

Overstorey leaf production and emergence of sassafras saplings in a southwest Missouri oak woodland: An analysis based upon long-term effects of fire

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Citation: Sharma S., Wait A., Khanal P. (2024): Overstorey leaf production and emergence of sassafras saplings in a southwest Missouri oak woodland: An analysis based upon long-term effects of fire. *J. For. Sci.*, 70: 407–419.

Abstract: Missouri Ozark woodlands are a unique, but imperilled ecosystem type due to fragmentation, lack of proper management and a changing climate. The management, restoration, and conservation of Ozark woodlands is a conservation priority. The Ozark woodlands contribute to the sequestration of carbon and nutrients through their robust productivity, effectively removing carbon dioxide from the atmosphere and storing it in the biomass and soil while cycling essential nutrients to support the ecosystem's health and vitality. We have assessed the over- and mid-storey leaf production, collecting leaves in baskets every autumn in a 1 200-ha conservation area in southwest Missouri since 2000. The leaf production data from 2000 to 2021 were compared among sites; control (not burnt for over 80 years), burnt (fire resumed in March of 1999 and repeated in 2001, 2003, 2008, 2010, 2013, and 2021) and reference (fire resumed in 1980 and repeated every 2 years). The average oak leaf production was statistically higher in the burnt site than the reference site, but only marginally higher than the control site. The leaf production varies statistically between the years. We applied a regression analysis among the productivity, temperature, and precipitation to associate the temporal variability in the weather with the productivity. The reference woodland showed statistical significance with the precipitation, but not with the temperature, while the other sites did not show any statistical significance with the precipitation. No statistically significance difference was observed between the productivity and temperature across any of the woodland burn histories. The March–June, March–May, and June–August precipitation statistically predicted the productivity. The results indicate that long-term burning is predictably associated with woodland leaf production and precipitation, but the precipitation is uncoupled with the productivity in woodlands that were more recently burnt or where burning has been suppressed. Sassafras saplings of approximately 1 m in height have emerged as the dominant species in the understorey of burnt woodlands while being completely absent from the control and reference woodlands. However, the productivity is the highest in the woodlands where burning has been suppressed and 20 years of prescribed fire does not significantly reduce the productivity. Oak regeneration over 20 years of burning is being suppressed by competition with sassafras, which may result in a significant shift in the ecosystem variables.

Keywords: ecosystem; precipitation; regression; saplings; woodland

The short- and long-term effects of prescribed burning require consideration of the fire effects on the stand dynamics and successional development. Following a disturbance, even-aged stands progress through predictable stages of stand development (i.e. stand dynamics), including density-dependent tree mortality driven

by increased competition as individual trees grow larger (Peet, Christensen 1987). Through time, tree mortality shifts from a density-dependent process to the outcome of local disturbances and stochastic events. This allows new trees to be established and successional change to occur (Oliver 1980). Studies describing temporal

patterns of forest responses to repeated burning have generally been limited to approximately 10–15-year periods (Hutchinson et al. 2005). In contrast, long-term studies more commonly report the chronic effects of different fire regimes simultaneously (Haywood et al. 2001). Studying the impact of prescribed burning on forest development through the stages of stand dynamics and subsequent successional change requires repeated measurements through extended periods.

Long-term studies (i.e. > 25 years) demonstrate that repeated prescribed burning at frequent fire return intervals (< 5 years) results in the reduction or removal of small-diameter woody vegetation and creates stands with open vertical structures in hardwood (Knapp et al. 2015) and conifer species (Haywood et al. 2001). Frequent fire events favour fire-tolerant species over fire-sensitive species (Knapp et al. 2015). The diversity of herbaceous ground layer vegetation increases with long-term fire events by reducing the abundance of small-class wood species and litter (Veldman et al. 2014). These structural and compositional features are considered defining characteristics of woodland ecosystems, suggesting frequent fire events are essential for woodland management. Anthropogenic fires have been influencing the dominance of the central hardwood region for many years (Fesenmyer, Christensen 2010). A recent model of the potential fire frequency, based on the precipitation, temperature, and oxygen, suggests that the eastern United States could support mean fire return intervals < 10 years (Guyette et al. 2012), which is also controlled by the topography and human intervention (Stambaugh, Guyette 2008).

The woodland in the central hardwood region of the eastern United States is shifting towards a lower dominance by oaks (*Quercus* spp.; Abrams 2003). The central hardwood region is distinguished by its diverse mix of hardwood tree species such as oak (*Quercus alba*, *Quercus rubra*), hickory (*Carya illinoensis*, *Carya ovata*), maple (*Acer saccharum*, *Acer rubrum*), cherry (*Prunus serotina*), and ash (*Fraxinus americana*), among others. These forests are often characterised by their relatively high species diversity and productivity compared to other forest types in the eastern United States (Nuzzo 1986). The successful regeneration of oak forests depends on the presence of adequate densities of oak seedlings before a canopy disturbance (Loftis 2004).

