



Seasonality of Biennial Burning Has No Adverse Effects on Mature Longleaf Pine Survival or Productivity

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Emulating natural disturbance has become an increasingly important restoration strategy. In the fire-maintained woodlands of the southeastern United States, contemporary restoration efforts have focused on approximating the historical fire regime by burning at short intervals. Due to concerns over escape and damage to mature trees, most prescribed burning has occurred in the dormant season, which is inconsistent with the historical prevalence of lightning-initiated fire in the region. This discordance between contemporary prescribed burning and what is thought to be the historical fire regime has led some to question whether dormant season burning should remain the most common management practice; however, little is known about the long-term effects of repeated growing season burning on the health and productivity of desirable tree species. To address this question, we report on a long-term experiment comparing the effects of seasonal biennial burning (winter, spring, and summer) and no burning on the final survival status, height, diameter, and volume growth of 892 mature longleaf pine (*Pinus palustris*) over 23 years in three mature even-aged stands in southern Alabama, United States. Overall, longleaf pine survival across all treatments averaged $81 \pm 2\%$ [s.e.]. Among seasonal burn treatments, survival was highest in the spring burns ($82 \pm 4\%$) but did not vary significantly from any other treatment (summer – $79 \pm 4\%$, winter – $81 \pm 4\%$, unburned – $84 \pm 4\%$). However, survival was statistically influenced by initial diameter at breast height, as survival of trees in the largest size class (30 cm) was 40% higher than trees in the smallest size class (5 cm). Productivity of longleaf pine was not significantly different among treatment averages in terms of volume ($38.9\text{--}44.1 \pm 6.0 \text{ m}^3 \text{ ha}^{-1}$), diameter ($6.0\text{--}6.7 \pm 0.3 \text{ cm}$), and height ($2.5\text{--}3.4 \pm 0.4 \text{ m}$) growth. Collectively, our results demonstrate that burning outside the dormant season will have little impact on mature longleaf pine survival and growth. This finding has important implications for the maintenance of restored southeastern woodlands, as interest in burning outside the dormant season continues to grow.

Keywords: *Pinus palustris*, woodland restoration pine, seasonal burning, prescribed fire, productivity

INTRODUCTION

Restoring degraded woodlands has become an international conservation priority (Dey et al., 2017; Buisson et al., 2019; Gordon et al., 2020). Prescribed fire often plays a key role in restoration prescriptions. Efforts to reestablish historical burning regimes have appropriately focused on fire frequency, which has been shown to have prominent effects on ecosystem response (Mitchell et al., 2006). For example, frequent, low intensity surface fire (2–4 years) is generally recommended for maintaining forest structure and promoting understory diversity in the longleaf pine ecosystem of the southeastern United States (Van Lear et al., 2005). However, a lack of consideration for other factors, such as fire season, may result in undesirable restoration outcomes. In fact, there is growing concern that contemporary burning operations are oversimplified and may be adversely affecting wildlife habitat and diversity (Lashley et al., 2015, 2017; Darracq et al., 2016; Hiers et al., 2016).

Prior to European settlement, fires in the southeastern United States were often created by lightning strikes in the growing season (Robbins and Myers, 1992; Outcalt, 2008; Ryan et al., 2013). Although application of prescribed fire in the growing season has increased over the past three decades (Ferguson, 1998; Cronan et al., 2015), dormant season burning remains the most common practice to mitigate risk (Stanturf et al., 2002; Knapp et al., 2009). This discordance in seasonal burning could have implications for fire behavior and subsequent fire effects. For example, while the risk of crown scorch increases with ambient temperature, growing season burns typically occur with lower available fuel loads, higher relative humidity, higher fine fuel moisture contributed by green herbaceous plants, and result in lower fire intensity compared to dormant season burns (Sparks et al., 2002; Govender et al., 2006). Moreover, growing season burns are considered beneficial for controlling hardwood encroachment and promoting wiregrass (*Aristida stricta*) reproduction, which are often objectives in woodland restoration (Outcalt, 1994; Glitzenstein et al., 1995; Haywood et al., 2001; Robertson and Hmielowski, 2014; Addington et al., 2015).

