** | 7,387** | 6,432 |
| Mean Fire Interval | | | | | |
| 1-3 years | 36,785 | 12,358** | 28,392** | 48,964** | 69,666** |
| 4-8 years | 50,138 | 24,537** | 29,747** | 26,559** | 17,081** |
| 9-20 years | 15,237 | 18,128** | 14,477** | 10,195** | 6,288** |
| >20 years | 63,172 | 110,311** | 92,717** | 79,616** | 72,297** |

Significance levels: ** $P < 0.01$; * $P = 0.01 - 0.05$

composition occurred with the 40k and 50k burn scenarios with a 10–16 percentage point transition from longleaf pine to sand pine and broadleaf species. This decline was unexpected given that stable or elevated rates of burning would be expected to yield stable or increasing cover of longleaf pine. Changes in understory conditions for the 40k and 50k burn scenarios were, however, in line with expectations; the distribution of fine surface fuel loading categories remained stable (± 5 percent). High and fire-excluded MFI categories increased at the expense of intermediate and low categories for the 40k and 50k burn scenarios with high-frequency MFI coverage increasing by 5–18 percentage points and fire-excluded coverage increasing by 4–10 percentage points. There was low variability among model simulations. As a result, there was little overlap in within and across-treatment outputs and few statistical tests generated non-significant results. Non-significant results are noted.

### 5.5.1 *Simulated disturbance*

The area of management units treated with prescribed fire closely tracked annual quotas and remained stable across the four different experimental treatments over the course of the simulations suggesting that the Eglin simulation landscape was sufficient in size to meet the burn unit management and burn unit prioritization criteria employed during the simulation period for all prescribed fire scenarios. This was expected given that FDM does not allow for feedback between annual area burned targets and other simulated phenomenon. The percent area burned decreased over the course of the simulations for the 20k and 30k scenarios. The median percent area burned across all scenarios was initially 65.5–66.0 percent, but this ratio diverged over time, decreasing to a median of 50.3 and 59.0 percent for the 20k and 30k scenarios, respectively, remaining unchanged at 65.7 percent for the 40k scenario, and increasing slightly to 67.9 percent for the 50k scenario.

Simulated wildfires matched parameterized values (Section 5.4.2) and area burned statistics and had no discernable temporal trends for any of the prescribed fire scenarios. Wildfires across Eglin were almost entirely surface fires (92.4 percent) with only a small amount of area classified as crown fire (7.6 percent). There was no difference in the ratio of surface fire to crown fire over time or among experimental treatment scenarios.

Area treated with PCT and herbicide was mostly as expected. Area of management units treated with precommercial thinning was 2122 ha yr$^{-1}$, (range: 2022–2792 ha), which closely matched the parameterized value (2025 ha). Mean percent area treated was stable among scenarios at 65.9 percent (range: 49.5–77.8 percent). Area of management units treated with herbicide was 2004 ha yr$^{-1}$ (range: 771–3213 ha), which closely matched annual parameterized value (2025 ha). This area doubled during the first 20 years from a mean of 1147 ha in year one to 2123 ha by year 25 for all experimental treatment scenarios. Mean percentage area treated was 66.0 percent (range: 52.5–80.2 percent) and did not differ among scenarios.

### 5.5.2 *Fine fuel loading*

Initially, fuelbeds with low fine fuel loading comprised 47.9 percent of the landscape, but by the tenth year of the simulation, the area of fuelbeds with low fine fuel loading began to diverge among prescribed fire scenarios (Figure 5-4A). The area of fuelbeds with low fine fuel loading declined for scenarios with lower levels of prescribed burning through year 30, then stabilized. Comparatively, the area of fuelbeds with low fine fuel loading changed far less for the 40k and 50k scenarios. By the end of the 50-year simulation period, land area with low fine fuel loading was greatest for the 50k scenario ($\bar{x}$ = 49.1; range: 48.3–49.7 percent) and successively lower until reaching a minimum with the 20k scenario ($\bar{x}$ = 33.2; range: 32.4–34.1 percent). Wilcoxon signed-rank tests comparing 50-year outputs with initial conditions were significant ($P < 0.05$) for all treatment scenarios and ARTc analysis results were significant ($P < 0.05$) for all among-treatment comparisons at 50 years.

Early in the simulations, low fine fuel loading fuelbeds transition to those with moderate fine fuel loading (4.5–9.0 Mg ha$^{-1}$) if MFI lengthened. Initially, 17.9 percent of the landscape was classified as moderate fine fuel loading and the area of these fuelbeds steadily increased through year 20: the rate of change was highest for the 20k and 30k scenarios (Figure 5-4B). By the twentieth year the extent of the landscape with moderate fuel loading peaked at an average of 25.1 percent (range: 24.3–25.8 percent) for the 20k scenario with peaks progressively decreasing as rates of prescribed burning increased to an average of 21.2 percent (range: 20.7–22.0 percent) for the 50k scenario. Differences in the landscape extent of fuelbeds with moderate loading were mostly not significant (P > 0.05) between the 40k and 50k scenarios and between the 20k and 30k scenarios throughout the simulation period. Wilcoxon signed-rank tests comparing 50-year

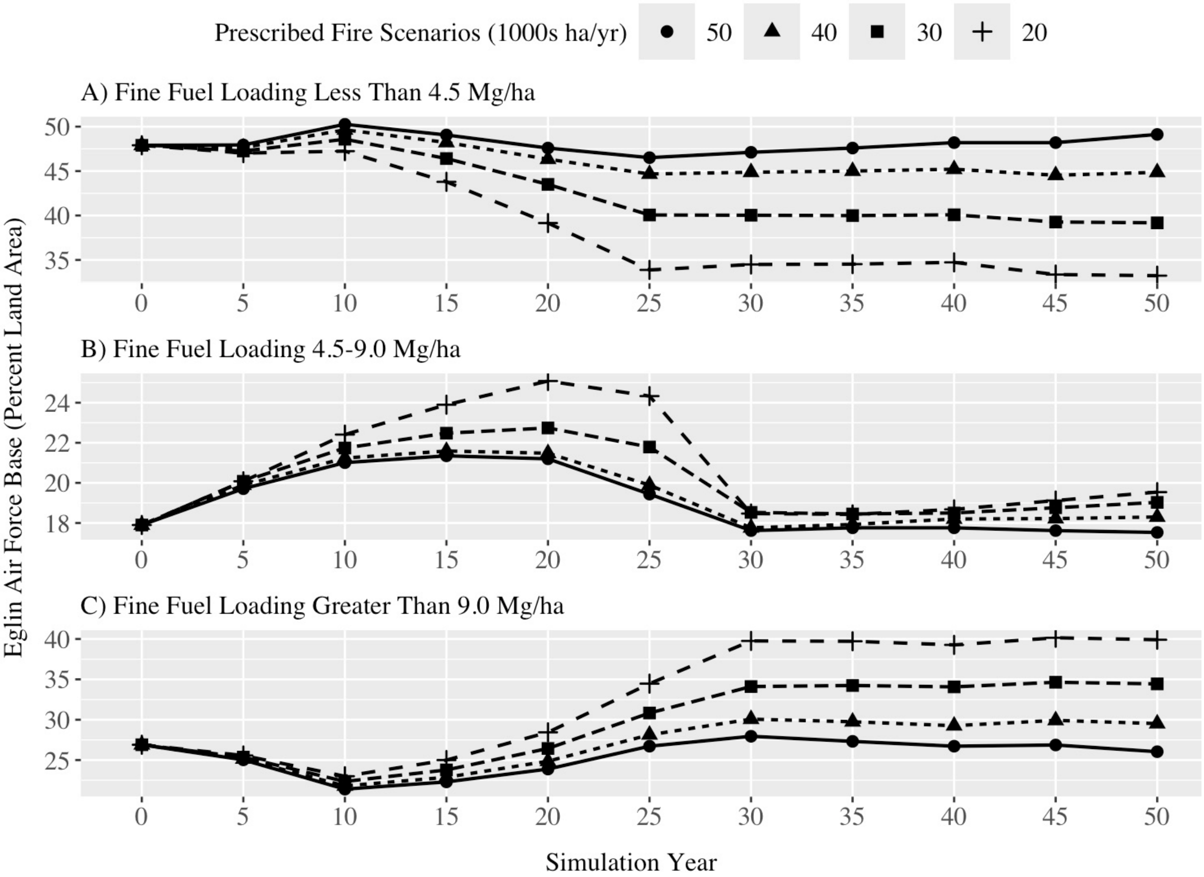


**Figure. 5-4.** Fine fuel loading distribution for Eglin Air Force Base, Florida under four prescribed fire scenarios for 50-year period. Each scenario has 10 replicates and modeled fine fuel loading is reported for 10-year intervals. Reported values exclude 10-km buffer zone.

outputs with initial conditions were significant for all treatment scenarios ($P < 0.05$) and Tukey's HSD analysis results were significant ($P < 0.05$) for all among-treatment comparisons at 50 years except for the 20k and 30k scenarios.

Land area of fuelbeds with high fine fuel loading showed an inverse trend with respect to fuelbeds with low fine fuel loading (Figure 5-4C). Coverage declined slightly from baseline conditions (26.9 percent) among all scenarios by year 10, steadily increased through year 30, and then remained stable through year 50. The largest increase was for the 20k scenario with 39.9 percent (range: 39.4–40.5 percent) of the landscape occupied by high fine fuel loading fuelbeds. For the 50k scenario percent landscape with high loading fuelbeds declined slightly to 26.0 percent (range: 25.4–26.9 percent). Wilcoxon signed-rank tests comparing 50-year outputs with initial conditions were significant ($P < 0.05$) for all treatment scenarios except the 50k scenario and ARTc analysis results were significant ($P < 0.05$) for all among-treatment comparisons at 50 years.

### 5.5.3 *Crown fire potential*

After 50 years of simulation the area of land with high crown fire potential (crown fire potential: 4–6) at Eglin increased for reduced burn scenarios and decreased for the 40k and 50k scenarios (Figure 5-5). Baseline coverage for high crown fire potential fuelbeds was 40.2 percent and area increased at higher rates and persisted for longer as rates of prescribed burning decreased. The amount of the landscape with high crown fire potential fuelbeds peaked in year 25 at 57.2 percent (range: 56.4–57.7 percent) for the 20k scenario and year 15 at 44.0 percent (range: 43.4–44.6 percent) for the 50k scenario. The area occupied by high crown fire potential fuelbeds then declined for the remainder of the simulation for all scenarios with the 20k and 30k scenarios remaining above baseline conditions and the 40k and 50k scenarios declining below baseline conditions. By the end of the simulations the percentage of Eglin occupied by fuelbeds with high crown fire potential was 49.1 percent (range: 48.2–49.8 percent) for the 20k scenario and 31.0 percent (range: 30.6–31.4 percent) for the 50k scenario. Wilcoxon signed-rank tests comparing 50-year outputs with initial conditions were significant ($P < 0.05$) for all treatment scenarios and Tukey's HSD analysis results were significant ($P < 0.05$) for all among-treatment comparisons at 50 years.

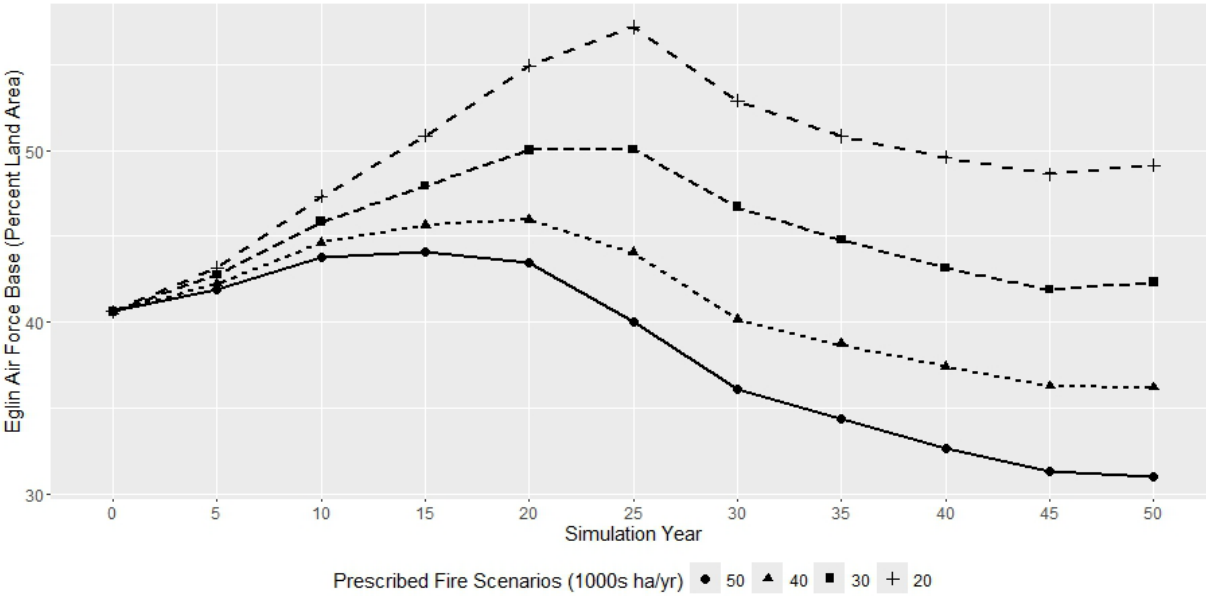


**Figure. 5-5.** Percent of Eglin Air Force Base with high crown fire hazard (FCCS crown fire potential: 4-6) under four prescribed fire scenarios for 50-year period. Each line represents the average of 10 replicates and modeled crown fire potentials is reported for 10-year intervals.

### 5.5.4 *Mean fire interval*

The distribution of MFI categories across the landscape for each scenario reflected the level of prescribed fire and prioritization of burn units. The baseline extent of high-frequency fire regimes (MFI: 1–3 years) was 19.5 percent and these increased for both 40k and 50k scenarios and decreased for the 20k and 30k scenarios (Figure 5-6A). Under the 50k scenario, coverage nearly doubled to 36.9 percent (range: 35.9–37.2 percent) by the end of the simulation period while coverage declined to 6.5 percent (range: 5.9–7.1 percent) for the 20k scenario.

The baseline extent of intermediate-frequency fire regimes (MFI: 4-8 years) was 26.5 percent and declined for all scenarios through year 30 before rebounding slightly (Figure 5-6B). The 50k scenario had the largest decline reaching a minimum of 5.7 percent (range: 5.1–6.4 percent) coverage at year 30. Among the other three scenarios, the change in intermediate-frequency fire regime extent showed a similar pattern, but a slightly less pronounced decline over time compared to the 50k scenario.