The function, composition, and structure of an oak-dominated ecosystem have been influenced by the fire regimes of the eastern United States (Stambaugh et al. 2015). Fire helps to maintain oak-hickory wood-

lands through selective mortality, or by altering the growth rates of the surviving trees (Crow 1988). However, fire may also kill and injure oaks. Fires may have both short- and long-term effects on tree mortality. The immediate stress imposed on plants by fires is high temperature; however longer-term risks posed by fires result from cambial injury and an associated increased susceptibility to insect attack and diseases (Johnson 1974). The increasing awareness of fire's historical role and the fire-adapted traits of oaks have led to the increased use of prescribed fire in oak woodlands and forests on public lands.

Burning in mature oak forests has yielded various outcomes concerning oak regeneration. Prescribed fire has been shown to increase the competitive status of oak regeneration in some studies (Fan et al. 2012). Still, other research has found that prescribed fire can decrease the oak's competitive position (Blankenship, Arthur 2006). This contrast is unsurprising given the range of the stand conditions and fire applications in those studies.

The bark of trees insulates the stem cambial tissues from the high temperatures of a fire and because bark thickness increases with the size, the size of the tree is correlated with the fire resistance (Hengst, Dawson 1994). The heat capacity of the bark, the capacity to sprout as seedlings, and storage are other important factors determining the fire resistance of a species (Spalt et al. 2017). The available storage reserves also increase with the tree size, tending to increase the survival of larger trees by promoting sprouting after top kill; physiological ageing reduces the inherent capacity to sprout in very large trees (Kozłowski et al. 1990). Oaks and the ecologically similar hickories (*Carya* spp.) gain an advantage in a regime of periodic fire, as they have relatively thick bark (Hengst, Dawson 1994), efficient wound compartmentalisation (Smith, Sutherland 1999), dormant root collar buds located more profound in the soil than those of most competing species (Brose, Van Lear 1998), and the capacity to sprout from these dormant buds using carbohydrate reserves achieved through 'root-centred' growth.

There are several limiting factors for oak regeneration in many areas: Fire along with the increasing abundance of shade-tolerant species in the understorey and midstorey, which reduces light availability to the forest floor (Fei, Steiner 2007). The abundance of shade-tolerant species in oak forests is due to the reduced fire frequency (Abrams 1992). Many land managers in the Midwest U.S. woodlands are interested in using prescribed burning to restore woodland ecosystems on sites that historically presumably supported

<https://doi.org/10.17221/8/2024-JFS>

frequent fires (Kabrick et al. 2014). Recently, Hanberry et al. (2014) suggested guidelines for classifying types of forested ecosystems based on the Gingrich stocking chart (Ginrich 1967), thus providing land managers with structural targets for woodland restoration.

The effects of fires on forest development are not well-known. Understanding the rate of change in woodland mid- and overstorey production and the understorey sapling density with repeated fire events would provide valuable information for potentially developing long-term silvicultural prescriptions. Our aim was to (i) identify the effect of fires on the leaf production of oak, hickory, and other species, (ii) study the sapling density of white oak (*Quercus alba*) and sassafras on the woodlands with three different burn histories, and (iii) study the effect of the temperature and precipitation on the leaf production on three sites (control, burnt, and reference sites).

MATERIAL AND METHODS

Study area. Woodland study sites: Bull Shoals Field Station (BSFS) is in the 1 200 ha Drury conservation area [Universal Transverse Mercator (UTM) 40°28'12"N, 4°55'48"E] in Taney County, Missouri, USA (adjacent to Bull Shoals Lake; Figure 1). The site is characterised as an upland oak-hickory forest. The average annual temperature ranges from 32 °C to –31.5 °C, and the average annual rainfall is 1 092.2 mm. The area has a karst topography, with elevation ranging from 180 m a.s.l. to 340 m a.s.l. We established the experimental habitat areas representing the following: (i) unburnt or control – last known fire in 1950; (ii) recently burnt or burnt – fire resumed in March of 1999 and repeated in 2001, 2003, 2008, 2010, 2013, and 2021; (iii) continuously burnt or reference – fire resumed in 1980 and repeated every 2 years.