While burning outside the dormant season corresponds more closely with historical burning patterns and may be beneficial for certain aspects of ecological restoration, concerns remain about the long-term impacts of repeated growing season fire on overstory health and productivity. Limiting root damage is an important consideration for protecting desirable tree species during prescribed burning (Hood et al., 2018). Longleaf pine (*Pinus palustris*), a foundational tree species in southeastern woodlands, is well-adapted to survive surface fire but is not impervious to fire effects (Boyer, 1990). Previous research has indicated that growing season burns can inhibit root growth leading to speculation that dormant season burns are preferable for maintaining longleaf pine productivity (Sayer and Haywood, 2006). Growing season burns may also negatively affect non-structural carbohydrate stocks, which could further constrain recovery and productivity (Guo et al., 2004; Sayer et al., 2020). Such negative effects may be magnified in locations where fire has long-been excluded,

as burning in stands with accumulated understory vegetation and duff can produce higher fire intensity (Menges and Deyrup, 2001), reduce non-structural carbohydrate reserves (Varner et al., 2009), and enhance post-fire physiological stress (O'Brien et al., 2010).

Recent evidence documenting the effects of fire seasonality on longleaf pine productivity has been inconclusive. After 10 years of dormant and growing-season biennial burning in young stands, Boyer (1987) reported an overall loss of productivity from burning but that burn season was of little consequence. Similarly, longleaf pine growth has been shown to recover rapidly after growing season burns regardless of fire frequency (Ford et al., 2010). However, after 37 years of growing-season biennial burning, Haywood et al. (2001) reported that summer burned longleaf pine were shorter and contained less volume than those burned in late spring. While our understanding of seasonal burning on longleaf pine productivity has improved, to our knowledge, no studies have examined the effects of repeated seasonal biennial burning at the latter stages of a timber rotation. Moreover, while it is generally accepted that the risk of mortality decreases with increasing size (Hare, 1965; Jackson et al., 1999; Hood et al., 2018), little is known if this relationship varies with fire season.

To answer these questions, we build upon a long-term experiment (Boyer, 1987) to assess survival and growth of longleaf pine after 23-years of seasonal biennial burning (winter, spring, and summer) and an unburned treatment in three 37-year-old even-aged stands in southern Alabama, United States. Specifically, we asked whether: (1) biennial burning outside the dormant season will negatively affect longleaf pine survival and productivity and, (2) fire resistance increases with tree size in all burn seasons. We hypothesized that: (1) burning outside the dormant season will not affect longleaf pine survival and productivity and, (2) fire resistance will increase with tree size in all burn seasons. The results of this study will contribute to our functional understanding of seasonal burning in the longleaf pine ecosystem and will address a fundamental debate surrounding the application of prescribed fire in the southeastern United States.

MATERIALS AND METHODS

Site Description

The study was conducted at the Escambia Experimental Forest near Brewton, Alabama, United States (31°01'N, 87°04'W). The climate is classified as humid subtropical with the hottest average temperatures occurring in August (22.7–32.8°C) and the coldest in January (4.4–16.7°C). Average growing season length is 250 days. Precipitation occurs almost exclusively in the form of rain and is abundant throughout the year (1,680 mm annual average). Soils at the site are generally classified as belonging to the Troup Series (loamy, kaolinitic, and thermic Grossarenic Kandiodults), which consist of sandy and loamy sediments that are somewhat excessively drained. Naturally regenerated longleaf pine is the dominant tree species at the site in

stands receiving frequent prescribed fire (3-year return interval) (approximately 95% of the experimental forest). In stands where fire is less frequent or is excluded (approximately 5% of the experimental forest) longleaf pine occurs in a mixture of water oak (*Quercus nigra*), dogwood (*Cornus florida*), and sweetgum (*Liquidambar styraciflua*). The understory is dominated by a mix of shrub and herbaceous species primarily consisting of gallberry (*Ilex* spp.), bracken fern (*Pteridium aquilinum*), shiny blueberry (*Vaccinium myrsinites*), narrowleaf silkgrass (*Pityopsis graminifolia*), gopher apple (*Geobalanus oblongifolius*), and greenbriers (*Smilax* spp.). Site index for longleaf pine is estimated to be 25 m at age 50.