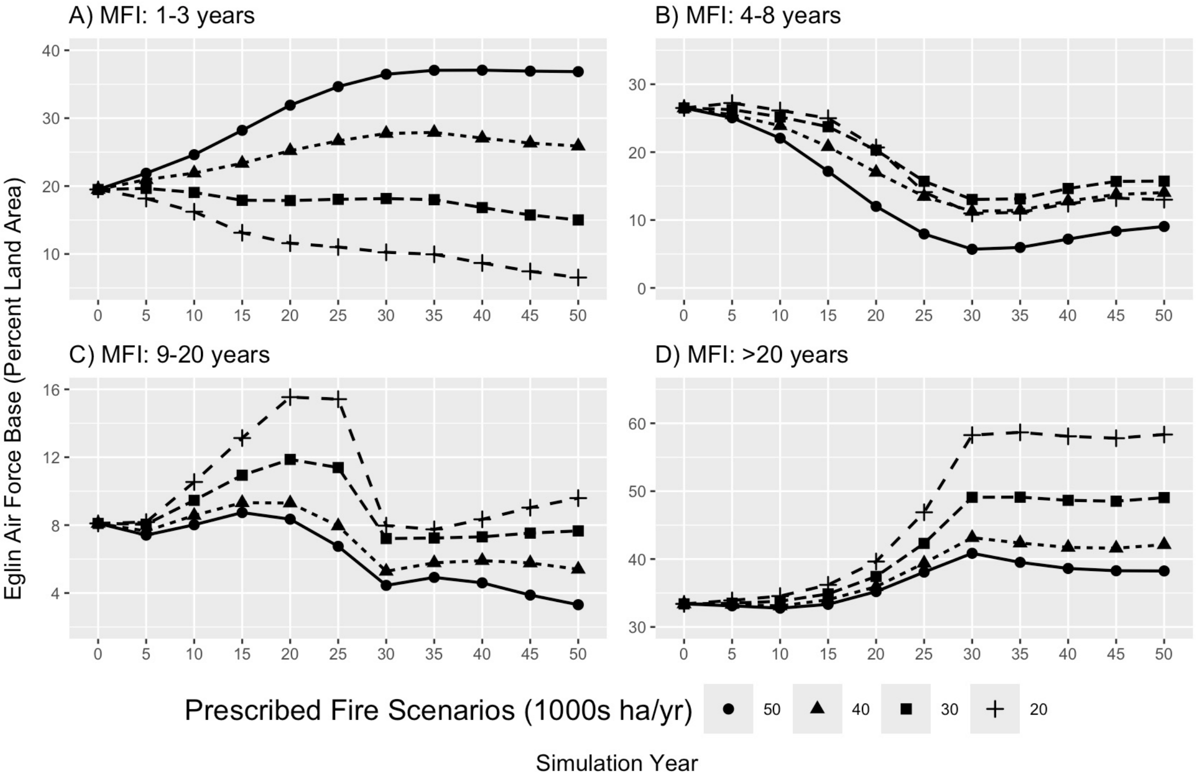


**Figure. 5-6.** Distribution of mean fire interval (MFI) categories across Eglin Air Force Base, Florida under four prescribed fire scenarios for 50-year period. MFI is plotted at 5-year intervals. Each line represents the average of 10 replicates. Reported values exclude 10-km buffer zone.

The baseline extent of fuelbeds with low-frequency fire regimes (MFI: 9–20 years) was 8.1 percent. The 20k and 30k scenario simulations showed a brief increase from year 5 to 20, before returning to near baseline levels (Figure 5-6C). Coverage of low-frequency fire regime fuelbeds peaked in year 20 at 15.5 percent (range: 14.8–16.5 percent) for the 20k scenario and 11.9 percent (range: 11.5–12.6 percent) for the 30k scenario. By year 50 coverage for the 20k scenario was slightly higher than baseline conditions at 9.6 percent (range: 9.0–10.2 percent) whereas the 50k scenario was lower at 3.3 percent (range: 3.0–3.6 percent).

The extent of fire-excluded fuelbeds (MFI: > 20 years) started at 33.4 percent and increased for all scenarios through year 30 before stabilizing (Figure 5-6D). By year 30 the extent of fire-excluded fuelbeds increased to 58.3 percent (range: 57.3–58.8 percent) for the 20k scenario, 49.1 percent (range: 48.1–50.7 percent) for the 30k scenario, 43.1 percent (range: 41.5–44.1 percent) for the 40k scenario, and 40.9 percent (range: 40.1–41.5 percent) for the 50k scenario.

For all MFI categories, Wilcoxon signed-rank tests comparing 50-year outputs with initial conditions were significant ($P < 0.05$) for all treatment scenarios and ARTc analysis results were significant ($P < 0.05$) for all among-treatment comparisons at 50 years.

### 5.5.5 *Vegetation cover types*

Longleaf pine coverage declined for all scenarios, but the rate of decline was greater with decreasing application of prescribed fire (Figure 5-7A). Corresponding increases were distributed among the other vegetation cover types with broadleaf-pine serving as an intermediate cover type between fire-maintained longleaf pine and fire-excluded broadleaf and sand pine forests. Larger increases corresponded with lower rates of simulated prescribed fire.

The baseline extent of longleaf pine coverage was 58.9 percent and declined steadily throughout the simulation period to 47.6 percent (range: 47.0–48.2 percent) for the 50k scenario,

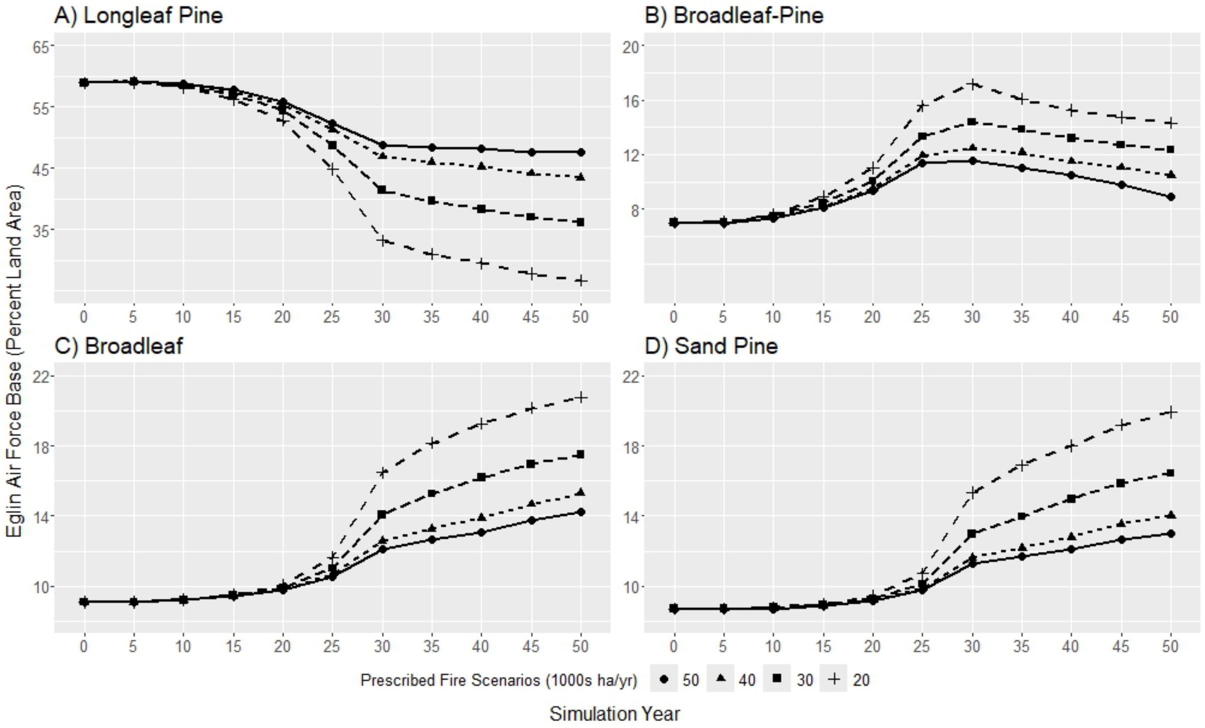


**Figure 5-7.** Distribution of forested vegetation cover types across Eglin Air Force Base, Florida under four prescribed fire scenarios for 50-year period. Cover is plotted at 5-year intervals. Each line represents the average of 10 replicates. Reported values exclude 10-km buffer zone.

43.5 percent (range: 43.0–44.1 percent) for the 40k scenario, 46.2 percent (range: 35.9—36.5 percent) for the 30k scenario, and 26.8 percent (range: 26.2–27.5 percent) for the 20k scenario. The fastest rate of loss occurred between 20 and 30 years and coincided with the fastest rates of increased coverage of mixed broadleaf-pine cover types.

The extent of fuelbeds with a mixed broadleaf-pine overstory remained near baseline (7.0 percent) for all scenarios through year 20 when coverage increased and then leveled off at year 30 (Figure 5-7B). Mixed broadleaf-pine vegetation cover types then declined slowly but remained above the baseline level through the end of the simulation. Highest coverage was for the 20k scenario when extent peaked at 17.2 percent (range: 16.6–18.5 percent) at year 30 before declining to 14.3 percent (range: 13.3–15.2 percent) by year 50. By comparison, lowest coverage was for the 50k scenario when extent peaked at 11.5 percent (range: 10.8–12.3 percent) at year 30 before declining to 8.9 percent (range: 8.5–9.6 percent).

Both broadleaf (Figure 5-7C) and sand pine cover types (Figure 5-7D) remained close to baseline extents of 9.1 and 8.7 percent, respectively, through year 20 before increasing steadily. These increases were most pronounced for the 20k scenario and were progressively lower as rate of burning increased. Extent of broadleaf forests peaked at 20.8 percent (range: 20.5–21.3 percent) in year 50 for the 20k scenario and 14.2 percent (range: 13.9 to 14.7 percent) in year 50 for the 50k scenario. The pattern for sand pine forests was the same. Extent was greatest for the 20k scenario with highest coverage of 19.9 percent (range: 19.2–20.9) at year 50 while the 50k scenario had highest coverage of 13.0 percent (range: 12.8–13.2) at year 50.

For all vegetation cover types, Wilcoxon signed-rank tests comparing 50-year outputs with initial conditions were significant ($P < 0.05$) for all treatment scenarios and ARTc analysis results were significant ($P < 0.05$) for all among-treatment comparisons at 50 years.

## 5.6 **Discussion**

Maintaining adequate levels of prescribed fire at the landscape-scale (Ferguson, 2005; New York Times, 2010) to manage hazardous fuels (Haines et al., 2001; Kobziar et al., 2015) in longleaf pine forests is challenging for land management organizations confronted with air quality standards and public dissatisfaction with smoke impacts (Goodrick et al., 2010; Kupfer et al., 2022; Liu and Achtemeier, 2003). Prescribed fire is an effective tool for mitigating hazardous fuels in the longleaf pine ecosystem (Brose and Wade, 2002; Haywood, 2010; Ottmar and Prichard, 2012) because repeated, frequent application maintains fine surface fuels (Andreu et al., 2012; Hiers et al., 2009; Hough and Albini, 1978) below levels that contribute to high-intensity surface fire behavior (Hough and Albini, 1978) and increased crown fire potential (Andreu et al., 2018). The FDM simulation results reported here quantify the impacts of different prescribed fire scenarios on the distribution of hazardous fuels at Eglin. Prescribed fire reductions of 25 to 50 percent (20k and 30k, respectively) produced substantial increases in the area of fuelbeds with high surface fuel loading and elevated crown fire hazard associated with fire exclusion, to the detriment of low-hazard longleaf pine fuelbeds. These increases in fire hazard may be temporary due to forest mesophication. This is indicated by the shift from longleaf pine and mixed pine-broadleaf to fire-impeding vegetation such as broadleaf and sand pine forests towards the end of the simulations for reduced prescribed fire scenarios. In contrast, fire-excluded and high hazard fuelbed types remained stable for the *status quo* (40k) and decreased for the increased prescribed fire (50k) scenarios. These trends align with current knowledge about the impacts of prescribed fire on fuel dynamics and fire hazard in southeastern US pine systems at the stand (Brose and Wade, 2002) and landscape scale (Ottmar and Prichard, 2012). Trends reported here echo outcomes of similar modeling exercises for the longleaf pine ecosystem (Costanza et al., 2015; Flanagan et al., 2019; Matusick et al., 2020) and other fire-adapted ecosystems across the US (Jones et al., 2025; Shang et al., 2004; Shinneman et al., 2012).

### 5.6.1 *Fine fuel loading and MFI*

For the 20k and 30k scenarios, the area of fuelbeds with high fine fuel loading increased because fire was effectively excluded from burn units with longleaf pine cover that were being regularly burned (i.e., there was not enough prescribed burn capacity available on an annual basis to include the number of units being regularly burned at baseline levels) , which permitted biomass to accumulate thereby changing the state of those locations on the Eglin landscape. This relationship between accumulating fine fuel loading and longer fire intervals has been observed across many fire-adapted ecosystems outside of the southeastern US including boreal regions (Cronan and Jandt, 2008; Schimmel and Granström, 1997), the Mediterranean Basin (Marino et al., 2011; Rego, 1991), and the western US (Stephens et al., 2012; Youngblood et al., 2008). In the southeastern US, fine fuels accumulate rapidly after the most recent fire, but rates plateau after 20 years (Brose and Wade, 2002). The Eglin landscape is dominated by longleaf pine flatwoods (18 percent) and sandhill (70 percent) cover types. Both are fire-adapted and depend on frequent fire to maintain an open understory with low fire hazard. In flatwoods, fine surface fuel loading for fuelbeds was 5.0–10.3 Mg $ha^{-1}$ for 1–3 year MFI, 10.9–13.0 Mg $ha^{-1}$ for 4–8 year MFI, and 20.9–26.7 Mg $ha^{-1}$ for 9–20 year MFI. These values are similar to those reported by Brose and Wade (2002), who observed that fine fuel loading nearly tripled from 7.2 to 19.0 Mg $ha^{-1}$ five years after fire in regularly burned longleaf pine flatwoods elsewhere in Florida. Likewise, McNab (1978) reported similar rates of increase in fine fuel loading following fire for slash and longleaf pine stands in northern Florida. Sandhills have lower fuel loads because they occur on well-drained, poor soils elevated above the water table; an environment with limited nutrient availability and physiological drought stress (Woods, 1957) that is less productive than flatwoods (Abrahamson and Hartnett, 1990). Fine surface fuel loading for sandhill fuelbeds was 3.3–8.0 Mg $ha^{-1}$ for 1–3 year MFI, 4.0–10.2 Mg $ha^{-1}$ for 4–8 year MFI, and 4.9–22.8 Mg $ha^{-1}$ for 9–20 year MFI. Unburned units in this simulation would transition to high fine surface fuel loading after as little as four years for flatwoods and after eight years for sandhills.

For fuel types in the southeastern US there is a well-established relationship between accumulating fine surface fuel loading and measures of fire behavior (Brose & Wade, 2002;

Gavazzi & McNulty, 2013; Hough & Albini, 1978; Robertson & Ostertag, 2007). Fire suppression tactics become difficult when fireline intensity values exceed 500–1500 kW $m^{-1}$. This occurs when fine fuel loading is greater than 9 Mg $ha^{-1}$. Of the fuelbeds included in the FDM simulations, 91.5 percent with loading greater than 9 Mg $ha^{-1}$ have infrequent MFI or are fire-excluded. FDM simulations projected the area of fuelbeds at Eglin that can support fireline intensity levels that exceed 1500 kW $m^{-1}$ will increase by 28 percent for the 30k scenario and 48 percent for the 20k scenario. This represents a substantial increase in land area capable of generating surface fire behavior that exceeds the capacity for typical fire suppression efforts and could necessitate the use of more costly suppression methods and pose greater fire risk to Eglin's infrastructure and to surrounding communities.

### 5.6.2 *Crown fire potential*

The increase in crown fire potential across Eglin under reduced prescribed fire scenarios is a product of changes to the quantity and arrangement of the surface and canopy fuel layers (Andreu et al., 2018). Accumulation of fine fuels, as outlined above, increases potential surface fire intensity which raises the likelihood of crown fire (Hoffman et al., 2013). Development of fuelbeds with fuel ladders and lower canopy base height reduce the surface fire intensity necessary for crown fire initiation, which further adds to crown fire hazard (Cruz et al., 2006). Long MFIs – exceeding 9 years – permit steep increases in surface fuel loading, and also lead to the development of a midstory layer of trees and shrubs that can act as fuel ladders that bridge the vertical gap between the surface and crown fuel layers (McNab et al., 1978) increasing the probability of crown fire initiation and spread. When fire is excluded, shade-tolerant midstory species continue to grow and slowly replace longleaf pine in the overstory, creating a fuelbed that can support high-intensity crown fires, albeit only under very dry conditions (Moser and Wade, 2005).

The fire-sensitive species that replace longleaf pine coupled with changes in understory vegetation, however, can have moderating effects on crown fire hazard in fire-excluded forests over longer time periods. This is because fire-excluded forests have dense canopies that maintain higher humidities (Moser and Wade, 2005) and the litter layer has a higher bulk density which is less prone to drying and burning at lower intensity (Kreye et al., 2013; Varner et al., 2021). Together these factors reduce the probability of ignition and limit fire spread to atypically hot and dry periods. This process of reduced flammability through changes in species composition, known as forest mesophication, is prevalent across the eastern US where frequent low-intensity fire has been removed from the landscape (Nowacki and Abrams, 2008). The impact of shifts in species composition is discussed further in the next section.