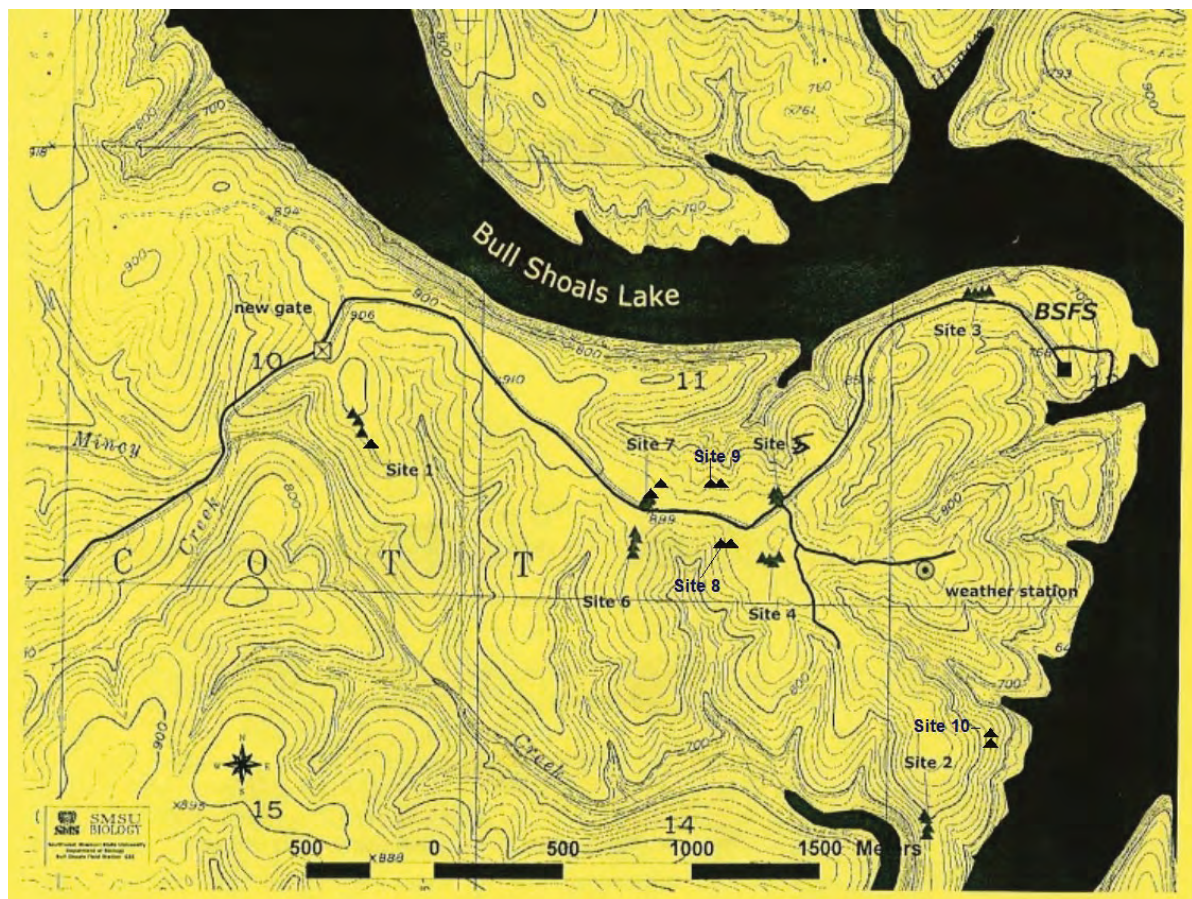


Figure 1. Map of woodland areas that includes woodlands with three different burn histories

Areas which have not been burnt in over 60 years (sites 5, 7, and 9) and are classified as degraded woodlands are considered 'control' woodland sites; degraded woodland areas where burning was prescribed in 1999 to open the canopy, promote wildlife and increase plant diversity (sites 4, 6, and 8) are classified as 'burnt' sites; sites which have been continuously burnt since 1980 and were selected based on being considered open woodlands with cover between 35–60% (sites 1, 2, 3, and 10) are classified as 'reference'

Data collection. The leaf litter was collected from suspended laundry baskets each year after all the leaves had fallen from trees from autumn 2000 to autumn 2021 from the Bull Shoals Field Station. Baskets were placed in 0.1 ha circular plots in the three treatment sites (control, burnt, and reference; see Figure 1). In total, 8 baskets were placed in each treatment site. In a circular plot, one basket is placed 10 m from the centre of the circle and another at the 17.5 m from the centre. Two baskets are placed in each direction: north, east, south, and west. In total, 24 baskets were placed in all three sites. The leaves and acorns from each basket were collected and brought to the lab. Each basket's leaves were placed in paper bags and then placed in the oven at 50 °C for 4 days until a constant dry weight was obtained. After 4 days, the weight of the leaves was recorded. This process was performed from 2000 to 2021, once per year in the autumn season of each year. The sapling density of the white oak was also counted only on 2018 to see the effect of the different treatments on the oak density. A 100-metre square line transect was conducted with the help of tape and the white oak saplings were counted on the three sites. Likewise, after the periodic fire was laid in the spring of 2021, we examined the trend in the potential community and ecosystem effects, and we assessed the sapling density of sassafras (*Sassafras albidum*) within the linear transect of 0.1 ha in the reference sites only as there is no sassafras in the control or burnt sites. The 0.1 ha was laid with the help of linear tape. A 0.1 ha linear transect was laid and divided into 10 blocks and counting was undertaken in the autumn of 2021. Flags were placed on the same transect and another counting was undertaken in the autumn of 2022. Visual counting was conducted based on the leaves as an indicator for the differentiation. The precipitation and temperature data were collected from the National Oceanic and Atmos-

pheric Administration (NOAA 2023) website for each month from the year 2000 through to 2021.

Data analysis. R-studio (Version 3.6.1., 2022) was used for the data analysis. We used an analysis of variance (ANOVA) to test for the mean differences as a function of the burn history for all types of litter: oak leaves, hickory leaves, total leaves, and acorns. We performed linear regression analyses (Sharma, Wait 2024) to examine the effect of the climate (temperature and precipitation) on the over- and mid-storey leaf production based on the yearly mean temperature and total precipitation; we also examined different combinations of months to look for significant relationships to explain the year to year variation in the productivity.