Experimental Design and Field Measurements

The study was originally established by Boyer (1987). Three even-aged longleaf pine stands (hereafter referred to as blocks) were used in the experiment. Each block naturally regenerated from the 1957–1958 seed crop with a seed tree harvest. At the initiation of the study in 1973 (stand age 15), the blocks were thinned to an average density of 1,236 trees ha⁻¹. Twelve plots (0.16 ha) were established in each block and randomly assigned a treatment featuring fully crossed combinations of four seasonal biennial burning and three non-fire hardwood control methods in a randomized complete block design. The plots were square and located adjacent to each other within the blocks. Season of biennial burning (hereafter referred to as seasonal burning treatments) included winter (November–March), spring (April–May), summer (July–August), and an unburned treatment. Biennial burning began in 1974 and continued through 2018 (22 total burns). Burning was primarily applied as a strip head fire with flame lengths averaging <1 m and a rate of spread <2 m min⁻¹. Non-fire hardwood control methods considered were 2, 4-D (a phenoxy herbicide, all woody stems in 1973), mechanical (hand clearing all woody stems > 1.3 m in height every 5 years), and no hardwood control. In 1990 (stand age 32), each plot was thinned to approximately 16–17 m² ha⁻¹ to reduce intraspecific competition.

In this report, the effect of non-fire hardwood control treatments was not considered, as they did not initially influence any growth metric (Boyer, 1987) and were not found to be statistically significant in preliminary analyses. Therefore, all non-fire hardwood control treatments were pooled within seasonal burning treatments in a split-plot design (three seasonal burn replicates per block). Beginning in 1995 (stand age 37), we remeasured total height (m) with a hypsometer, diameter (cm) at breast height (1.37 m) with a diameter tape, and visually assessed survival status of marked longleaf pine trees in an internal measurement plot (0.1 ha) (Figure 1). Additional measurements of each metric were also taken in 1998, 2003, 2009, 2014, and 2018. Survival was determined by the presence of a living crown. Changes in growth and survival were calculated over the entire 23-year increment (1995–2018). At the start of this study, average longleaf pine diameter and height across treatments ranged from 19.3–22.1 cm and 20.0–22.2 m, respectively. For further detail on the experimental design see Boyer (1987) or Kush et al. (1999).

Statistical Methods

We used a mixed-effects analysis of variance (ANOVA) to compare the height, diameter, volume growth, and final survival percentage of longleaf pine established in different seasonal burning treatments over 23 years (1995–2018). Prior to analysis, all metrics of growth and survival were averaged at the plot level. Additionally, all longleaf pine that died over the duration of the experiment were removed from the height, diameter, and volume analyses. In each model, seasonal burning treatment was considered a fixed effect, while the interaction between block and seasonal burning treatment was considered a random effect. Significant treatment effects were further investigated with Tukey's adjusted multiple comparison tests. Differences among seasonal treatments were considered significant at $\alpha = 0.05$. These analyses were performed with the MIXED procedure in SAS 9.4 software (SAS Institute, Cary, NC, United States).

A generalized linear mixed-effects logistic regression was used to explore the effect of initial size on final survival status (1995–2018). The model assumed a binomial distribution with a logit link and estimated the probability of survival of individual longleaf pine ($n = 892$) with an odds ratio statistic. Parameter estimation was accomplished through Laplace approximation. Fixed effects in the model included seasonal burning treatment, initial diameter (tree age 37), and the interaction between seasonal burning treatment and initial diameter. The interaction between block and seasonal burning treatment was considered a random effect in the model. Factors were considered statistically significant at $\alpha = 0.05$. This analysis was performed with the GLIMMIX procedure in SAS 9.4 software (SAS Institute, Cary, NC, United States).

RESULTS

Treatment Effects on Growth

Over 23 years, longleaf pine diameter growth averaged across all treatments was 6.1 ± 0.3 cm (30% increase). Diameter growth of longleaf pine ranged from 6.0 – 6.7 ± 0.3 cm and did not differ statistically among treatments ($F = 0.51$, $P = 0.6889$, Hedges' $g = 0.39$) (Table 1 and Figure 2). Overall, longleaf pine height growth averaged 3.0 ± 0.2 m across all treatments (14% increase). Among treatments, height growth ranged from 2.5 – 3.4 ± 0.4 m and was not statistically significant ($F = 0.95$, $P = 0.4630$, Hedges' $g = 0.53$) (Table 1 and Figure 2). Longleaf pine volume growth across all treatments averaged 41.0 ± 3.0 m³ ha⁻¹ (62% increase). Volume growth ranged from 38.9 – 44.1 ± 6.0 m³ ha⁻¹ and did not differ significantly among treatments ($F = 0.14$, $P = 0.9357$, Hedges' $g = 0.20$) (Table 1 and Figure 2).