### 5.6.3 *Vegetation cover types*

The extent to which crown fire potential increases depends on which species replace longleaf pine in the absence of frequent prescribed fire. In sandhills multiple species can overtake longleaf pine during periods of fire exclusion. In instances where sand pine becomes dominant, crown fire hazard increases relative to frequently burned longleaf pine but is reduced relative to infrequently burned longleaf pine stands with dense understory and midstory fuels. Sand pine was historically uncommon at Eglin, but colonized the area extensively during the period of fire suppression in the mid- to late-1900s (McCay, 2000; Provencher et al., 2000). The variety of sand pine (*P. clausa* var. *immuginata*) that occurs throughout the Florida panhandle (Ward, 1963) is not as susceptible to fire as the peninsular variety (*Pinus clausa* (Chapm. Ex

Engelm.) Vasey ex Sarg. Var. *clausa*), which is adapted to infrequent, but catastrophic stand replacing crown fires (Myers, 1990) that tend to occur in the early spring (Hough, 1973). However, it has higher crown fire hazard relative to frequently burned longleaf pine forest types but will only burn under abnormally dry conditions. Thus, when sand pine becomes established the risk of crown fires increases but, as a fire impeder, it is less prone to ignition. This represents a potential shift from a fire regime characterized by frequent, relatively small, low intensity prescribed surface fires to one with infrequent fires that can potentially transition into the canopy. This pattern is common for fire-excluded forests in the southeast (Moser and Wade, 2005) and similar to what was documented across the southern Appalachians in 2016 when over 36,000 ha burned in a severe drought-induced outbreak of wildfires (Reilly et al., 2022). Sand pine forests may have lower crown fire hazard (relative to infrequently burned longleaf sandhills) because they have dense litter with low flammability (Fonda, 2001), low understory fuel loading and a high canopy base height, which reduces the probability of crown fire initiation. These characteristics explain why crown fire potentials peak halfway through the simulation period and then decline nearly back to baseline levels as sand pine and broadleaf species become established. These intermediate fuelbeds with higher fire hazard are characterized by fire-excluded longleaf pine with high surface fine fuel biomass and a dense understory of trees and shrubs that act as fuel ladders (Sections 5.5.4 & 5.5.5).

With a few exceptions, broadleaf trees also behave like fire impeders. Oaks, including sand live oak (*Quercus geminata* Small), bluejack oak (*Quercus incana* W. Bartram), and turkey oak (*Quercus laevis* Walter), can also become established in the absence of frequent fire (Provencher et al., 2001) in sandhills. Foliage flammability is low for sand live oak, intermediate for bluejack oak, and high for turkey oak (Varner et al., 2021). Sand live oak is considered a fire-sensitive species and, as with sand pine, its litter inhibits fire spread except in anomalously dry conditions. Bluejack oak and turkey oak are adapted to frequent fire and litter derived from these species ignites easily and readily supports fire spread (Hannon et al., 2020). In instances were fire-sensitive oaks replace longleaf pine, fire hazard may decrease as both surface and canopy fuels become less flammable (Whelan et al., 2021) whereas replacement by fire-adapted oaks maintain high flammability and easily ignitable fuels (Wenk, 2009). At Eglin all three successional tracks (i.e., sand pine, fire-sensitive oaks, and fire-adapted oaks) are equally likely (Provencher et al., 2001, 2000) and the STMs in FDM incorporate this uncertainty. Given that the outcome on fuelbed development and fire hazard for each of these tracks is different, there is a degree of uncertainty surrounding the effect of fire exclusion and forest succession on fire potential and flammability.

In the absence of fire, longleaf pine in flatwoods cover types can also be replaced, in this case by baygalls or bottomland forests. Like fire-excluded sandhills both of these cover types are less prone to fire. Baygalls, especially if titi is dominant, can support high-intensely crown fires in spring when chemical changes in the foliage substantially increase flammability whereas bottomland forests are fire-resistant. Thus, relative to frequently burned longleaf pine flatwoods, baygalls lead to higher crown fire potential while bottomland forests have lower crown fire potential. As with sandhills, intermediate fuelbeds in flatwoods transitioning from pyrophytic to mesophytic forest types can have higher fire hazard relative to fire-excluded fuelbeds because readily ignitable longleaf pine litter and a dense layer of shrubs and grasses remain significant components of the surface fuel layer and can contribute to high surface fire intensity relative to surface fuels in fire-excluded stands.

The pattern of crown fire potential over time for the reduced prescribed fire scenarios (Figure 5-5) is a function of the simulated successional changes described above. High crown fire potential reached its maximum at year 20 before declining, nearly back to baseline levels by year 50 for the 20k and 30k scenarios. This early peak occurs because in units that have become fire-excluded, surface fuels build up and the midstory develops within 25 years. There may be few if any changes in the overstory at this stage, but the high potential surface fireline intensity associated with elevated surface fuel loading and the development of fuel ladders in the form of a developing midstory increases the potential for crown fire – a shift in fuel structure that has been observed at other sites in the southeastern US (Andreu et al., 2018). The process of mesophication (Alexander et al., 2021) occurs in the last half of simulations for fire-excluded stands. Midstory species move into the overstory and, depending on the species composition and topographic position, the forest type shifts from longleaf pine to either fire-sensitive oaks, sand pine, or lowland hardwoods. Crown fire potential in oak-dominated uplands (2.1) is lower than fire-excluded longleaf pine sandhill (3.8) and sand pine (5.2). The net effect is a slow overall decline in crown fire potential from the 25-year peak as fire-sensitive hardwoods with relatively lower crown fire potential replace conifers (Whelan et al., 2018). However, the percentage of fuelbeds with high crown fire potential is higher than baseline conditions due to the development of sand pine stands with relatively higher canopy fuel continuity, but lower probability of ignition. This shift from easily ignitable fuels to fire-inhibiting fuels has been observed throughout eastern forests when fire is removed as a disturbance agent (Alexander et al., 2021; Nowacki and Abrams, 2008). Once the overstory shift starts to occur it becomes substantially more difficult and costly to restore fire-adapted longleaf pine fuelbeds with low fuel hazard.

Other simulations in the region have shown similar results when prescribed fire is reduced. A 100-yr simulation for longleaf pine in the Dougherty Plan ecoregion in Georgia, Alabama, and Florida found that baseline levels of prescribed fire maintained current forest cover while an absence of prescribed fire caused near disappearance of open canopy longleaf pine within 25 years (Costanza et al., 2015). Another modeling exercise that assessed longleaf pine in the same ecoregion found that longleaf pine was replaced by oak species for scenarios where MFI was 20 years or greater (Flanagan et al., 2019). Similarly, a 200-yr simulation for Fort Benning, Georgia showed that longleaf pine was largely replaced by hardwood in the absence of fire (Matusick et al., 2020). Both Flanagan et al. (2019) and Matusick et al. (2020) found that longleaf pine cover and forest structure (i.e., open canopy with low surface fuel loads) increased under prescribed burn scenarios with a 2-3 year MFI, which agree with simulations in this study that show persistence and development of open-canopy longleaf pine cover types with short-MFI on burnable lands at Eglin for the 40k (3.9 yr MFI) and 50k (3.1 yr MFI) scenarios.

### 5.6.4 *Model parameterization and limitations*

Regardless of burn scenario, the FDM simulations project that the current landscape will shift from burn units with an even distribution of MFI towards a bimodal distribution of high-frequency fire (MFI: 1–3 years) and fire-excluded (MFI: >20 years) burn units. This is seen in the decline in area of the intermediate-fire frequency MFI (4–8 years) and of longleaf pine cover types for all modeled prescribed burn scenarios. For the 40k and 50k scenarios, most intermediately burned burn units shift to frequently burned while fire is excluded from the remainder. The resulting unburned units eventually shift to fire-sensitive species causing a decline in the longleaf pine cover type but an increase in high MFI fuelbeds within the remaining longleaf stands. In the 20k and 30k scenarios the effect is more pronounced as prescribed fire is removed from a much greater number of burn units. There is a near doubling in the area of fire-excluded MFI (>20 years; Figure 5-6) and a commensurate decrease in area of the longleaf pine cover type (Figure 5-7). This trend occurs because the prescribed fire prioritization parameters used by Eglin and incorporated into FDM place a high priority on maintaining short MFIs in the BANSA and CCA units (60.2 percent of Eglin). These trends, especially for the 40k and 50k scenarios, suggest that the parameters governing unit selection in the FDM burn prioritization model do not adequately reflect actual burn unit selection, otherwise we would expect a more stable distribution of MFI categories and longleaf pine cover over the simulation period for the 40k scenario.

There are two potential modeling limitations that may explain this trend. The first is that FDM is overestimating area burned by using area of the burn unit treated rather than the actual area burned within in each unit to meet annual area burned quotas for prescribed burning. Using burn unit area rather than actual area burned, in these simulations effectively underestimated actual burning by 35 percent (Section 5.5.1). This would explain the result that shows a decline in area of longleaf pine without a change in the distribution of MFI categories. Although possible, this explanation  is unlikely because land managers generally do not map intra-unit area burned in detail following prescribed fires. The second is that Eglin does not rigidly adhere to the burn priority parameters used for the FDM simulations. They instead, like most land managers, focus on a larger array of factors when selecting units (Kupfer et al., 2022), resulting in a wider range of MFI values across burn units eligible for prescribed burning. The rigid interpretation of burn unit selection parameters used in the simulations does illustrate the implications that distribution of prescribed fire can have even if area burned remains unchanged.

Mean area for high-frequency MFI categories was roughly double that of low fine surface fuel loading categories by the end of the simulation despite the association of high-frequency MFI categories with low fine surface fuel loading. While this may appear contradictory, it is a product of the 4.5 Mg ha$^{-1}$ upper limit for the low fine surface fuel loading category. This category threshold was below fine surface fuel loads of high-frequency MFI categories for more productive fuelbeds in wet flatwoods. There is also a significant portion (60 percent) of fuelbeds from other MFI categories in the low fine fuel loading category. Simulated trends for MFI categories and cover types under the 40k and 50k prescribed fire scenarios result in a loss of fuelbeds with intermediate fire frequency, producing a landscape with a larger share of high-frequency and fire-excluded fire regimes (Figure 5-6).

## 5.7 Management implications

The results of this simulation experiment suggest that reducing the amount of prescribed fire at Eglin is likely to expand areal coverage of hazardous fuels at Eglin, increase fire hazard, and reduce the extent of longleaf pine. This is supported by work showing that prescribed fire activity is negatively correlated with the incidence of wildfires (Addington et al., 2015). While reducing the area burned in prescribed fires may reduce smoke impacts from prescribed burning and save costs associated with a prescribed fire program, this must be reconciled with the potential for higher intensity, more severe, longer duration wildfires. Impacts from these wildfires may outweigh the benefits of a reduction in prescribed burning and include: fire hazard to on-base infrastructure and surrounding WUI communities, smoke events with longer durations and higher pollutant concentrations than prescribed fires, increased firefighting costs, degraded wildlife habitat, and an overall reduction in ecosystem services.

Potential reductions in smoke emissions from decreases in prescribed burning are likely to be offset to some degree by an increase in smoke emissions from additional wildfire activity (Hurteau and North, 2009; Stephens et al., 2009; Volkova et al., 2021). Smoke impacts from wildfires can be more severe than prescribed fires due to unfavorable ventilation such as inversions that trap smoke close to the surface for extended periods or winds such as nighttime downslope winds that transport smoke into populated or other sensitive areas (Guan et al., 2020). Wildfires may also produce much larger quantities of smoke over longer periods of time relative to prescribed fires (Reilly et al., 2022).

Another cost associated with potential reductions in prescribed burning is that changes to vegetation that affect fire hazard and wildlife habitat are not easily reversed. For example, longleaf pine forest with high wiregrass coverage can provide some protection from woody encroachment (Fill et al., 2017), however, once woody plants are established extensive and time-consuming efforts are necessary to shift forests back to longleaf pine (Cox et al., 2004; Freeman and Jose, 2009; Outcalt, 2005; Provencher et al., 2001, 2000). Prescribed fire cannot simply be re-introduced without significant mortality risk to mature longleaf pine (Slack et al., 2016; Varner et al., 2007). Furthermore, climate change and increasing urban pressure are projected to decrease opportunities for prescribed burning across the longleaf pine ecosystem (Hutchens et al., 2024) increasing the importance of maintaining and even enhancing existing prescribed fire programs.

## 5.8 **References**

Abatzoglou, J.T., Williams, A.P., 2016. Impact of anthropogenic climate change on wildfire across western US forests. Proc. Natl. Acad. Sci. U. S. A. 113, 11770–11775.

https://doi.org/10.1073/pnas.1607171113

Abrahamson, W.G., Hartnett, D.C., 1990. Pine flatwoods and dry prairies, in: Meyers, R.L., Ewel, J.J. (Eds.), Ecosystems of Florida. University of Central Florida Press, Orlando, Florida, pp. 103–149.

Addington, R.N., Hudson, S.J., Hiers, J.K., Hurteau, M.D., Hutcherson, T.F., Matusick, G., Parker, J.M., 2015. Relationships among wildfire, prescribed fire, and drought in a fire-prone landscape in the south-eastern United States. Int. J. Wildl. Fire 24, 778–783.

Afrin, S., Garcia-Menendez, F., 2021. Potential impacts of prescribed fire smoke on public health and socially vulnerable populations in a Southeastern U.S. state. Sci. Total Environ. 794, 1–10. https://doi.org/10.1016/j.scitotenv.2021.148712

Agee, J.K., 1993. Fire ecology of Pacific Northwest forests. Island Press, Washington, D.C.

Agee, J.K., Skinner, C.N., 2005. Basic principles of forest fuel reduction treatments. For. Ecol. Manage. 211, 83–96. https://doi.org/10.1016/j.foreco.2005.01.034

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

Alexander, M.E., 1998. Crown fire thresholds in exotic pine plantations of Australasia. Australian National University, Canberra, Australia. https://doi.org/https://doi.org/10.25911/5d78daa095b33

An, H., Gan, J., Cho, S.J., 2015. Assessing climate change impacts on wildfire risk in the United States. Forests 6, 3197–3211. https://doi.org/10.3390/f6093197

Andreu, A.G., Blake, J.I., Zarnoch, S.J., 2018. Estimating canopy fuel characteristics for predicting crown fire potential in common forest types of the Atlantic Coastal Plain, USA. Int. J. Wildl. Fire 27, 742–755.

Andreu, A.G., Shea, D., Parresol, B.R., Ottmar, R.D., 2012. Evaluating fuel complexes for fire hazard mitigation planning in the southeastern United States. For. Ecol. Manage. 273, 4–16. https://doi.org/DOI 10.1016/j.foreco.2011.06.040

Aponte, C., de Groot, W.J., Wotton, B.M., 2016. Forest fires and climate change: causes, consequences and management options. Int. J. Wildl. Fire 25, 1–2. https://doi.org/10.1071/WF15026

Arno, S.F., Allison-Bunnell, S., 2002. Fire on the landscape: past, present, and future, in: Flames in Our Forest: Disaster or Renewal? Island Press, Washington, DC, pp. 27–36.

Baker, W.L., 2009. People and fire: land-use legacies across the landscape, in: Fire Ecology in Rocky Mountain Landscapes. Island Press, Washington, DC, pp. 356–414.

Bar Massada, A., Radeloff, V.C., Stewart, S.I., 2011. Allocating fuel breaks to optimally protect structures in the wildland-urban interface. Int. J. Wildl. Fire 20, 59–68. https://doi.org/Doi 10.1071/Wf09041

Behm, A.L., Duryea, M.L., Long, A.J., Zipperer, W.C., 2004. Flammability of native understory species in pine flatwood and hardwood hammock ecosystems and implications for the wildland-urban interface. Int. J. Wildl. Fire 13, 355–365. https://doi.org/https://doi.org/10.1071/WF03075

Brodie, E.G., Knapp, E.E., Brooks, W.R., Drury, S.A., Ritchie, M.W., 2024. Forest thinning and prescribed burning treatments reduce wildfire severity and buffer the impacts of severe fire weather. Fire Ecol. 20. https://doi.org/10.1186/s42408-023-00241-z

Brose, P., Wade, D., 2002. Potential fire behavior in pine flatwood forests following three different fuel reduction techniques. For. Ecol. Manage. 163, 71–84. https://doi.org/https://doi.org/10.1016/S0378-1127(01)00528-X

Brown, R.T., Agee, J.K., Franklin, J.F., 2004. Forest restoration and fire: principles in the context of place. Conserv. Biol. 18, 903–912. https://doi.org/https://doi.org/10.1111/j.1523-1739.2004.521_1.x

Butry, D.T., Mercer, D.E., Prestemon, J.P., Pye, J.M., Holmes, T.P., 2001. What is the price of catastrophic wildfire? J. For. 9–17. https://doi.org/https://doi.org/10.1093/jof/99.11.9

Chafin, L.G., Kindell, C.E., Herring, B.J., Nordman, C., Jense, J., Schotz, A.R., 1997. Natural community survey of Eglin Air Force Base, 1993-1996: final report. Florida Natural Areas Inventory, Tallahassee, Florida.