RESULTS AND DISCUSSION

In the case of oak, the periodically burnt sites have greater leaf productivity compared to the control and reference sites or the continuously burnt sites. A significant difference (Figures 2 and 3) was observed between the control and reference ($P < 0.05$) and the reference and burnt ($P < 0.05$), while no significant difference was observed between the control and burnt ($P > 0.05$) sites. Oak is considerably more resistant to fire as it has thick bark. However, oak seedlings and saplings are susceptible to fire as they do not have very good bark formation (Hengst, Dawson 1994). Due to the continuous fire, the oak seedlings and saplings were killed, and the productivity of the oak leaves was low in the continuously burnt sites. The productivity in the burnt sites was high because the fire destroyed the other susceptible species and favoured the resistant species like oak. The diminished competition with fire-sensitive species following the fires facilitated a rapid mineral uptake by the Ozark woodlands, fostering accelerated leaf production and promoting the overall

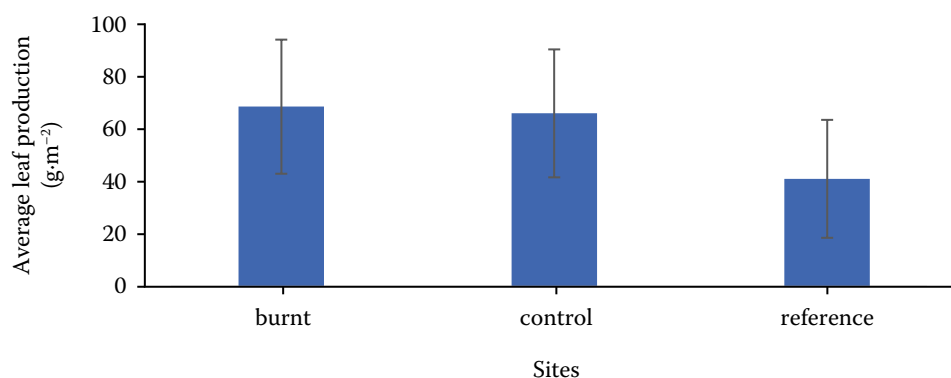


Figure 2. Mean (\pm standard deviation) over- and mid-storey leaf production of oak on three sites with different burn histories across an oak woodland from 2000 to 2021

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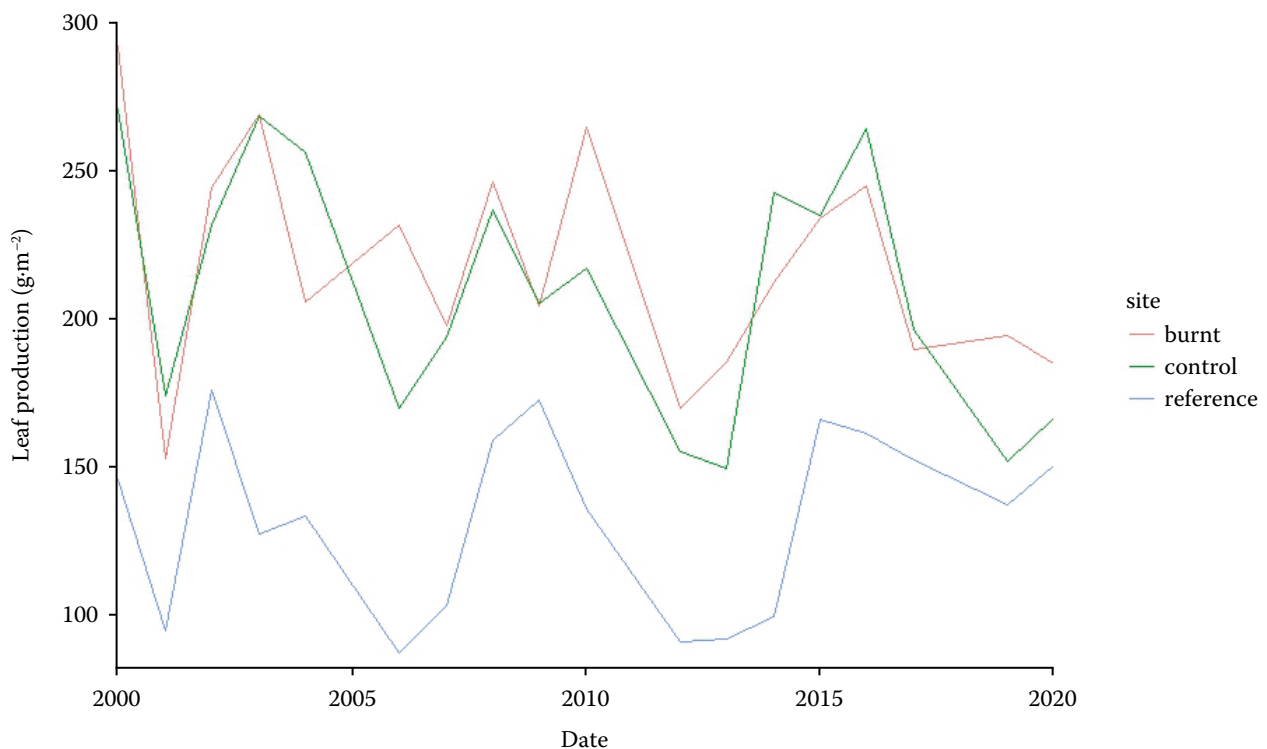


Figure 3. Oak litter production a 2000 to 2021 across three burn histories control, burnt, and reference

ecosystem resilience and regeneration. Similarly, the burnt sites were burnt in periods that allowed the saplings to grow bigger. As they grew, they developed more bark and were resistant to fire. Wait and Aubrey (2014) recommend longer intervals between prescribed fires coupled with the deliberate creation of physical gaps to facilitate oak regeneration into the canopy. Similarly, Wait (2016) suggested that oak saplings in forests are potentially more susceptible to herbivore damage than oaks managed in savannas (woodlands), espe-

cially following a prescribed burn. This might be the case for the burnt sites as they have higher average leaf productivity for oaks compared to other sites.