Survival

Overall, longleaf pine survival averaged across all treatments was $81 \pm 2\%$. Longleaf pine survival ranged from 79 – $84 \pm 4\%$ and did not differ statistically among treatments ($F = 0.17$, $P = 0.9138$, Hedges' $g = 0.22$) (Table 1 and Figure 2). Initial diameter had a statistically significant positive association with survival across all treatments ($F = 19.43$, $P < 0.0001$) (Table 2 and Figure 3). The positive effect of initial diameter on survival was more evident



FIGURE 1 | An example of a 0.1 ha measurement plot in a winter biennial burn treatment.

TABLE 1 | Results of mixed-effects analyses of variance (ANOVA) for the effect of seasonal biennial fire (winter, spring, summer) and the unburned treatment on longleaf pine diameter growth, height growth, volume growth, and survival.

Response variable	Effect	Degrees of freedom	F ratio	Prob > F
Diameter growth	Seasonal biennial burning	3, 8	0.51	0.6889
Height growth	Seasonal biennial burning	3, 8	0.95	0.4630
Volume growth	Seasonal biennial burning	3, 8	0.14	0.9357
Survival	Seasonal biennial burning	3, 8	0.17	0.9138

Effects < 0.05 were considered statistically significant.

in the winter and growing season burns compared to spring burns and the unburned treatment (data not shown); however, the interaction between initial diameter and seasonal treatment was not statistically significant ($F = 1.35$, $P = 0.2558$) (Table 2).

DISCUSSION

Dormant season burning has been a conventional management practice in the southeastern United States for decades. The rationale behind this paradigm is partially based on an ingrained cultural belief that growing season burning presents a greater risk to productivity than dormant season burning (Cary, 1932; Garren, 1943). Yet, studies examining the effects of seasonal burning on longleaf pine have produced conflicting evidence supporting (Haywood et al., 2001) and refuting this notion (Boyer, 1987; Ford et al., 2010). Our results indicate that biennially burned longleaf pine diameter, height, and volume

growth were not affected by burn season, and thus provide further evidence that fire seasonality has little influence on longleaf pine productivity in a biennial burning regime. Finally, at least under the conditions of fire application and behavior studied, fire seasonality had no discernable impact on longleaf pine survival indicating that burning outside the dormant season does not inherently increase the risk of mortality in mature longleaf pine. However, it should be recognized that prescribed burning in this study was applied under favorable climatic conditions with conservative ignition techniques to minimize crown scorch. Burning under less-optimal conditions or with different ignition patterns may have resulted in a different outcome.

Two factors may have strongly contributed to our results. First, the trees evaluated in this experiment were 37 years-old at the start of the sampling period, and therefore likely possessed sufficient bark thickness and crown height to confer resistance to surface fire at the start of this study (Jackson et al., 1999). Evidence from a previous study reported an overall decline