Cook, C.W., 1939. Scenery of Florida interpreted by a geologist. No. 17. Pub. for the state Geological survey.

Costanza, J.K., Terando, A.J., Mckerrow, A.J., Collazo, J.A., 2015. Modeling climate change, urbanization, and fire effects on *Pinus palustris* ecosystems of the southeastern U.S. J. Environ. Manage. 151, 186–199. https://doi.org/10.1016/j.jenvman.2014.12.032

Cox, A.C., Gordon, D.R., Slapcinsky, J.L., Seamon, G.S., 2004. Understory restoration in longleaf pine sandhills. Nat. Areas J. 24, 4–14.

Cronan, J.B., Jandt, R., 2008. How succession affects fire behavior in boreal black spruce forests of Alaska. USDI Bureau of Land Management, Alaska Fire Service, Alaska Technical Report 59, Anchorage, AK.

Cronan, J.B., Wright, C.S., Petrova, M., 2015. Effects of dormant and growing season burning on surface fuels and potential fire behavior in northern Florida longleaf pine (*Pinus palustris*) flatwoods. For. Ecol. Manage. 354, 318–333.

https://doi.org/10.1016/j.foreco.2015.05.018

Cruz, M.G., Butler, B.W., Alexander, M.E., 2006. Predicting the ignition of crown fuels above a spreading surface fire. Part II: model evaluation. Int. J. Wildl. Fire 15, 61–72. https://doi.org/https://doi.org/10.1071/WF04061

Dale, L., 2010. The true cost of wildfire in the Western U.S. Western Forestry Leadership Coalition, Lakewood, Colorado.

Davis, K.T., Dobrowski, S.Z., Higuera, P.E., Holden, Z.A., Veblen, T.T., Rother, M.T., Parks, S.A., Sala, A., Maneta, M.P., 2019. Wildfires and climate change push low-elevation forests across a critical climate threshold for tree regeneration. PNAS 116, 6193–6198. https://doi.org/10.1073/pnas.1815107116

Davis, L.S., Cooper, R.W., 1963. How prescribed burning affects wildfire occurrence. J. For. 61, 915–917. https://doi.org/https://doi.org/10.1093/jof/61.12.915

Duncan, B.W., Adrian, F.W., Stolen, E.D., 2010. Isolating the lightning ignition regime from a contemporary background fire regime in east-central Florida, USA. Can. J. For. Res. 40, 286–297. https://doi.org/Doi 10.1139/X09-193

Emery, R.K., Hart, J.L., 2020. Flammability characteristics of surface fuels in a longleaf pine (*Pinus palustris* Mill.) woodland. Fire 3, 1–18. https://doi.org/10.3390/fire3030039

Fenneman, N.M., Johnson, D.W., 1946. Physiographic divisions of the conterminous US [Map]. US Geological Survey, Reston, Virginia. https://doi.org/https://doi.org/10.5066/P9B1S3K8

Ferguson, J.P., 2005. Building a landscape-level prescribed fire program. Fire Manag. Notes 65, 16–18.

Fernandes, P.M., 2015. Empirical support for the use of prescribed burning as a fuel treatment. Curr. For. Reports 1, 118–127. https://doi.org/10.1007/s40725-015-0010-z

Fill, J.M., Glitzenstein, J.S., Streng, D.R., Stowe, J., Mousseau, T.A., 2017. Wiregrass (*Aristida beyrichiana*) may limit woody plant encroachment in longleaf pine (*Pinus palustris*) ecosystems. Am. Midl. Nat. 177, 153–161. https://doi.org/10.1674/0003-0031-177.1.153

Flanagan, S.A., Bhotika, S., Hawley, C., Starr, G., Wiesner, S.W., Hiers, J.K., O'Brien, J.J., Goodrick, S.G., Callaham Jr., M.A., Scheller, R.M., Klepzig, K.D., Taylor, R.S., Loudermilk, E.L., 2019. Quantifying carbon and species dynamics under different fire regimes in a southeastern U.S. pineland. Ecosphere 10. https://doi.org/10.1002/ecs2.2772

Flannigan, M., Cantin, A.S., de Groot, W.J., Wotton, M., Newbery, A., Gowman, L.M., 2013. Global wildland fire season severity in the 21st century. For. Ecol. Manage. 294, 54–61. https://doi.org/10.1016/j.foreco.2012.10.022

Florida Natural Areas Inventory, 2012. Florida Cooperative Land Cover Map version 2.3.

Fonda, R.W., 2001. Burning characteristics of needles from eight pine species. For. Sci. 47, 390–396. https://doi.org/https://doi.org/10.1093/forestscience/47.3.390

Freeman, J.E., Jose, S., 2009. The role of herbicide in savanna restoration: Effects of shrub reduction treatments on the understory and overstory of a longleaf pine flatwoods. For. Ecol. Manage. 257, 978–986. https://doi.org/10.1016/j.foreco.2008.10.041

Frost, C.C., 1993. Four centuries of changing landscape patterns in the longleaf pine ecosystem, in: Hermann, S. (Ed.), Tall Timbers Fire Ecology Conference Proceedings No. 18. Tall Timbers Research Station, Tallahassee, Florida, pp. 17–44.

Gavazzi, M.J., McNulty, S.G., 2013. The influence of prescribed fire and burn interval on fuel loads in four North Carolina forest ecosystems, in: Proceedings of 4th Fire Behavior and Fuels Conference. International Association of Wildland Fire, Raleigh, North Carolina, USA, pp. 26–48.

Glitzenstein, J.S., Streng, D.R., Wade, D.D., 2003. Fire frequency effects on longleaf pine (*Pinus palustris*, P. Miller) vegetation in South Carolina and northeast Florida, USA. Nat. Areas J. 23, 22–37.

Goodrick, S., Shea, D., Blake, J.I., 2010. Estimating fuel consumption for the Upper Coastal Plain of South Carolina. South. J. Appl. For. 34, 5–12. https://doi.org/https://doi.org/10.1093/sjaf/34.1.5

Greenhouse, S.W., Geisser, S., 1959. On methods in the analysis of profile data. Psychometrika 24, 95–112. https://doi.org/10.1007/BF02289823

Guan, S., Wong, D.C., Gao, Y., Zhang, T., Pouliot, G., 2020. Impact of wildfire on particulate matter in the southeastern United States in November 2016. Sci. Total Environ. 724, 1–11. https://doi.org/10.1016/j.scitotenv.2020.138354

Gude, P., Rasker, R., van den Noort, J., 2008. Potential for future development on fire-prone lands. J. For. 106, 198–205. https://doi.org/https://doi.org/10.1093/jof/106.4.198

Haines, T.K., Busby, R.L., Cleaves, D.A., 2001. Prescribed burning in the South: trends, purpose, and barriers. South. J. Appl. For. 25, 149–153. https://doi.org/10.1093/sjaf/25.4.149

Halofsky, J.E., Peterson, D.L., Harvey, B.J., 2020. Changing wildfire, changing forests: the effects of climate change on fire regimes and vegetation in the Pacific Northwest, USA. Fire Ecol. 16, 1–26. https://doi.org/https://doi.org/10.1186/s42408-019-0062-8

Hannon, D.R., Moorman, C.E., Schultz, A.D., Gray, J.M., DePerno, C.S., 2020. Predictors of fire-tolerant oak and fire-sensitive hardwood distribution in a fire-maintained longleaf pine ecosystem. For. Ecol. Manage. 477, 118468. https://doi.org/10.1016/j.foreco.2020.118468

Haywood, J.D., 2010. Effects of prescribed fire on vegetation and fuel loads in longleaf pine stands in the bluestem range, in: Stanturf, J.A. (Ed.), Proceedings of the 14th Biennial Southern Silvicultural Research Conference. USDA Forest Service, Gen. Tech. Rep. SRS-121., Asheville, North Carolina, pp. 213–217. https://doi.org/https://doi.org/10.2737/SRS-GTR-121

Henderson, J.P., 2006. Dendroclimatological analysis and fire history of longleaf pine (*Pinus palustris* Mill.) in the Atlantic and Gulf Coastal Plain. Dissertation. University of Tennessee, Knoxville, Tennessee.

Hendricks, J.J., Wilson, C.A., Boring, L.R., 2002. Foliar litter position and decomposition in a fire-maintained longleaf pine-wiregrass ecosystem. Can. J. For. Res. 32, 928–941. https://doi.org/Doi 10.1139/X02-020

Heyward, F., 1939. The relation of fire to stand composition of longleaf pine forests. Ecology 20, 287–304. https://doi.org/https://doi.org/10.2307/1930747

Hiers, J.K., O'Brien, J.J., Mitchell, R.J., Grego, J.M., Loudermilk, E.L., 2009. The wildland fuel cell concept: an approach to characterize fine-scale variation in fuels and fire in frequently burned longleaf pine forests. Int. J. Wildl. Fire 18, 315–325. https://doi.org/https://doi.org/10.1071/WF08084

Hiers, J.K., O'Brien, J.J., Will, R.E., Mitchell, R.J., 2007. Forest floor depth mediates understory vigor in xeric *Pinus palustris* ecosystems. Ecol. Appl. 17, 806–814. https://doi.org/https://doi.org/10.1890/06-1015

Hoffman, C.M., Morgan, P., Mell, W., Parsons, R., Strand, E., Cook, S., 2013. Surface fire intensity influences simulated crown fire behavior in lodgepole pine forests with recent mountain pine beetle-caused tree mortality. For. Sci. 59, 390–399. https://doi.org/10.5849/forsci.11-114

Hough, W.A., 1973. Fuel and weather influence wildfires in sand pine forests. USDA Forest Service, Res. Pap. SE-106, Asheville, North Carolina.

Hough, W.A., Albini, F.A., 1978. Predicting fire behavior in palmetto-gallberry fuel complexes. USDA Forest Service, Res. Pap. SE-174, Asheville, North Carolina.

Huang, R., Hu, Y., Russell, A.G., Mulholland, J.A., Odman, M.T., 2019. The impacts of prescribed fire on $PM_{2.5}$ air quality and human health: application to asthma-related emergency room visits in Georgia, USA. Int. J. Environ. Res. Public Health 16, 1–14. https://doi.org/https://doi.org/10.3390/ijerph16132312

Hunter, M.E., Robles, M.D., 2020. Tamm review: the effects of prescribed fire on wildfire regimes and impacts: a framework for comparison. For. Ecol. Manage. 475, 1–13. https://doi.org/10.1016/j.foreco.2020.118435

Hurteau, M., North, M., 2009. Fuel treatment effects on tree-based forest carbon storage and emissions under modeled wildfire scenarios. Front. Ecol. Environ. 7, 409–414. https://doi.org/https://doi.org/10.1890/080049

Hutchens, L., Kupfer, J.A., Gao, P., Sanchez, G.M., Meentemeyer, R.K., Terando, A.J., Hiers, J.K., 2024. Projecting the long-term effects of large-scale human influence on the spatial and functional persistence of extant longleaf pine ecosystems in the Florida Flatwoods Pyrome. Conserv. Sci. Pract. 1–17. https://doi.org/10.1111/csp2.13187

Jaffe, D.A., O’Neill, S.M., Larkin, N.K., Holder, A.L., Peterson, D.L., Halofsky, J.E., Rappold, A.G., 2020. Wildfire and prescribed burning impacts on air quality in the United States. J. Air Waste Manag. Assoc. 70, 583–615. https://doi.org/10.1080/10962247.2020.1749731

Johnson, A.S., Hale, P.E., 2002. The historical foundations of prescribed burning for wildlife: a southeastern perspective, in: Ford, W.M., Russell, K.R., Moorman, C.E. (Eds.), The Role of

Fire in Nongame Wildlife Management and Community Restoration: Traditional Uses and New Directions Proceedings of a Special Workshop. USDA Forest Service, Gen. Tech. Rep. NE-288, Newtown Square, Pennsylvania, pp. 11–23. https://doi.org/https://doi.org/10.2737/NE-GTR-288

Jones, B.A., Berrens, R.P., 2020. Prescribed burns, smoke exposure, and infant health. Contemp. Econ. Policy 39, 292–309. https://doi.org/10.1111/coep.12509

Jones, B.A., McDermott, S., Champ, P.A., Berrens, R.P., 2022. More smoke today for less smoke tomorrow ? We need to better understand the public health benefits and costs of prescribed fire. Int. J. Wildl. Fire 10, 918–926. https://doi.org/10.1071/WF22025

Jones, K., Vukomanovic, J., Robbins, Z.J., Scheller, R.M., 2025. Prescribed fire management impacts on forest succession trajectories in future southern Appalachian forests. Ecol. Modell. 510, 111323. https://doi.org/10.1016/j.ecolmodel.2025.111323

Kane, J.M., Varner, J.M., Hiers, J.K., 2008. The burning characteristics of southeastern oaks: discriminating fire facilitators from fire impeders. For. Ecol. Manage. 256, 2039–2045. https://doi.org/10.1016/j.foreco.2008.07.039

Karafyllidis, I., Thanailakis, A., 1997. A model for predicting forest fire spreading using cellular automata. Ecol. Modell. 99, 87–97. https://doi.org/Doi 10.1016/S0304-3800(96)01942-4

Keane, R.E., Agee, J.K., Fuĺ, P., Keeley, J.E., Key, C., Kitchen, S.G., Miller, R., Schulte, L.A., 2008. Ecological effects of large fires on US landscapes: Benefit or catastrophe? Int. J. Wildl. Fire 17, 696–712. https://doi.org/10.1071/WF07148

Keane, R.E., Holsinger, L.M., Pratt, S.D., 2006. Simulating historical landscape dynamics using the landscape fire succession model LANDSUM version 4.0. USDA Forest Service, Gen. Tech. Rep. RMRS-GTR-171CD, Fort Collins, Colorado.

Keane, R.E., Parsons, R.A., Hessburg, P.F., 2002. Estimating historical range and variation of landscape patch dynamics: limitations of the simulation approach. Ecol. Modell. 151, 29–49. https://doi.org/https://doi.org/10.1016/S0304-3800(01)00470-7

Kennard, D.K., Outcalt, K., 1996. Modeling spatial patterns of fuels and fire behavior in a longleaf pine forest inthe southeastern USA. Fire Ecol. 2, 31–52. https://doi.org/https://doi.org/10.4996/fireecology.0201031

Knight, G.R., Knight, A., Hipes, D., NeSmith, K., Gulledge, K., Jenkins, A., Elam, C., Diamond, P., Oetting, J., Newberry, A., 2010. Development of a cooperative land cover map: final report. Florida's Wildlife Legacy Initiative Project 08009.