In the case of hickory trees, the control site has greater productivity than the other sites. Statistically significant differences were observed in the means across all the burn histories (Figures 4 and 5): control and reference ($P < 0.05$), control and burnt ($P < 0.05$), and reference and burnt ($P < 0.05$) sites. It shows a massive gap between the production at the control site and the

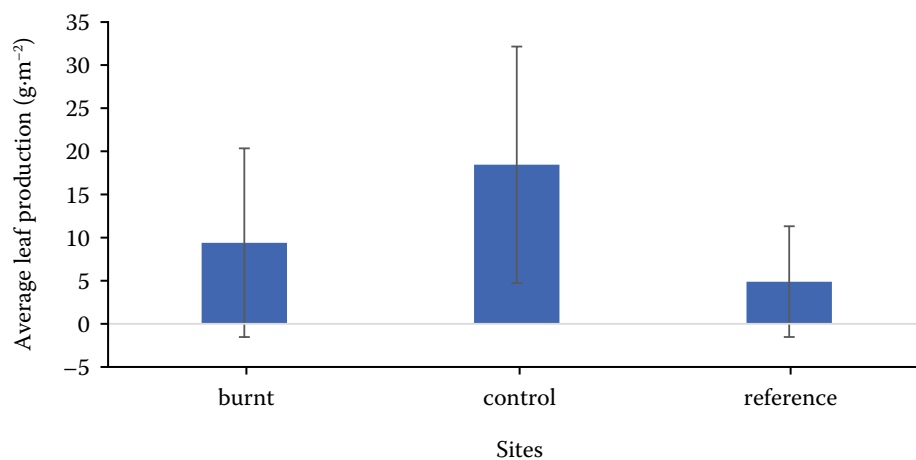


Figure 4. Mean (\pm standard deviation) over- and mid-storey leaf production of hickory on three sites with different burn histories across an oak woodland from 2000 to 2021

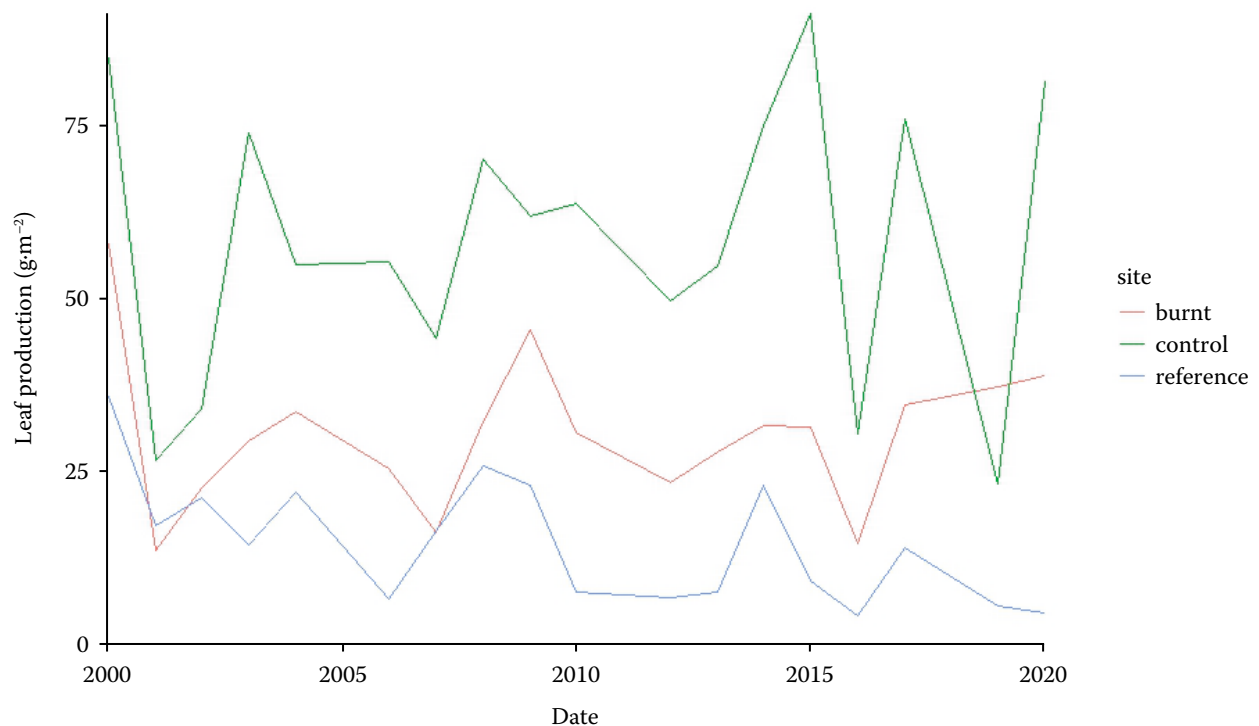


Figure 5. Hickory litter production from 2000 to 2021 across three burn histories control, burnt, and reference

other applied fire regime sites. Ozark forests are mainly dominated by oak. The application of fire in this forest has a significant role in managing the oak regeneration. However, the hickory did not show any positive change in the productivity. This might be due to the smaller number of hickory trees compared to oaks, as the Ozark forest is an oak-dominated forest. The fire killed a limited number of hickory saplings.