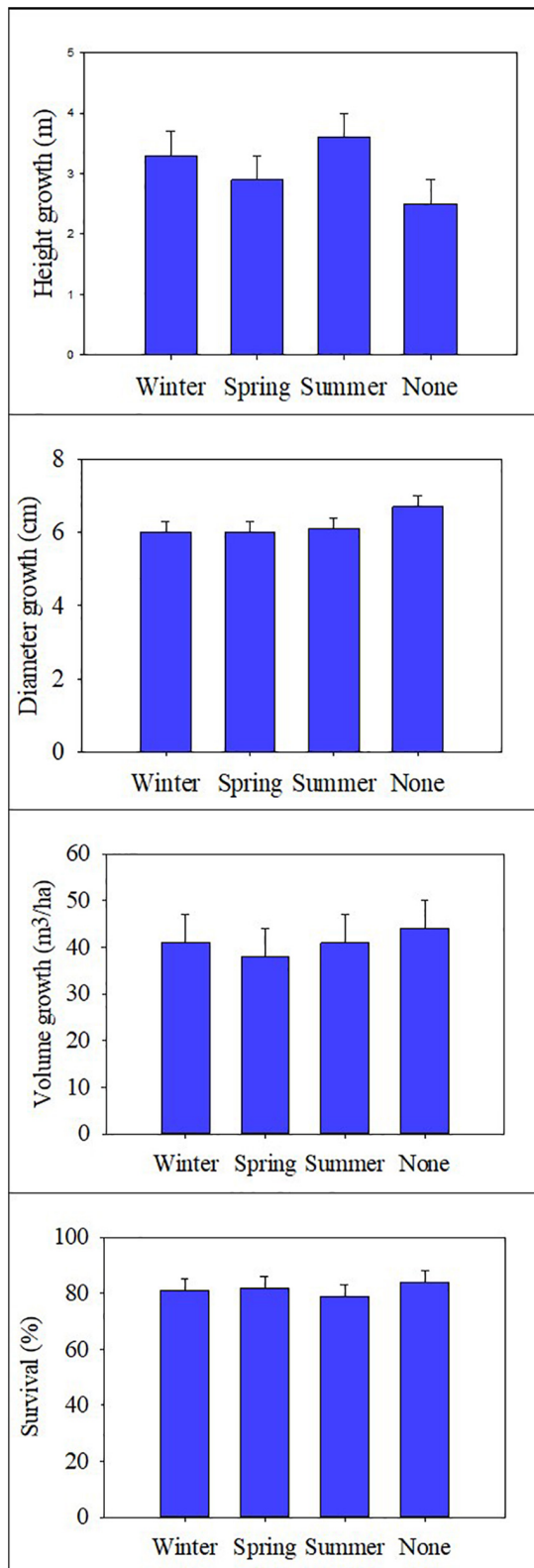


FIGURE 2 | The estimated survival, diameter growth, height growth, and volume growth ± 1 SE of longleaf pine after 23 years of winter, spring, summer biennial burning and an unburned treatment.

TABLE 2 | Results of a generalized linear mixed-effects analysis of variance (ANOVA) for the effects of seasonal biennial burning (winter, spring, summer) and the unburned treatment, diameter, the interaction between seasonal biennial burning and diameter on the odds of survival for individual longleaf pine.

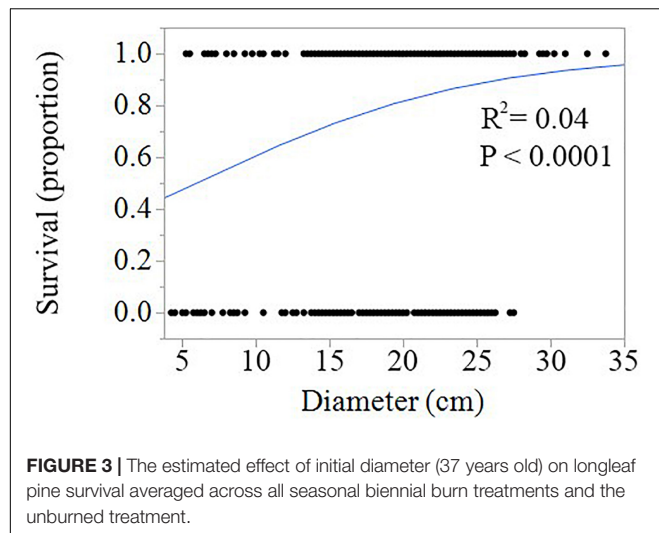
Effect	Degrees of freedom	F ratio	Prob > F
Seasonal biennial burning	3, 8	1.26	0.3505
Diameter	1, 877	19.43	<0.0001
Seasonal biennial burning $\times$ diameter	3, 877	1.35	0.2558

Effects < 0.05 were considered statistically significant.

in productivity in all seasonal burning treatments at age 14–24 relative to the unburned treatment, which indicates that longleaf pine is more susceptible to negative fire effects at a younger age (Boyer, 1987). In similar studies featuring younger longleaf pine, Grelen (1975) and Haywood et al. (2001) found that summer burning negatively affected longleaf pine height and volume production compared to late spring burning. Outside the longleaf ecosystem, studies examining the influence of repeated prescribed fire have also reported minimal impacts on burning on larger, older trees (Peterson et al., 1994; Hutchinson et al., 2012; Bottero et al., 2017). Based on these collective findings, we hypothesize that biennial growing season burns present minimal risk to productivity once longleaf pine reaches 25 cm dbh in even-aged stands.