Kobziar, L.N., Godwin, D., Taylor, L., Watts, A.C., 2015. Perspectives on trends, effectiveness, and impediments to prescribed burning in the southern U.S. Forests 6, 561–580. https://doi.org/10.3390/f6030561

Kottek, M., Grieser, J., Beck, C., Rudolf, B., Rubel, F., 2006. World map of the Koppen-Geiger climate classification updated. Meteorol. Zeitschrift 15, 259–263. https://doi.org/10.1127/0941-2948/2006/0130

Kreye, J.K., Kobziar, L.N., Camp, J.M., 2014. Immediate and short-term response of understory fuels following mechanical mastication in a pine flatwoods site of Florida, USA. For. Ecol. Manage. 313, 340–354. https://doi.org/10.1016/j.foreco.2013.10.034

Kreye, J.K., Varner, J.M., Hiers, J.K., Mola, J., 2013. Toward a mechanism for eastern North American forest mesophication: differential litter drying across 17 species. Ecol. Appl. 23, 1976–1986. https://doi.org/10.1890/13-0503.1

Kupfer, J.A., Lackstrom, K., Grego, J.M., Dow, K., Terando, A.J., Hiers, J.K., 2022. Prescribed fire in longleaf pine ecosystems: fire managers' perspectives on priorities, constraints, and future prospects. Fire Ecol. 18, 1–19. https://doi.org/10.1186/s42408-022-00151-6

Lafon, C.W., 2010. Fire in the American South: vegetation impacts, history, and climatic relations. Geogr. Compass 4, 919–944. https://doi.org/https://doi.org/10.1111/j.1749-8198.2010.00363.x

Lee, C., Schlemme, C., Murray, J., Unsworth, R., 2015. The cost of climate change: ecosystem services and wildland fires. Ecol. Econ. 116, 261–269. https://doi.org/10.1016/j.ecolecon.2015.04.020

Levene, H., 1960. Robust tests for equality of variances, in: Olkin, I. (Ed.), Contributions to Probability and Statistics. Stanford University Press, Palo Alto, pp. 278–292.

Liu, Y.Q., Achtemeier, G., 2003. Impacts of smoke from prescribed fire on regional air quality in the South. Abstr. Pap. Am. Chem. Soc. 226, U91–U91.

Maliakal, S.K., Menges, E.S., Denslow, J.S., 2000. Community composition and regeneration of Lake Wales Ridge wiregrass flatwoods in relation to time-since-fire. J. Torrey Bot. Soc. 127, 125–138. https://doi.org/10.2307/3088690

Marino, E., Guijarro, M., Hernando, C., Madrigal, J., Díez, C., 2011. Fire hazard after prescribed burning in a gorse shrubland: implications for fuel management. J. Environ. Manage. 92, 1003–1011. https://doi.org/10.1016/j.jenvman.2010.11.006

Matusick, G., Hudson, S.J., Garrett, C.Z., Samuelson, L.J., Kent, J.D., Addington, R.N., Parker, J.M., 2020. Frequently burned loblolly – shortleaf pine forest in the southeastern United States lacks the stability of longleaf pine forest. Ecosphere 11. https://doi.org/10.1002/ecs2.3055

Mauchly, J.W., 1940. Significance test for sphericity of a normal n-variate distribution. Ann. Math. Stat. 11, 204–209.

McCay, D.H., 2000. Effects of chronic human activities on invasion of longleaf pine forests by sand pine. Ecosystems 3, 283–292. https://doi.org/DOI 10.1007/s100210000026

McNab, W.H., Edwards, M.B., Hough, W.A., 1978. Estimating fuel weights in slash pine-palmetto stands. For. Sci. 24, 345–358. https://doi.org/https://doi.org/10.1093/forestscience/24.3.345

Melvin, M.A., 2020. 2020 national prescribed fire use report. Coalition of Prescribed Fire Councils, Inc., Technical Bulletin 04-20, Newton, Georgia.

Menges, E.S., Abrahamson, W.G., Givens, K.T., Gallo, N.P., Layne, J.N., 1993. Twenty years of vegetation change in five long-unburned Florida plant communities. J. Veg. Sci. 4, 375–386. https://doi.org/10.2307/3235596

Menges, E.S., Gordon, D.R., 2010. Should mechanical treatments and herbicides be used as fire surrogates to manage Florida’s uplands: a review. Florida Sci. 73, 147–174.

Mitchener, L.J., Parker, A.J., 2005. Climate, lightning, and wildfire in the national forests of the southeastern United States: 1989-1998. Phys. Geogr. 26, 147–162. https://doi.org/Doi 10.2747/0272-3646.26.2.147

Moser, W.K., Wade, D.D., 2005. Fire exclusion as a disturbance in the temperate forests of the USA: examples from longleaf pine forests. Scand. J. For. Res. 20, 17–26. https://doi.org/Doi 10.1080/14004080510041048

Myers, R.L., 1990. Scrub and high pine, in: Ecosystems of Florida. University of Central Florida Press, Orlando, Florida, pp. 150–193.

Navarro, K.M., Schweizer, D., Balmes, J.R., Cisneros, R., 2018. A review of community smoke exposure from wildfire compared to prescribed fire in the United States. Atmosphere 9, 1–11. https://doi.org/10.3390/atmos9050185

New York Times, 2010. Endangered species thrive on U.S. military bases. http://www.nytimes.com/video/2010/02/21/science/earth/1247467036149/military-bases-as-wildlife-havens.html

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/Doi 10.1641/B580207

O'Brien, J.J., Butler, B., Hiers, J.K., Mitchell, R.J., 2013. Fuel lifecycle and long term fire behavior responses to fuel treatments in southeastern US pine ecosystems. Joint Fire Science Program, Final Report: Joint Fire Science Program Project 09-1-01-7.

O'Brien, J.J., Hiers, J.K., Mitchell, R.J., Varner, J.M., Mordecai, K., 2010. Acute physiological stress and mortality following fire in a long-unburned longleaf pine ecosystem. Fire Ecol. 6, 1–12. https://doi.org/10.4996/fireecology.0602001

Oswalt, C.M., Cooper, J.A., Brockway, D.G., Brooks, H.W., Walker, J.L., Connor, K.F., Oswalt, S.N., Conner, R.C., 2012. History and current condition of longleaf pine in the southern United States. USDA Forest Service, Gen. Tech. Rep. SRS–166, Asheville, North Carolina.

Ottmar, R.D., Prichard, S.J., 2012. Fuel treatment effectiveness in forests of the upper Atlantic Coastal Plain - An evaluation at two spatial scales. For. Ecol. Manage. 273, 17–28. https://doi.org/10.1016/j.foreco.2011.09.040

Ottmar, R.D., Sandberg, D.V., Riccardi, C.L., Prichard, S.J., 2007. An overview of the Fuel Characteristic Classification System - quantifying, classifying, and creating fuelbeds for resource planning. Can. J. For. Res. 37, 2383–2393. https://doi.org/https://doi.org/10.1139/X07-077

Ottmar, R.D., Vihnanek, R.E., 2000. Stereo photo series for quantifying natural fuels. Volume VI: longleaf pine, pocosin, and marshgrass types in the Southeast United States, PMS 835.

ed. National Wildfire Coordinating Group, National Interagency Fire Center, Boise, Idaho.

Ottmar, R.D., Vihnanek, R.E., Mathey, J.W., 2003. Stereo photo series for quantifying fuels. Volume VIa: sand hill, sand pine scrub, and hardwoods with white pine types in the southeast United States with supplmental sites for Volume VI, PMS 838. National Wildfire Coordinating Group, Boise, Idaho.

Outcalt, K.W., 2005. Restoring structure and composition of longleaf pine ecosystems of the Gulf Coastal Plains, in: Kush, J.S. (Ed.), Proceedings of the 5th Longleaf Alliance Regional Conference, Longleaf Alliance Report No. 8. Hattiesburg, Mississippi, pp. 97–100.

Overing, J.D., Watts, F.C., 1989. Soil survey of Walton County, Florida. USDA Soil Conservation Service, Washington, DC.

Parker, A.J., Parker, K.C., McCay, D.H., 2004. Disturbance-mediated variation in stand structure between varieties of Pinus clausa (sand pine). Ann. Assoc. Am. Geogr. 28–47. https://doi.org/https://doi.org/10.1111/0004-5608.00232

Parks, S.A., Abatzoglou, J.T., 2020. Warmer and drier fire seasons contribute to increases in area burned at high severity in western US forests from 1985 to 2017. Geophys. Res. Lett. 1–10. https://doi.org/10.1029/2020GL089858

Peet, R.K., 2006. Ecological classification of longleaf pine woodlands, in: Jose, S., Jokela, E.J., Miller, D.L. (Eds.), The Longleaf Pine Ecosystem: Ecology, Silviculture, and Restoration. Springer, New York, pp. 51–93. https://doi.org/10.1007/978-0-387-30687-2

Peterson, G.D., 2002. Forest dynamics in the southeastern United States: managing multiple stable states, in: Gunderson, L.H., Pritchard Jr, L. (Eds.), Resilience and the Behavior of Large-Scale Systems. Island Press, London, pp. 227–246. https://doi.org/https://doi.org/10.1108/meq.2003.14.3.423.3

Piqué, M., Domènech, R., 2018. Effectiveness of mechanical thinning and prescribed burning on fire behavior in *Pinus nigra* forests in NE Spain. Sci. Total Environ. 618, 1539–1546. https://doi.org/10.1016/j.scitotenv.2017.09.316

Prichard, S.J., Karau, E.C., Ottmar, R.D., Kennedy, M.C., Cronan, J.B., Wright, C.S., Keane, R.E., 2014. Evaluation of the CONSUME and FOFEM fuel consumption models in pine and mixed hardwood forests of the eastern United States. Can. J. For. Res. 44, 784–795. https://doi.org/DOI 10.1139/cjfr-2013-0499

Prichard, S.J., Ottmar, R.D., Sandberg, D.V., Eagle, P.C., Andreu, A.G., Swedin, K., 2011. FCCS User's Guide, Version 2.2.

Provencher, L., Herring, B.J., Gordon, D.R., Rodgers, H.L., Galley, K.E.M., Tanner, G.W., Hardesty, J.L., Brennan, L.A., 2001. Effects of hardwood reduction techniques on longleaf pine sandhill vegetation in northwest Florida. Restor. Ecol. 9, 13–27. https://doi.org/DOI 10.1046/j.1526-100x.2001.009001013.x

Provencher, L., Herring, B.J., Gordon, D.R., Rodgers, H.L., Tanner, G.W., Brennan, L.A., Hardesty, J.L., 2000. Restoration of northwest Florida sandhills through harvest of invasive Pinus clausa. Restor. Ecol. 8, 175–185. https://doi.org/https://doi.org/10.1046/j.1526-100x.2000.80025.x

Quinn-Davidson, L.N., Varner, J.M., 2012. Impediments to prescribed fire across agency, landscape and manager: an example from northern California. Int. J. Wildl. Fire 21, 210–218. https://doi.org/Doi 10.1071/Wf11017

R Development Core Team, 2008. R: a language and environment for statistical computing. https://www.r-project.org/.

Radeloff, V.C., Helmers, D.P., Kramer, H.A., Mockrin, M.H., Alexandre, P.M., Bar-Massada, A., Butsic, V., Hawbaker, T.J., Martinuzzi, S., Syphard, A.D., Stewart, S.I., 2018. Rapid growth of the US wildland-urban interface raises wildfire risk. PNAS 115, 3314–3319. https://doi.org/10.1073/pnas.1718850115

Rego, F.C., 1991. Fuel management, in: ECE/FAO/ILO Seminar on Forest Fire Prevention, Land Use and People. Athens, Greece, pp. 209–221.

Reilly, M.J., Norman, S.P., O'Brien, J.J., Loudermilk, E.L., 2022. Drivers and ecological impacts of a wildfire outbreak in the southern Appalachian Mountains after decades of fire exclusion. For. Ecol. Manage. 524, 1–12. https://doi.org/10.1016/j.foreco.2022.120500

Reinhardt, E.D., Keane, R.E., Calkin, D.E., Cohen, J.D., 2008. Objectives and considerations for wildland fuel treatment in forested ecosystems of the interior western United States. For. Ecol. Manage. 256, 1997–2006. https://doi.org/DOI 10.1016/j.foreco.2008.09.016

Reisen, F., Meyer, C.P., McCaw, L., Powell, J.C., Tolhurst, K., Keywood, M.D., Gras, J.L., 2011. Impact of smoke from biomass burning on air quality in rural communities in southern Australia. Atmos. Environ. 45, 3944–3953. https://doi.org/DOI 10.1016/j.atmosenv.2011.04.060

Riebold, R.J., 1971. The early history of wildfires and prescribed burning, in: Prescribed Burning Symposium Proceedings. USDA Forest Service, Asheville, North Carolina, pp. 11–20.

Robertson, K.M., Ostertag, T.E., 2007. Effects of land use on fuel characteristics and fire behavior in pinelands of southwest Georgia, in: Masters, R.E., Galley, K.E.M. (Eds.), Proceedings of the 23rd Tall Timbers Fire Ecology Conference. Tall Timbers Research Station, Tallahassee, Florida, pp. 181–191.

Ryan, K.C., Opperman, T.S., 2013. LANDFIRE - a national vegetation/fuels data base for use in fuels treatment, restoration, and suppression planning. For. Ecol. Manage. 294, 208–216.

https://doi.org/DOI 10.1016/j.foreco.2012.11.003

Salguero, J., Li, J., Farahmand, A., Reager, J.T., 2020. Wildfire trend analysis over the contiguous United States using remote sensing observations. Remote Sens. 12, 1–16. https://doi.org/https://doi.org/10.3390/rs12162565

Sandberg, D.V., Riccardi, C.L., Schaaf, M.D., 2007. Fire potential rating for wildland fuelbeds using the Fuel Characteristic Classification System. Can. J. For. Res. 37, 2456–2463. https://doi.org/https://doi.org/10.1139/X07-093

Schimmel, J., Granström, A., 1997. Fuel succession and fire behavior in the Swedish boreal forest. Can. J. For. Res. 27, 1207–1216.

Science Applications International Corporation, 2010. Eglin integrated natural resources management plan. Shalimar, Florida.

Science Applications International Corporation, 2008. Long-term vegetation control for Eglin Air Force Base, Florida - final environmental assessment. Shalimar, Florida.

Scott, J.H., Reinhardt, E.D., 2001. Assessing crown fire potential by linking models of surface and crown fire behavior. USDA Forest Service, Res. Pap. RMRS-29, Fort Collins, Colorado. https://doi.org/https://doi.org/10.2737/RMRS-RP-29

Shang, B.Z., He, H.S., Crow, T.R., Shifley, S.R., 2004. Fuel load reductions and fire risk in central hardwood forests of the United States: a spatial simulation study. Ecol. Modell. 180, 89–102. https://doi.org/10.1016/j.ecolmodel.2004.01.020

Shapiro, S.S., Wilk, M.B., 1965. An analysis of variance test for normality (complete samples). Biometrika 52, 591–611. https://doi.org/10.2307/2333709

Shaw, J.D., Long, J.N., 2007. A density management diagram for longleaf pine stands with application to red-cockaded woodpecker habitat. South. J. Appl. For. 31, 28–38.

https://doi.org/https://doi.org/10.1093/sjaf/31.1.28

Shinneman, D.J., Palik, B.J., Cornett, M.W., 2012. Can landscape-level ecological restoration influence fire risk? A spatially-explicit assessment of a northern temperate-southern boreal forest landscape. For. Ecol. Manage. 274, 126–135. https://doi.org/10.1016/j.foreco.2012.02.030

Slack, A.W., Zeibig-Kichas, N.E., Kane, J.M., Varner, J.M., 2016. Contingent resistance in longleaf pine (*Pinus palustris*) growth and defense 10 years following smoldering fires. For. Ecol. Manage. 364, 130–138. https://doi.org/10.1016/j.foreco.2016.01.014

Stephens, S.L., Collins, B.M., Roller, G., 2012. Fuel treatment longevity in a Sierra Nevada mixed conifer forest. For. Ecol. Manage. 285, 204–212. https://doi.org/10.1016/j.foreco.2012.08.030

Stephens, S.L., Moghaddas, J.J., Edminster, C., Fiedler, C.E., Haase, S., Harrington, M., Keeley, J.E., Knapp, E.E., McIver, J.D., Metlen, K., Skinner, C.N., Youngblood, A., 2009. Fire treatment effects on vegetation structure, fuels, and potential fire severity in western US forests. Ecol. Appl. 19, 305–320. https://doi.org/https://doi.org/10.1890/07-1755.1

Strabo, F., Reimer, M.N., 2024. Before the Burn: The Economic Benefits of Fuel-Reduction Treatments in Wildfire-Prone Forests. Available SSRN. https://doi.org/https://dx.doi.org/10.2139/ssrn.5064565

Theobald, D.M., Romme, W.H., 2007. Expansion of the US wildland-urban interface. Landsc. Urban Plan. 83, 340–354. https://doi.org/DOI 10.1016/j.landurbplan.2007.06.002

Thomas, D., Butry, D., Gilbert, S., Webb, D., Fung, J., 2017. The costs and losses of wildfires: a literature review. Department of Commerce, National Institute of Standards and Technology, NIST Special Publication 1215. https://doi.org/10.6028/NIST.SP.1215

Tukey, J.W., 1949. Comparing individual means in the analysis of variance. Biometrics 5, 99–114. https://doi.org/10.2307/3001913

US Air Force, 2017. U.S. Air Force Integrated Natural Resources Management Plan - Eglin Air Force Base, Florida (August 2017 to July 2022).