Acorn production is more significant in the periodically burnt site (Figures 6 and 7) than in the other sites. Statistically significant mean differences in the reference and burnt sites ($P < 0.05$), while no significant mean differences were observed between the reference and control ($P > 0.05$) and control and burnt ($P > 0.05$) sites. The burnt sites favour oak as it helps in nutrient absorption and has fewer competitive spe-

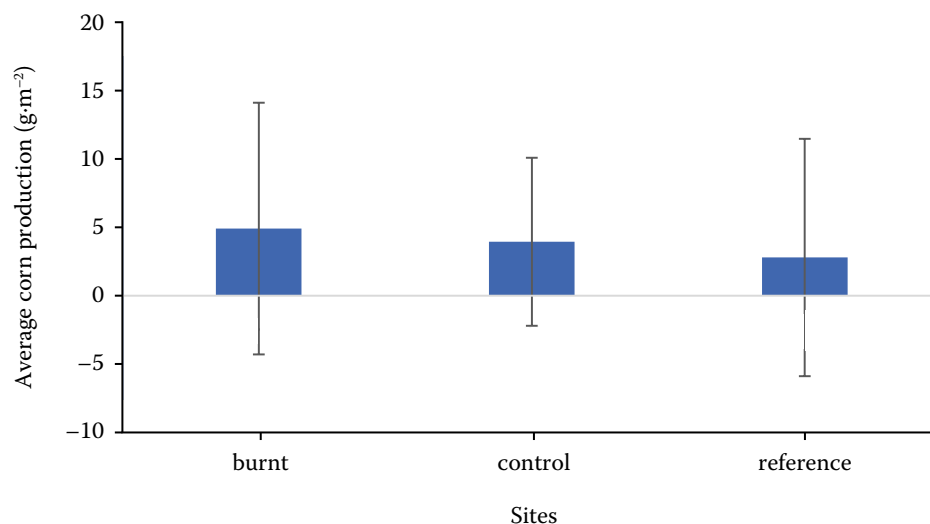


Figure 6. Mean (\pm standard deviation) acorn production on three sites with different burn histories across an oak woodland from 2000 to 2021

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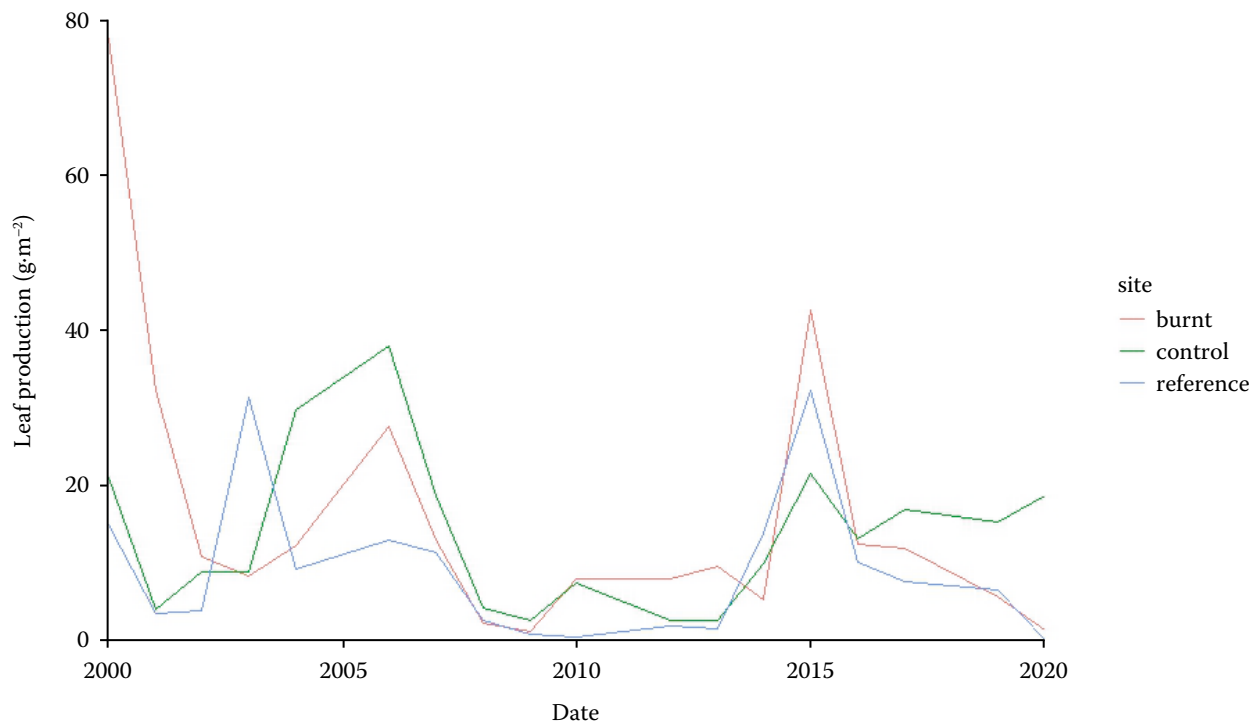


Figure 7. Acorn production from 2000 to 2021 across three burn histories control, burnt, and reference

cies, leading to higher acorn production. The periodically burnt sites also select the seedlings and saplings as they grow bigger and produce acorns.