A second explanation for the minimal effect of fire seasonality may be related to the burning regime. Studies reporting high post-fire mortality in mature longleaf pine have generally occurred in stands where duff has accumulated after decades of fire exclusion (Kush et al., 2004; Varner et al., 2005, 2009; O'Brien et al., 2010). Such conditions promote smoldering fire behavior, which can damage trees through extended transfer of heat to the roots and cambium (Varner et al., 2009). In this study, plots were subjected to biennial burning for over two decades, which resulted in the exposure of mineral soil and little duff accumulation. While we can only speculate on the potential mechanisms influencing fire effects in our burn treatments, observational evidence of limited surface organic matter, scant midstory development, and relatively low flame lengths suggest that biennial burning maintained conditions that prevented smoldering and reduced crown scorch and consumption. Limiting damaging fire behavior may be particularly important for maintaining long term productivity, as prolonged soil heating has been shown to have negative short-term effects on radial growth and adverse long-term effects on growth when combined with drought (Varner et al., 2009; Slack et al., 2016). Moreover, crown scorch is considered the primary factor influencing mortality for some conifer species (Stephens and Finney, 2002; Hull-Sieg et al., 2006). Thus, it is possible that the fuel conditions created by repeated biennial burning may have overwhelmed any potential effects associated with seasonal burning.

Although mortality was generally low and did not differ across seasonal treatments, our results clearly demonstrate that risk of mortality diminished with increasing initial diameter.



Similar results have been reported from other frequently burned ecosystems and is an expected result with longleaf pine given its rapid ability to accumulate bark thickness (Peterson and Reich, 2001; Ordóñez et al., 2005; Schafer et al., 2015). However, our results suggest that intraspecific competition rather than biennial burning was likely responsible for the death of smaller-diameter longleaf pine, as survival in the unburned treatment did not differ significantly from any seasonal biennial burning treatment. In support of this interpretation, calculations of stand density index revealed that all biennially burned plots had nearly reached or exceeded the self-thinning range of intraspecific competition by 2018 (Stand Density Index > 250) (Shaw and Long, 2007). Competition in the unburned treatments was undoubtedly higher due to the presence of established hardwood stems. Given that the smaller-diameter trees were almost always found in suppressed growing positions, and the relatively high light demands of longleaf pine (Boyer, 1990), it is not surprising that smaller-diameter trees were at greater risk of mortality.

CONCLUSION AND IMPLICATIONS

The importance of incorporating regular prescribed fire in southeastern woodland restoration is well established (Van Lear et al., 2005). However, what remains relatively unknown is how other features of the burning regime, such as burn season, impact key ecosystem properties. Due to its importance for understory flammability, maintaining a productive longleaf pine overstory is a restoration objective (Mitchell et al., 2006). Thus, understanding the response of mature longleaf pine to fire seasonality is an important consideration in restoration prescriptions.

Under the conditions of fire application and behavior studied, our findings suggest a continuance of seasonal biennial burning has minimal impact on the survival and productivity of mature (37–60-year-old) longleaf pine. Similar findings have also been reported for longleaf pine in the 14–23 age range (Boyer, 1987). Collectively, these findings have important implications

for woodland restoration at the regional scale, as many of the stands established in previous decades have reached the age where accumulated fire resistance minimizes the impact of fire seasonality in a biennial burn regime. Incorporating spring and summer burning into stands featuring low duff accumulation and longleaf pine at least 25 cm in diameter, would alleviate strain on local burning capacity, which often struggles to meet demand for dormant season burning. Moreover, burning outside the dormant season could benefit other restoration objectives such as promoting wire grass expansion and reducing hardwood encroachment (Outcalt, 1994; Addington et al., 2015). While climate change is expected to reduce the availability of summer burning days (Kupfer et al., 2020), we expect growing season burning will become an increasingly important practice for maintaining restoration efforts in southeastern woodlands.

In addition, our results may have important implications for other fire-prone ecosystems where prescribed fire is used to reduce hazardous fuels (Boer et al., 2009; Prichard et al., 2017). Our results do not directly link fire frequency with wildfire resistance; however, they do provide further evidence that damaging fire behavior is minimal in areas receiving frequent fire (Fernandes and Rigolot, 2007; Fernandes et al., 2015). Consequently, implementing a frequent prescribed fire regime would likely aid management efforts focused on mitigating wildfire risk.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

JW developed the research questions, wrote the first draft of the manuscript, and performed the statistical analyses. AS and JK collected data and revised drafts of the manuscript. All authors contributed to the article and approved the submitted version.

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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