USDA, USDI, 2021. Hazardous Fuels Reduction and Landscape Restoration Accomplishments Fiscal Years (FY) 2003-2021.

Van Wagner, C.E., 1977. Conditions for the start and spread of crown fire. Can. J. For. Res. 7, 23–24. https://doi.org/https://doi.org/10.1139/x77-004

Varner, J.M., Hiers, J.K., Ottmar, R.D., Gordon, D.R., Putz, F.E., Wade, D.D., 2007. Overstory tree mortality resulting from reintroducing fire to long-unburned longleaf pine forests: the importance of duff moisture. Can. J. For. Res. 37, 1349–1358. https://doi.org/10.1139/xo6-315

Varner, J.M., Kane, J.M., Kreye, J.K., Shearman, T.M., Dean, T.J., Nowacki, G.J., 2021. Litter flammability of 50 southeastern North American tree species: evidence for mesophication gradients across multiple ecosystems. Front. For. Glob. Chang. 4, 1–11. https://doi.org/10.3389/ffgc.2021.727042

Volkova, L., Roxburgh, S.H., Weston, C.J., 2021. Effects of prescribed fire frequency on wildfire emissions and carbon sequestration in a fire adapted ecosystem using a comprehensive carbon model. J. Environ. Manage. 290, 1–10. https://doi.org/10.1016/j.jenvman.2021.112673

Vorster, A.G., Stevens-Rumann, C., Young, N., Woodward, B., Choi, C.T.H., Chambers, M.E., Cheng, A.S., Caggiano, M., Schultz, C., Thompson, M., Greiner, M., Aplet, G., Addington, R.N., Battaglia, M.A., Bowker, D., Bucholz, E., Buma, B., Evangelista, P., Huffman, D., Mueller, S., Rhoades, C., Romme, W.H., Sánchez Meador, A.J., Tinkham, W.T., Tuten, M., West Fordham, A., 2024. Metrics and considerations for evaluating how forest treatments alter wildfire behavior and effects. J. For. 122, 13–30. https://doi.org/10.1093/jofore/fvad036

Wade, D.D., Lunsford, J.D., 1989. A guide for prescribed fire in southern forests. USDA Forest Service, Tech. Pub. R8-TP 11, Atlanta, Georgia.

Waldrop, T.A., Van Lear, D.H., Lloyd, F.T., Harms, W.R., 1987. Long-term studies of prescribed burning in loblolly pine forests of the Southeastern Coastal Plain. USDA Forest Service, Gen. Tech. Rep. SE-45, Asheville, North Carolina. https://doi.org/https://doi.org/10.2737/SE-GTR-45

Ward, D.B., 1963. Contributions to the flora of Florida: 2, Pinus (Pinaceae). Castanea 28, 1–10.

Ware, S., Frost, C.C., Doerr, P.D., 1993. Southern mixed hardwood forest: the former longleaf pine forest, in: Martin, W.H., Boyce, S.G., Echternacht, A.C. (Eds.), Biodiversity of the Southeastern United States: Lowland Terrestrial Communities. John Wiley & Sons, Inc, New York.

Weinhold, B., 2011. Fields and forests in flames: vegetation, smoke and human health. Environ. Health Perspect. 119, A386–A393. https://doi.org/Doi 10.1289/Ehp.119-A386

Wenk, E.S., 2009. Effects of vegetation structure on fire behavior and wiregrass seedling establishment in xeric sandhills. Masters Thesis. Clemson University, Clemson, South Carolina.

Westerling, A.L., Hidalgo, H.G., Cayan, D.R., Swetnam, T.W., 2006. Warming and earlier spring increase western US forest wildfire activity. Science 313, 940–943. https://doi.org/10.1126/science.1128834

Whelan, A.W., Bigelow, S.W., Nieminen, M.F., Jack, S.B., 2018. Fire season, overstory density and groundcover composition affect understory hardwood sprout demography in longleaf pine woodlands. Forests 9. https://doi.org/10.3390/f9070423

Whelan, A.W., Bigelow, S.W., O'Brien, J.J., Hudak, A.T., 2021. Overstory longleaf pines and hardwoods create diverse patterns of energy release and fire effects during prescribed fire. Front. For. Glob. Chang. 4, 1–14. https://doi.org/10.3389/ffgc.2021.658491

Woods, F.W.., 1957. Factors limiting root penetration in deep sands of the Southeastern Coastal Plain. Ecology 38, 357–359. https://doi.org/https://doi.org/10.2307/1931699

Wright, C.S., 2010. Effects of disturbance and fuelbed succession on spatial patterns of fuel, fire hazard, and carbon; and fuel consumption in shrub dominated ecosystems. Dissertation. University of Washington, Seattle Washington.

Wu, X., Sverdrup, E., Mastrandrea, M.D., Wara, M.W., Wager, S., 2023. Low-intensity fires mitigate the risk of high-intensity wildfires in California's forests. Sci. Adv. 9, 1–9. https://doi.org/10.1126/sciadv.adi4123

Youngblood, A., Wright, C.S., Ottmar, R.D., McIver, J.D., 2008. Changes in fuelbed characteristics and resulting fire potentials after fuel reduction treatments in dry forests of the Blue Mountains, northeastern Oregon. For. Ecol. Manage. 255, 3151–3169. https://doi.org/https://doi.org/10.1016/j.foreco.2007.09.032

Zhang, Y.J., He, H.S., Yang, H., 2008. The wildland-urban interface dynamics in the southeastern U.S. from 1990 to 2000. Landsc. Urban Plan. 85, 155–162. https://doi.org/DOI 10.1016/j.landurbplan.2007.11.007

# Appendix A: FCCS custom fuelbeds for each treatment plot at each sampling period

**Table A-1.** Mean understory live fuel variables for each treatment plot at each sampling time at EAFB in mesic longleaf pine flatwoods in northern Florida, US used as inputs to create custom FCCS fuelbeds.

| | | Shrubs | | | Herbs | | |
|---|---|---|---|---|---|---|---|
| Plot No. | Sample time | Cover (%) | Biomass (Mg $ha^{-1}$) | Height (m) | Cover (%) | Biomass (Mg $ha^{-1}$) | Height (m) |
| Dormant season plots | | | | | | | |
| 1 | Pre | 39 | 4.48 | 0.75 | 13 | 0.44 | 0.32 |
| | 1-year post | 27 | 1.90 | 0.47 | 12 | 0.62 | 0.24 |
| | 2-years post | 34 | 1.80 | 0.60 | 12 | 0.84 | 0.13 |
| 2 | Pre | 32 | 2.67 | 0.67 | 48 | 1.96 | 0.35 |
| | 1-year post | 20 | 1.16 | 0.49 | 29 | 1.53 | 0.25 |
| | 2-years post | 21 | 1.10 | 0.63 | 39 | 2.39 | 0.23 |
| 3 | Pre | 41 | 2.10 | 0.57 | 23 | 1.51 | 0.33 |
| | 1-year post | 39 | 2.32 | 0.50 | 21 | 0.71 | 0.26 |
| | 2-years post | 30 | 2.17 | 0.52 | 21 | 1.33 | 0.23 |
| 4 | Pre | 44 | 3.46 | 0.60 | 7 | 0.14 | 0.20 |
| | 1-year post | 34 | 1.63 | 0.45 | 6 | 0.23 | 0.14 |
| | 2-years post | 34 | 1.69 | 0.52 | 7 | 0.25 | 0.17 |
| Growing season plots | | | | | | | |
| 5 | Pre | 36 | 1.55 | 0.53 | 7 | 0.21 | 0.19 |
| | 1-year post | 31 | 1.32 | 0.50 | 6 | 0.34 | 0.21 |
| | 2-years post | 35 | 1.55 | 0.50 | 8 | 0.20 | 0.17 |
| 6 | Pre | 43 | 2.56 | 0.87 | 19 | 0.60 | 0.25 |
| | 1-year post | 24 | 1.04 | 0.55 | 15 | 0.54 | 0.17 |
| | 2-years post | 33 | 1.97 | 0.61 | 15 | 0.59 | 0.11 |
| 7 | Pre | 36 | 1.57 | 0.63 | 24 | 1.13 | 0.24 |
| | 1-year post | 24 | 1.48 | 0.51 | 19 | 1.33 | 0.22 |
| | 2-years post | 43 | 1.77 | 0.55 | 23 | 1.10 | 0.25 |
| 8 | Pre | 42 | 2.26 | 0.51 | 38 | 1.80 | 0.29 |
| | 1-year post | 29 | 1.74 | 0.44 | 22 | 1.46 | 0.15 |
| | 2-years post | 26 | 1.71 | 0.50 | 19 | 1.03 | 0.23 |

**Table A-2.** Mean understory live fuel variables for each treatment plots at each sampling time at APSM in mesic longleaf pine flatwoods in northern Florida, US used as inputs to create custom FCCS fuelbeds.

| | | Shrubs | | | Herbs | | |
|---|---|---|---|---|---|---|---|
| Plot No. | Sample time | Cover (%) | Biomass (Mg ha$^{-1}$) | Height (m) | Cover (%) | Biomass (Mg ha$^{-1}$) | Height (m) |
| Dormant season plots | | | | | | | |
| 9 | Pre | 31 | 1.75 | 0.51 | 42 | 1.36 | 0.22 |
| | 1-year post | 35 | 1.59 | 0.38 | 15 | 1.09 | 0.18 |
| | 2-years post | 39 | 2.36 | 0.40 | 20 | 1.24 | 0.16 |
| 10 | Pre | 52 | 2.78 | 0.60 | 4 | 0.10 | 0.25 |
| | 1-year post | 46 | 3.28 | 0.43 | 2 | 0.13 | 0.11 |
| | 2-years post | 58 | 2.43 | 0.51 | 3 | 0.22 | 0.11 |
| 11 | Pre | 57 | 3.58 | 0.53 | 4 | 0.22 | 0.29 |
| | 1-year post | 54 | 2.62 | 0.44 | 4 | 0.19 | 0.10 |
| | 2-years post | 61 | 2.99 | 0.48 | 4 | 0.22 | 0.11 |
| 12 | Pre | 35 | 2.40 | 0.51 | 10 | 0.68 | 0.32 |
| | 1-year post | 32 | 1.83 | 0.39 | 8 | 0.28 | 0.19 |
| | 2-years post | 37 | 2.03 | 0.44 | 8 | 0.26 | 0.16 |
| Growing season plots | | | | | | | |
| 13 | Pre | 43 | 1.61 | 0.43 | 34 | 0.79 | 0.27 |
| | 1-year post | 39 | 1.95 | 0.42 | 11 | 0.75 | 0.22 |
| | 2-years post | 46 | 1.68 | 0.44 | 14 | 0.78 | 0.18 |
| 14 | Pre | 28 | 0.94 | 0.52 | 37 | 0.78 | 0.25 |
| | 1-year post | 29 | 1.37 | 0.48 | 17 | 0.99 | 0.24 |
| | 2-years post | 40 | 1.28 | 0.48 | 25 | 1.14 | 0.27 |
| 15 | Pre | 45 | 2.62 | 0.50 | 9 | 0.64 | 0.28 |
| | 1-year post | 40 | 1.83 | 0.42 | 11 | 0.54 | 0.14 |
| | 2-years post | 54 | 2.11 | 0.42 | 20 | 0.84 | 0.12 |
| 16 | Pre | 67 | 5.15 | 0.63 | 6 | 0.53 | 0.29 |
| | 1-year post | 61 | 4.06 | 0.54 | 5 | 0.28 | 0.13 |
| | 2-years post | 80 | 4.43 | 0.67 | 8 | 0.28 | 0.12 |

**Table A-3.** Mean understory dead fuel variables for each treatment plot each sampling time at EAFB in mesic longleaf pine flatwoods in northern Florida, US used as inputs to create custom FCCS fuelbeds.

| | | Litter | | | Duff | | Woody fuel biomass (Mg ha$^{-1}$) | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Plot No. | Sample time | Cover (%) | Biomass (Mg ha$^{-1}$) | Depth (mm) | Cover (%) | Depth (mm) | 1-hr | 10-hr | 100-hr | 1000-hr |
| Dormant season plots | | | | | | | | | | |
| 1 | Pre | 89 | 3.67 | 23 | 48 | 35 | 0.21 | 0.97 | 1.45 | 10.00 |
| | 1-year post | 88 | 2.39 | 18 | 56 | 23 | 0.10 | 0.76 | 1.13 | 8.83 |
| | 2-years post | 92 | 3.09 | 23 | 42 | 23 | 0.07 | 0.59 | 1.30 | 7.53 |
| 2 | Pre | 53 | 2.66 | 25 | 25 | 11 | 0.13 | 0.51 | 0.77 | 5.52 |
| | 1-year post | 70 | 1.77 | 15 | 28 | 12 | 0.05 | 0.54 | 0.74 | 4.66 |
| | 2-years post | 61 | 2.07 | 15 | 22 | 11 | 0.09 | 0.37 | 0.62 | 4.25 |
| 3 | Pre | 78 | 3.13 | 20 | 68 | 23 | 0.13 | 0.72 | 1.07 | 4.77 |
| | 1-year post | 79 | 3.54 | 23 | 45 | 19 | 0.10 | 0.70 | 0.76 | 4.81 |
| | 2-years post | 80 | 4.39 | 25 | 68 | 19 | 0.08 | 0.42 | 0.82 | 2.65 |
| 4 | Pre | 92 | 3.77 | 28 | 77 | 40 | 0.20 | 0.55 | 1.04 | 0.22 |
| | 1-year post | 93 | 2.42 | 15 | 45 | 33 | 0.16 | 0.67 | 1.05 | 0.22 |
| | 2-years post | 93 | 3.08 | 18 | 46 | 49 | 0.10 | 0.53 | 1.19 | 0.36 |
| Growing season plots | | | | | | | | | | |
| 5 | Pre | 96 | 4.90 | 20 | 44 | 9 | 0.07 | 0.71 | 0.66 | 1.65 |
| | 1-year post | 97 | 2.22 | 15 | 52 | 16 | 0.08 | 0.45 | 0.59 | 0.74 |
| | 2-years post | 96 | 2.92 | 13 | 42 | 15 | 0.05 | 0.52 | 0.59 | 0.84 |
| 6 | Pre | 80 | 3.99 | 25 | 48 | 42 | 0.15 | 0.96 | 1.36 | 4.53 |
| | 1-year post | 88 | 2.18 | 15 | 34 | 27 | 0.13 | 0.89 | 0.88 | 4.11 |
| | 2-years post | 89 | 4.09 | 20 | 49 | 36 | 0.21 | 0.59 | 1.05 | 3.40 |
| 7 | Pre | 79 | 3.19 | 20 | 29 | 14 | 0.06 | 1.00 | 0.31 | 0.65 |
| | 1-year post | 82 | 1.88 | 15 | 20 | 13 | 0.09 | 0.54 | 0.42 | 0.49 |
| | 2-years post | 78 | 2.49 | 13 | 8 | 13 | 0.02 | 0.33 | 0.36 | 0.58 |
| 8 | Pre | 63 | 3.12 | 23 | 18 | 17 | 0.07 | 0.57 | 0.43 | 0.75 |
| | 1-year post | 78 | 1.14 | 13 | 24 | 7 | 0.06 | 0.22 | 0.43 | 0.58 |
| | 2-years post | 82 | 2.29 | 13 | 15 | 17 | 0.04 | 0.17 | 0.51 | 0.11 |