Other plant productivity was higher in the control site than in the other sites. Statistically significant differences were observed in the means (Figure 8) across all the burn histories: control and reference ($P < 0.05$), control and burnt ($P < 0.05$), and reference and burnt ($P < 0.05$). In the Ozark forests, there were other spe-

cies susceptible to fire, such as maple. They grow better in the control sites as they do not have good bark to protect them from fire. These species died in the burnt and reference sites as they are susceptible, so the overall productivity was lower.

The total leaf production is higher in the control sites than in the other sites. Statistically significant differences (Figures 9 and 10) were observed in the means across all the burn histories: control and refer-

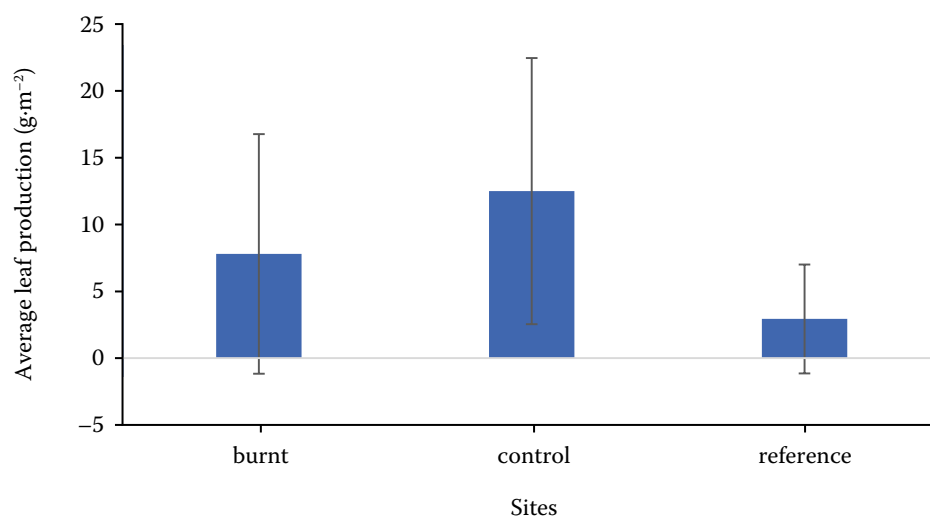


Figure 8. Mean (\pm standard deviation) over- and mid-storey leaf production of the 'other' category on three sites with different burn histories across an oak woodland from 2000 to 2021

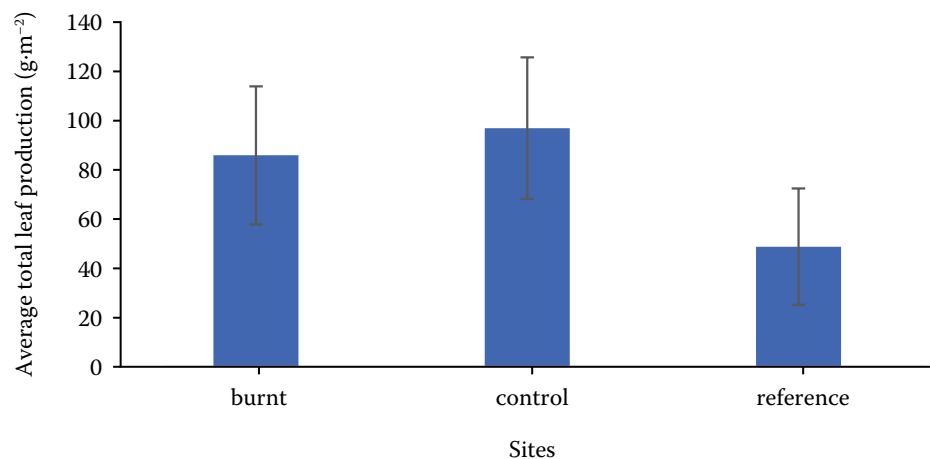


Figure 9. Mean (\pm standard deviation) over- and mid-storey leaf production of the 'other' category on three sites with different burn histories across an oak woodland from 2000 to 2021

ence ($P < 0.05$), control and burnt ($P < 0.05$), and reference and burnt ($P < 0.05$). The control site has high production compared to the other sites. It is because the control site has all species of oak, hickory, and maple, as well as other herbaceous species as it has never been burnt. All these species lead to higher productivity in the control site, while the fires kill the fire-susceptible species in the case of the burnt and reference sites.

Sapling estimation. The oak sapling density reflects the preference for oak for the periodical fire sites.