**Table A-4.** Mean understory dead fuel variables for each treatment plot each sampling time at EAFB in mesic longleaf pine flatwoods in northern Florida, US used as inputs to create custom FCCS fuelbeds.

| | | Litter | | | Duff | | Woody fuel biomass (Mg ha$^{-1}$) | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Plot No. | Sample time | Cover (%) | Biomass (Mg ha$^{-1}$) | Depth (mm) | Cover (%) | Depth (mm) | 1-hr | 10-hr | 100-hr | 1000-hr |
| Dormant season plots | | | | | | | | | | |
| 9 | Pre | 57 | 2.11 | 15 | 8 | 13 | 0.04 | 0.36 | 0.32 | 0.26 |
| | 1-year post | 85 | 1.06 | 8 | 2 | 4 | 0.02 | 0.48 | 0.29 | 0.37 |
| | 2-years post | 81 | 2.59 | 8 | 46 | 2 | 0.04 | 0.39 | 0.39 | 0.36 |
| 10 | Pre | 94 | 4.80 | 20 | 35 | 9 | 0.03 | 0.32 | 0.73 | 2.86 |
| | 1-year post | 96 | 1.47 | 10 | 10 | 16 | 0.04 | 0.34 | 0.71 | 2.22 |
| | 2-years post | 96 | 2.93 | 8 | 44 | 4 | 0.04 | 0.29 | 0.88 | 2.27 |
| 11 | Pre | 98 | 4.90 | 23 | 62 | 19 | 0.22 | 0.41 | 0.57 | 1.19 |
| | 1-year post | 99 | 2.00 | 10 | 34 | 6 | 0.06 | 0.57 | 0.62 | 1.11 |
| | 2-years post | 99 | 3.93 | 10 | 78 | 8 | 0.08 | 0.50 | 0.66 | 0.83 |
| 12 | Pre | 91 | 6.52 | 23 | 41 | 8 | 0.08 | 0.73 | 0.54 | 0.61 |
| | 1-year post | 92 | 2.34 | 15 | 24 | 12 | 0.12 | 0.64 | 0.51 | 0.63 |
| | 2-years post | 92 | 4.71 | 10 | 65 | 5 | 0.15 | 0.79 | 0.51 | 0.51 |
| Growing season plots | | | | | | | | | | |
| 13 | Pre | 76 | 2.66 | 13 | 2 | 4 | 0.00 | 0.24 | 0.68 | 1.48 |
| | 1-year post | 93 | 1.53 | 13 | 3 | 10 | 0.01 | 0.35 | 0.57 | 1.05 |
| | 2-years post | 91 | 2.33 | 10 | 22 | 4 | 0.01 | 0.38 | 0.62 | 0.96 |
| 14 | Pre | 73 | 4.01 | 15 | 18 | 7 | 0.01 | 0.37 | 0.80 | 1.43 |
| | 1-year post | 91 | 2.21 | 13 | 20 | 10 | 0.00 | 0.54 | 0.51 | 2.04 |
| | 2-years post | 87 | 3.36 | 15 | 17 | 10 | 0.01 | 0.74 | 0.53 | 1.58 |
| 15 | Pre | 95 | 2.50 | 13 | 12 | 8 | 0.06 | 0.32 | 0.59 | 1.37 |
| | 1-year post | 96 | 1.51 | 10 | 16 | 7 | 0.02 | 0.62 | 0.45 | 0.97 |
| | 2-years post | 94 | 2.57 | 18 | 32 | 9 | 0.07 | 0.61 | 0.54 | 0.75 |
| 16 | Pre | 95 | 2.74 | 13 | 58 | 18 | 0.25 | 0.29 | 0.20 | 1.07 |
| | 1-year post | 98 | 1.37 | 10 | 54 | 13 | 0.10 | 0.50 | 0.29 | 0.76 |
| | 2-years post | 97 | 1.96 | 15 | 38 | 21 | 0.16 | 0.67 | 0.43 | 0.53 |

# Appendix B. Ancillary statistical test results.

**Table B-1.** Season or burn (growing vs. dormant season) and geographic region (APSM vs. EAFB) comparisons of mean (± SE) Maximum Thermocouple Temperature (MTT).

| Treatment | | MTT (˚ C) | *P* |
|---|---|---|---|
| Season-of-burn | | | |
| | Growing season | 403 ± 19 | 0.190 |
| | Dormant season | 443 ± 19 | |
| Geographic region | | | |
| | APSM | 439 ± 21 | 0.299 |
| | EAFB | 407 ± 21 | |

## Appendix C: Paired plot sampling to adjust for phenological differences of live fuels

Post-fire sampling times were spaced at annual increments after treatment burns to allow for a full growing season for vegetation recovery, which resulted in plots being sampled from January to July. This provided equal periods of recovery among plots, but phenological differences in live fuels between plots sampled in the dormant and growing seasons may have been present and could have affected hypothesis testing. Differences in live fuels between the dormant and growing seasons have been observed elsewhere in the southeastern United States (Sparks et al. 2002). We felt that phenological differences in shrubs were minor and limited to cover. At our plots, the majority of understory shrubs (i.e., saw palmetto, gallberry, dwarf live oak, and Darrow's blueberry) were evergreen and unlikely to express strong phenological differences that would affect our response variables. As such, changes in loading and height would be attributable completely to growth rather than seasonal changes and were not tested. However, some deciduous species were present in small numbers including huckleberry (*Gaylussacia* Kunth), gopher apple (*Licania michauxii* Prance), and highbush blueberry (*Vaccinium corymbosum* L.) and this could have significantly influenced cover estimates beyond increases attributable only to growth. The herb layer was dominated by wiregrass which retains foliage throughout the year and phenological differences would likely be limited to height as plants tend to flatten during the dormant season. Some perennial forbs, whose foliage decomposes rapidly after the plant enters dormancy, were also present at our plots. Phenology of these plants could affect cover, fuel loading, and height of the herb layer.

To account for these differences, we sampled 10 paired February (sampled before leaf emergence) and May (leaves fully emerged) subplots at two locations in each region in 2012.

Odd numbered subplots from the main study were used as paired plots. Shrub cover and herb cover and height data were sampled along subplot transects before (February) and after (May) leaf emergence. For herb fuel loading, additional biomass subplots were paired with existing subplots (within 2 m) at locations where density and structure of live fuels were visually similar. Measurements of shrub cover and herb cover, biomass, and height were collected by using the same techniques outlined in the methods (Section 3.3.3). A paired *t* test was conducted to determine whether differences in fuel variables existed between the February and May sampling times (Table C-1). Shrub cover, and herb cover, loading, and height were adjusted by applying the ratio of mean February-to-May values on a weighted scale according to time-since-leaf emergence to plots for which sample times fell between initial leaf emergence (defined as March 15, the beginning of the growing season) and full leaf emergence (defined as May 15) to remove phenological effects. For instance, to adjust a hypothetical plot measured on April 15 with 45 percent shrub cover for phenological differences, the adjustment ratio of 0.822 (Table C-1; February shrub cover divided by May shrub cover from paired plots), is scaled to mid-April by adding it to the product of the ratio of time to full leaf emergence from the sampling date (30 days) to time between initial and full leaf emergence (61 days) and the inverse of the adjustment ratio (1 – 0.822). This gives a time-weighted adjustment ratio of 0.910 (0.822 + (0.492 × 0.178)) and an adjusted shrub cover of 41 percent. Live fuels analyses were re-calculated with adjusted data to test whether the phenological differences in fuels we detected had an effect on statistical results. There was no change in significance for terms in the overall repeated measures analysis of variance tests or post-hoc multiple comparison tests for any live fuel variable (Tables C-2 – C-3).

**Table C-1.** Live fuel ($\bar{x} \pm \mathrm{SE}$) cover, loading, and height for paired February (before leaf emergence) and May (after leaf emergence) plots, results of Student's t-test, and adjustment ratio used for fuels sampled after leaf out (mean ratio value applied on weighted scale based on time-since-leaf emergence).

| Fuel layer | Fuel property | February | May | *P* | Adjustment ratio |
|---|---|---|---|---|---|
| Shrub | Cover (%) | 42.00 ± 9.60 | 51.00 ± 9.40 | <0.001 | 0.822 (0.901) |
| | Loading (Mg $ha^{-1}$) | 2.24 ± 0.83 | 2.42 ± 0.88 | 0.298 | n.a. |
| | Height (m) | 1.30 ± 0.30 | 1.50 ± 0.30 | 0.011 | n.a. |
| Herbaceous | Cover (%) | 17.20 ± 5.60 | 21.20 ± 5.00 | <0.001 | 0.811 (0.893) |
| | Loading (Mg $ha^{-1}$) | 0.84 ± 0.54 | 1.05 ± 0.53 | 0.039 | 0.798 (0.890) |
| | Height (m) | 0.60 ± 0.20 | 0.70 ± 0.20 | 0.080 | 0.906 (0.946) |

**Table C-2.** Comparison of significant terms for overall repeated measures ANOVA statistical tests for raw data and data adjusted for phenological differences in shrub cover and herb cover, and height.

| Fuel stratum | Term | *P* | |
|---|---|---|---|
| | | Raw data | Adjusted data |
| Shrubs | | | |
| Cover (%) | Region | 0.026 | 0.031 |
| | Time | < 0.001 | < 0.001 |
| | Season × time | 0.057 | 0.043 |
| | Region × time | < 0.001 | < 0.001 |
| Herbs | | | |
| Cover (%) | Time | 0.009 | 0.002 |
| Loading (Mg $ha^{-1}$) | No significant terms | n.a. | n.a. |
| Height (m) | Time | < 0.001 | < 0.001 |

**Table C-3.** Comparison of significant terms for Tukey's HSD multiple comparison statistical tests for raw data and data adjusted for phenological differences in shrub cover and herb cover and height.

| Fuel stratum | Term | *P* | |
|---|---|---|---|
| | | Raw data | Adjusted data |
| Shrubs | | | |
| Cover (%) | APSM – 2-year post<br>EAFB – 2-year post | 0.004 | 0.007 |
| Herbs | | | |
| Cover (%) | n.a. | | |
| Height (m) | n.a. | | |

# Appendix D: Site-level biomass data

**Table D-1.** Biomass and percent of total understory biomass by site for all species and plant functional groups. Column A: Biomass (Mg ha$^{-1}$). Column B: Percent of total living aboveground biomass.

| Site | Understory Tree | | *Acer rubrum* | | *Cornus florida* | | *Chionanthus virginicus* | | *Diospyros virginiana* | | *Ilex opaca* | | *Liquidambar styraciflua* | | *Magnolia grandiflora* | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | A | B | A | B | A | B | A | B | A | B | A | B | A | B | A | B |
| A01 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| A02 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| A03 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| A04 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| A05 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| A06 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| A07 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| A08 | 0.01 | 0.33 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| A09 | 0.02 | 0.79 | 0.00 | 0.00 | 0.02 | 0.80 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| A10 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| A11 | 0.01 | 0.50 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| E01 | 0.01 | 0.26 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| E02 | 0.23 | 7.72 | 0.00 | 0.00 | 0.00 | 0.00 | 0.04 | 1.30 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| E03 | 0.19 | 4.24 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| E04 | 0.01 | 0.21 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| E05 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| E06 | 0.01 | 0.37 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| E07 | 0.02 | 1.06 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.02 | 0.90 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| E08 | 0.00 | 0.12 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| E09 | 0.14 | 4.15 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| E11 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |

**Table D-1 (cont.).** Biomass and percent of total understory biomass by site for all species and plant functional groups. Column A: Biomass (Mg ha$^{-1}$). Column B: Percent of total living aboveground biomass.

| Site | *Magnolia virginiana* | | *Pinus elliottii* | | *Pinus serotina* | | *Rhus copallinum* | | *Symplocos tinctoria* | | Shrub | | *Aronia arbutifolia* | | *Asimina angustifolia* | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | A | B | A | B | A | B | A | B | A | B | A | B | A | B | A | B |
| A01 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 1.54 | 62.73 | 0.01 | 0.40 | 0.00 | 0.00 |
| A02 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 3.27 | 86.95 | 0.00 | 0.00 | 0.00 | 0.00 |
| A03 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 4.31 | 79.75 | 0.00 | 0.00 | 0.00 | 0.00 |
| A04 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 2.20 | 67.48 | 0.00 | 0.00 | 0.00 | 0.00 |
| A05 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 2.45 | 63.65 | 0.00 | 0.00 | 0.00 | 0.00 |
| A06 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 2.70 | 69.09 | 0.00 | 0.00 | 0.00 | 0.00 |
| A07 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 2.80 | 90.22 | 0.00 | 0.00 | 0.00 | 0.00 |
| A08 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 2.40 | 71.23 | 0.00 | 0.00 | 0.00 | 0.00 |
| A09 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 1.30 | 48.73 | 0.00 | 0.00 | 0.00 | 0.00 |
| A10 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 1.61 | 63.04 | 0.00 | 0.00 | 0.00 | 0.00 |
| A11 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 2.33 | 90.36 | 0.00 | 0.00 | 0.00 | 0.00 |
| E01 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 1.48 | 70.70 | 0.00 | 0.00 | 0.00 | 0.00 |
| E02 | 0.06 | 2.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.01 | 0.30 | 0.01 | 3.30 | 1.62 | 54.34 | 0.00 | 0.00 | 0.00 | 0.00 |
| E03 | 0.06 | 1.30 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 3.28 | 71.66 | 0.00 | 0.00 | 0.00 | 0.00 |
| E04 | 0.01 | 0.30 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 2.47 | 62.52 | 0.02 | 0.50 | 0.00 | 0.00 |
| E05 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 1.73 | 53.43 | 0.00 | 0.00 | 0.00 | 0.00 |
| E06 | 0.01 | 0.30 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 1.11 | 30.92 | 0.00 | 0.00 | 0.00 | 0.00 |
| E07 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 1.69 | 79.01 | 0.00 | 0.00 | 0.00 | 0.00 |
| E08 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 1.79 | 61.48 | 0.00 | 0.00 | 0.00 | 0.00 |
| E09 | 0.14 | 4.20 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 2.33 | 69.31 | 0.00 | 0.00 | 0.00 | 0.00 |
| E11 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 3.43 | 86.99 | 0.00 | 0.00 | 0.00 | 0.00 |

**Table D-1 (cont.).** Biomass and percent of total understory biomass by site for all species and plant functional groups. Column A: Biomass (Mg ha$^{-1}$). Column B: Percent of total living aboveground biomass.

| Site | *Baccharis halimifolia* | | *Callicarpa americana* | | *Clethra alnifolia* | | *Clinopodium coccineum* | | *Conradina canescens* | | *Cyrilla racemiflora* | | *Garberia heterophylla* | | *Hypericum hypericoides* | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | A | B | A | B | A | B | A | B | A | B | A | B | A | B | A | B |
| A01 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.03 | 1.2 | 0.00 | 0.00 | 0.03 | 1.20 |
| A02 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| A03 | 0.00 | 0.00 | 0.00 | 0.00 | 0.04 | 0.70 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.01 | 0.20 |
| A04 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.01 | 0.30 |
| A05 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.01 | 0.30 |
| A06 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| A07 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| A08 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| A09 | 0.00 | 0.00 | 0.01 | 0.40 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| A10 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| A11 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.02 | 0.80 | 0.00 | 0.00 | 0.01 | 0.40 |
| E01 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| E02 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| E03 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| E04 | 0.00 | 0.00 | 0.00 | 0.00 | 0.01 | 0.30 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| E05 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| E06 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| E07 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| E08 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.01 | 0.30 |
| E09 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| E11 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |

**Table D-1 (cont.).** Biomass and percent of total understory biomass by site for all species and plant functional groups. Column A: Biomass (Mg ha$^{-1}$). Column B: Percent of total living aboveground biomass.

| Site | *Hypericum tetrapetalum* | | *Ilex coriacea* | | *Ilex glabra* | | *Ilex vomitoria* | | *Lyonia ferruginea* | | *Lyonia lucida* | | *Morella cerifera* | | *Quercus minima* | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | A | B | A | B | A | B | A | B | A | B | A | B | A | B | A | B |
| A01 | 0.00 | 0.00 | 0.00 | 0.00 | 0.65 | 26.40 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.01 | 0.40 | 0.55 | 22.40 |
| A02 | 0.00 | 0.00 | 0.00 | 0.00 | 0.10 | 2.70 | 0.00 | 0.00 | 0.53 | 14.10 | 0.01 | 0.30 | 0.04 | 1.11 | 0.95 | 25.30 |
| A03 | 0.00 | 0.00 | 0.00 | 0.00 | 1.13 | 21.0. | 0.00 | 0.00 | 0.84 | 15.60 | 0.00 | 0.00 | 0.00 | 0.00 | 0.62 | 11.50 |
| A04 | 0.00 | 0.00 | 0.00 | 0.00 | 0.25 | 7.60 | 0.00 | 0.00 | 0.23 | 7.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.94 | 28.70 |
| A05 | 0.00 | 0.00 | 0.00 | 0.00 | 0.12 | 3.10 | 0.00 | 0.00 | 0.99 | 25.80 | 0.00 | 0.00 | 0.04 | 1.00 | 0.70 | 18.50 |
| A06 | 0.00 | 0.00 | 0.06 | 1.60 | 0.23 | 5.90 | 0.00 | 0.00 | 0.93 | 24.00 | 0.00 | 0.00 | 0.03 | 0.80 | 0.67 | 17.80 |
| A07 | 0.00 | 0.00 | 0.00 | 0.00 | 0.21 | 6.70 | 0.00 | 0.00 | 0.05 | 1.60 | 0.00 | 0.00 | 0.00 | 0.00 | 0.94 | 30.10 |
| A08 | 0.00 | 0.00 | 0.00 | 0.00 | 0.24 | 7.10 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 1.36 | 40.50 |
| A09 | 0.00 | 0.00 | 0.00 | 0.00 | 0.06 | 2.30 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.01 | 0.40 | 0.46 | 17.30 |
| A10 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 1.27 | 49.80 |
| A11 | 0.00 | 0.00 | 0.00 | 0.00 | 0.16 | 6.20 | 0.00 | 0.00 | 0.19 | 7.40 | 0.07 | 2.70 | 0.05 | 1.90 | 1.33 | 51.60 |
| E01 | 0.00 | 0.00 | 0.00 | 0.00 | 0.79 | 38.0 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.22 | 10.60 |
| E02 | 0.00 | 0.00 | 0.17 | 5.70 | 0.46 | 15.30 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.15 | 5.00 |
| E03 | 0.00 | 0.00 | 0.00 | 0.00 | 0.91 | 20.00 | 0.00 | 0.00 | 0.54 | 11.80 | 0.00 | 0.00 | 0.00 | 0.00 | 0.79 | 17.10 |
| E04 | 0.00 | 0.00 | 0.25 | 6.30 | 0.74 | 18.80 | 0.01 | 0.30 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.12 | 3.00 |
| E05 | 0.00 | 0.00 | 0.03 | 0.90 | 0.16 | 5.00 | 0.04 | 1.20 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.62 | 19.20 |
| E06 | 0.00 | 0.00 | 0.00 | 0.00 | 0.81 | 22.60 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.09 | 2.50 |
| E07 | 0.00 | 0.00 | 0.04 | 1.90 | 0.41 | 19.10 | 0.00 | 0.00 | 0.08 | 3.70 | 0.04 | 1.90 | 0.00 | 0.00 | 0.08 | 3.70 |
| E08 | 0.00 | 0.00 | 0.00 | 0.00 | 0.60 | 20.50 | 0.04 | 1.40 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.62 | 21.20 |
| E09 | 0.00 | 0.00 | 0.00 | 0.00 | 0.50 | 14.90 | 0.10 | 3.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.20 | 6.00 |
| E11 | 0.00 | 0.00 | 0.05 | 1.30 | 0.29 | 7.40 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 2.15 | 54.70 |

**Table D-1 (cont.).** Biomass and percent of total understory biomass by site for all species and plant functional groups. Column A: Biomass (Mg ha$^{-1}$). Column B: Percent of total living aboveground biomass.

| Site | *Quercus* spp. | | *Serenoa repens* | | *Vaccinium arboreum* | | *Vaccinium corymbosum* | | Vine | | *Gelsemium sempervirens* | | *Smilax auriculata* | | *Toxicodendron radicans* | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | A | B | A | B | A | B | A | B | A | B | A | B | A | B | A | B |
| A01 | 0.03 | 1.20 | 0.00 | 0.00 | 0.06 | 2.40 | 0.00 | 0.00 | 0.03 | 1.32 | 0.00 | 0.00 | 0.03 | 1.20 | 0.00 | 0.00 |
| A02 | 0.39 | 10.40 | 0.95 | 25.30 | 0.00 | 0.00 | 0.00 | 0.00 | 0.02 | 0.46 | 0.00 | 0.00 | 0.02 | 0.50 | 0.00 | 0.00 |
| A03 | 0.10 | 1.90 | 1.30 | 24.10 | 0.00 | 0.00 | 0.01 | 0.20 | 0.00 | 0.02 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| A04 | 0.00 | 0.00 | 0.74 | 22.60 | 0.00 | 0.00 | 0.00 | 0.00 | 0.01 | 0.20 | 0.00 | 0.00 | 0.01 | 0.30 | 0.00 | 0.00 |
| A05 | 0.00 | 0.00 | 0.45 | 11.70 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| A06 | 0.03 | 0.80 | 0.53 | 13.70 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.13 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| A07 | 0.18 | 5.80 | 1.30 | 41.30 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.01 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| A08 | 0.21 | 6.20 | 0.46 | 13.70 | 0.01 | 0.30 | 0.00 | 0.00 | 0.06 | 1.67 | 0.03 | 0.90 | 0.02 | 0.60 | 0.00 | 0.00 |
| A09 | 0.14 | 5.30 | 0.58 | 21.80 | 0.00 | 0.00 | 0.00 | 0.00 | 0.15 | 5.42 | 0.00 | 0.00 | 0.14 | 5.30 | 0.00 | 0.00 |
| A10 | 0.03 | 1.20 | 0.24 | 9.40 | 0.03 | 1.20 | 0.00 | 0.00 | 0.02 | 0.62 | 0.00 | 0.00 | 0.02 | 0.80 | 0.00 | 0.00 |
| A11 | 0.01 | 0.40 | 0.51 | 19.80 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| E01 | 0.05 | 2.40 | 0.28 | 13.50 | 0.03 | 1.40 | 0.00 | 0.00 | 0.16 | 7.51 | 0.13 | 6.20 | 0.03 | 1.40 | 0.00 | 0.00 |
| E02 | 0.11 | 3.70 | 0.47 | 15.70 | 0.02 | 0.70 | 0.02 | 0.70 | 0.25 | 8.43 | 0.01 | 3.30 | 0.04 | 1.30 | 0.00 | 0.00 |
| E03 | 0.43 | 9.40 | 0.56 | 12.30 | 0.00 | 0.00 | 0.00 | 0.00 | 0.29 | 6.36 | 0.05 | 1.10 | 0.17 | 3.70 | 0.00 | 0.00 |
| E04 | 0.00 | 0.00 | 1.07 | 27.20 | 0.09 | 2.30 | 0.10 | 2.50 | 0.01 | 0.32 | 0.00 | 0.00 | 0.01 | 0.30 | 0.00 | 0.00 |
| E05 | 0.11 | 3.40 | 0.59 | 18.30 | 0.00 | 0.00 | 0.00 | 0.00 | 0.39 | 11.98 | 0.38 | 11.80 | 0.00 | 0.00 | 0.00 | 0.00 |
| E06 | 0.00 | 0.00 | 0.16 | 4.50 | 0.00 | 0.00 | 0.01 | 0.30 | 0.00 | 0.06 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| E07 | 0.04 | 1.90 | 0.85 | 39.50 | 0.00 | 0.00 | 0.00 | 0.00 | 0.01 | 0.52 | 0.00 | 0.00 | 0.01 | 0.50 | 0.00 | 0.00 |
| E08 | 0.01 | 0.30 | 0.40 | 14.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.03 | 1.03 | 0.00 | 0.00 | 0.02 | 0.70 | 0.00 | 0.00 |
| E09 | 0.07 | 2.10 | 0.25 | 7.40 | 0.02 | 0.60 | 0.43 | 12.8 | 0.30 | 8.93 | 0.02 | 0.60 | 0.19 | 5.70 | 0.00 | 0.00 |
| E11 | 0.03 | 0.80 | 0.70 | 18.10 | 0.00 | 0.00 | 0.01 | 0.30 | 0.03 | 0.81 | 0.00 | 0.00 | 0.03 | 0.80 | 0.00 | 0.00 |

**Table D-1 (cont.).** Biomass and percent of total understory biomass by site for all species and plant functional groups. Column A: Biomass (Mg ha$^{-1}$). Column B: Percent of total living aboveground biomass.

| Site | *Vitis rotundifolia* | | Sub-shrub | | *Gaylussacia dumosa* | | *Kalmia hirsuta* | | *Licania michauxii* | | *Vaccinium darrowii* | | *Yucca filamentosa* | | Graminoid | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | A | B | A | B | A | B | A | B | A | B | A | B | A | B | A | B |
| A01 | 0.00 | 0.00 | 0.62 | 25.28 | 0.05 | 2.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.57 | 23.20 | 0.00 | 0.00 | 0.23 | 9.54 |
| A02 | 0.00 | 0.00 | 0.25 | 6.77 | 0.04 | 1.10 | 0.00 | 0.00 | 0.00 | 0.00 | 0.21 | 5.60 | 0.00 | 0.00 | 0.08 | 2.10 |
| A03 | 0.00 | 0.00 | 0.81 | 14.96 | 0.23 | 4.30 | 0.02 | 0.40 | 0.00 | 0.00 | 0.55 | 10.2 | 0.00 | 0.00 | 0.10 | 1.86 |
| A04 | 0.00 | 0.00 | 0.21 | 6.46 | 0.04 | 1.20 | 0.00 | 0.00 | 0.00 | 0.00 | 0.17 | 5.20 | 0.00 | 0.00 | 0.48 | 14.73 |
| A05 | 0.00 | 0.00 | 0.16 | 4.06 | 0.08 | 2.10 | 0.00 | 0.00 | 0.00 | 0.00 | 0.07 | 1.80 | 0.00 | 0.00 | 1.09 | 28.43 |
| A06 | 0.00 | 0.00 | 0.18 | 4.63 | 0.07 | 1.80 | 0.00 | 0.00 | 0.00 | 0.00 | 0.11 | 2.80 | 0.00 | 0.00 | 0.89 | 22.93 |
| A07 | 0.00 | 0.00 | 0.08 | 2.64 | 0.04 | 1.30 | 0.00 | 0.00 | 0.00 | 0.00 | 0.05 | 1.60 | 0.00 | 0.00 | 0.20 | 6.36 |
| A08 | 0.00 | 0.00 | 0.15 | 4.32 | 0.04 | 1.20 | 0.00 | 0.00 | 0.00 | 0.00 | 0.11 | 3.30 | 0.00 | 0.00 | 0.60 | 17.75 |
| A09 | 0.00 | 0.00 | 0.06 | 2.38 | 0.04 | 1.50 | 0.00 | 0.00 | 0.00 | 0.00 | 0.02 | 0.80 | 0.00 | 0.00 | 0.65 | 24.25 |
| A10 | 0.00 | 0.00 | 0.15 | 5.70 | 0.02 | 0.80 | 0.00 | 0.00 | 0.00 | 0.00 | 0.12 | 4.70 | 0.00 | 0.00 | 0.57 | 22.17 |
| A11 | 0.00 | 0.00 | 0.14 | 5.32 | 0.01 | 0.40 | 0.00 | 0.00 | 0.00 | 0.00 | 0.13 | 5.00 | 0.00 | 0.00 | 0.08 | 2.95 |
| E01 | 0.00 | 0.00 | 0.20 | 9.57 | 0.03 | 1.40 | 0.08 | 3.80 | 0.00 | 0.00 | 0.09 | 4.30 | 0.00 | 0.00 | 0.22 | 10.43 |
| E02 | 0.11 | 3.70 | 0.04 | 1.42 | 0.01 | 0.30 | 0.00 | 0.00 | 0.00 | 0.20 | 0.04 | 1.30 | 0.00 | 0.00 | 0.64 | 21.48 |
| E03 | 0.07 | 1.50 | 0.35 | 7.70 | 0.06 | 1.30 | 0.00 | 0.00 | 0.01 | 0.80 | 0.28 | 6.10 | 0.00 | 0.00 | 0.45 | 9.73 |
| E04 | 0.00 | 0.00 | 0.12 | 3.15 | 0.01 | 0.30 | 0.00 | 0.00 | 0.03 | 0.00 | 0.09 | 2.30 | 0.00 | 0.00 | 1.32 | 33.50 |
| E05 | 0.00 | 0.00 | 0.02 | 0.57 | 0.02 | 0.60 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 1.01 | 31.27 |
| E06 | 0.00 | 0.00 | 0.07 | 1.99 | 0.07 | 1.90 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 2.33 | 64.87 |
| E07 | 0.00 | 0.00 | 0.22 | 10.13 | 0.14 | 6.50 | 0.00 | 0.00 | 0.00 | 0.00 | 0.07 | 3.30 | 0.00 | 0.00 | 0.14 | 6.6 |
| E08 | 0.01 | 0.30 | 0.06 | 1.90 | 0.02 | 0.70 | 0.00 | 0.00 | 0.02 | 0.70 | 0.01 | 0.30 | 0.00 | 0.00 | 0.95 | 32.53 |
| E09 | 0.08 | 2.40 | 0.01 | 0.21 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.46 | 13.61 |
| E11 | 0.00 | 0.00 | 0.02 | 0.56 | 0.02 | 0.50 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.40 | 10.11 |

**Table D-1.** Biomass and percent of total understory biomass by site for all species and plant functional groups. Column A: Biomass (Mg ha-1). Column B: Percent of total living aboveground biomass.

| Site | *Andropogon glaucopsis* | | *Aristida beyrichiana* | | Forb | |
|---|---|---|---|---|---|---|
| | A | B | A | B | A | B |
| A01 | 0.07 | 2.80 | 0.02 | 0.80 | 0.03 | 1.13 |
| A02 | 0.00 | 0.00 | 0.05 | 1.30 | 0.14 | 3.72 |
| A03 | 0.00 | 0.00 | 0.02 | 0.40 | 0.18 | 3.41 |
| A04 | 0.00 | 0.00 | 0.34 | 10.40 | 0.36 | 11.13 |
| A05 | 0.00 | 0.00 | 0.59 | 15.40 | 0.15 | 3.86 |
| A06 | 0.01 | 0.30 | 0.51 | 13.20 | 0.13 | 3.22 |
| A07 | 0.00 | 0.00 | 0.19 | 6.10 | 0.02 | 0.77 |
| A08 | 0.00 | 0.00 | 0.50 | 14.60 | 0.16 | 4.69 |
| A09 | 0.03 | 1.10 | 0.55 | 20.70 | 0.49 | 18.43 |
| A10 | 0.01 | 0.40 | 0.52 | 20.40 | 0.22 | 8.48 |
| A11 | 0.00 | 0.00 | 0.07 | 2.70 | 0.02 | 0.86 |
| E01 | 0.07 | 3.40 | 0.08 | 3.80 | 0.03 | 1.53 |
| E02 | 0.37 | 12.30 | 0.17 | 5.70 | 0.20 | 6.61 |
| E03 | 0.12 | 2.60 | 0.13 | 2.90 | 0.01 | 0.32 |
| E04 | 0.03 | 0.80 | 1.23 | 31.20 | 0.01 | 0.31 |
| E05 | 0.06 | 1.90 | 0.78 | 24.10 | 0.09 | 2.75 |
| E06 | 0.24 | 6.70 | 0.81 | 50.70 | 0.06 | 1.79 |
| E07 | 0.11 | 5.10 | 0.03 | 1.40 | 0.06 | 2.68 |
| E08 | 0.15 | 5.10 | 0.72 | 24.70 | 0.09 | 3.04 |
| E09 | 0.17 | 5.10 | 0.25 | 7.40 | 0.13 | 3.80 |
| E11 | 0.03 | 0.80 | 0.27 | 6.90 | 0.06 | 1.52 |