Oak is fire resistant (Smith, Sutherland 1999), and the fires provide more benefits for oak seed germination. However, if the fire is continuous, it might kill the seedling or sapling; due to this, the productivity was good on the periodic fire sites as it helps increase the sapling density. The oak sapling density was high (Table 1) in the burnt site, followed by the reference and control sites. A burnt site favours germination as it removes the litter above the seed, and the fire plays a role in the germination of oak seeds as it reduces the seed dormancy. However, the fire kills the

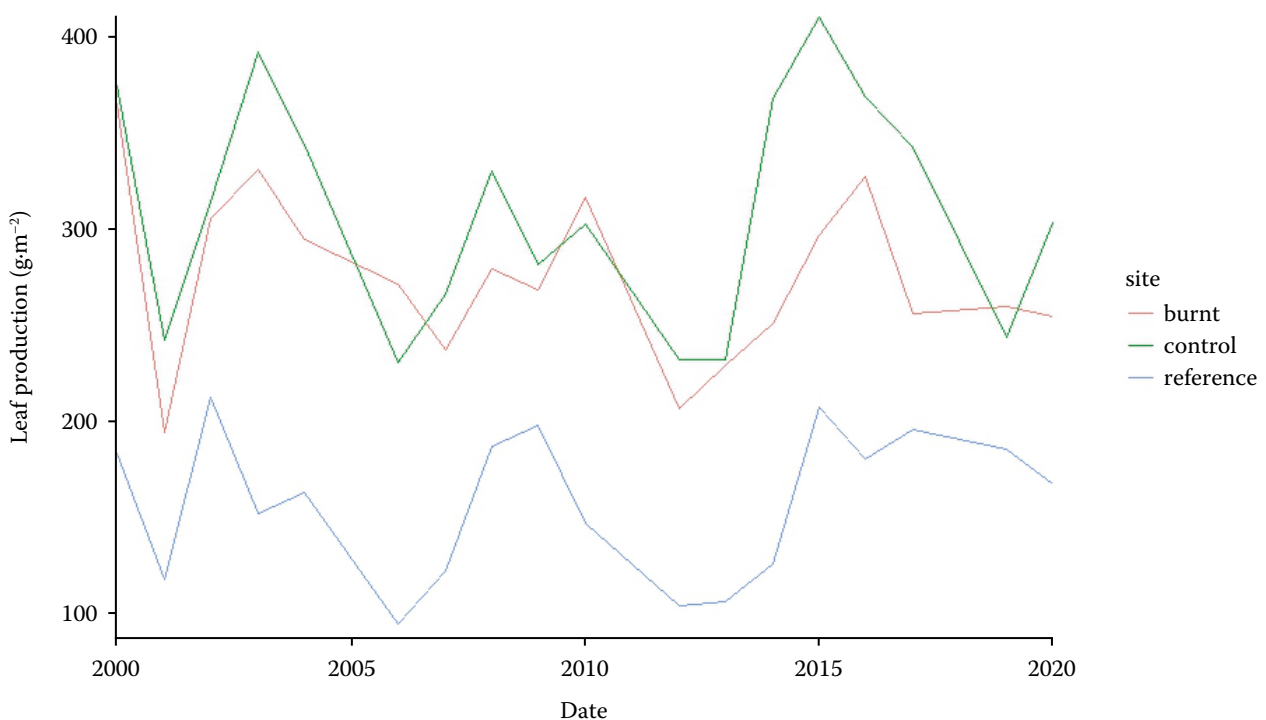


Figure 10. Total litter production from 2000 to 2021 across three burn histories control, burnt, and reference

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Table 1. White oak (*Quercus alba*) sapling density on a 100 m² line transects on each site

Population characteristics	Site		
	control	burnt	reference
Density (m ²)	0.22	0.34	0.30

saplings in the case of the reference sites, so saplings are found a little less than at the burnt site.

Only the burnt woodlands were found to contain sassafras. The oak and sassafras sapling density was counted in the autumn of 2021 and 2022. A higher sassafras density (Table 2) was observed in both years, almost two times as much. This study provides unique insights into both the burnt and reference effects on an oak-hickory forest ecosystem. The burnt sites have a greater number of sassafras saplings compared to the oak ones. The results show the burnt sites are ultimately not favouring oak regeneration. In addition, the elimination of ingrowth introduces a potential regeneration challenge if the canopy cover is desired in perpetuity, suggesting that a fire-free interval would be necessary for oak tree recruitment. The emergence of the sassafras in the burnt woodland sites has emerged as a focus for new research, including the impacts on decomposition and nutrient cycling.

Table 2. Sapling density of sassafras and oak in a burnt site within a 0.1 ha linear line transect

Date	Sapling density (stems·ha ⁻¹)	
	sassafras	oak
Autumn 2021	560	171
Autumn 2022	582	213

Regression analysis of the total productivity with the temperature and precipitation. Statistically significant regression was not observed between the total average temperature and leaf productivity across the three treatment sites. A statistically significant regression was observed (Figure 11) between the total average precipitation and reference site leaf productivity ($P = 0.011$). However, statistically significant regression was not observed between total average precipitation and burnt sites or control sites.

For average March–June: Statistically significant regression was not observed between average March–June temperature and productivity across any of the three woodland sites. However, a statistically significant regression was observed (Figure 12) between March–June average precipitation and the reference site ($P = 0.004$). Statistically significant regression was not observed between March–June average precipitation and burnt sites or control sites.

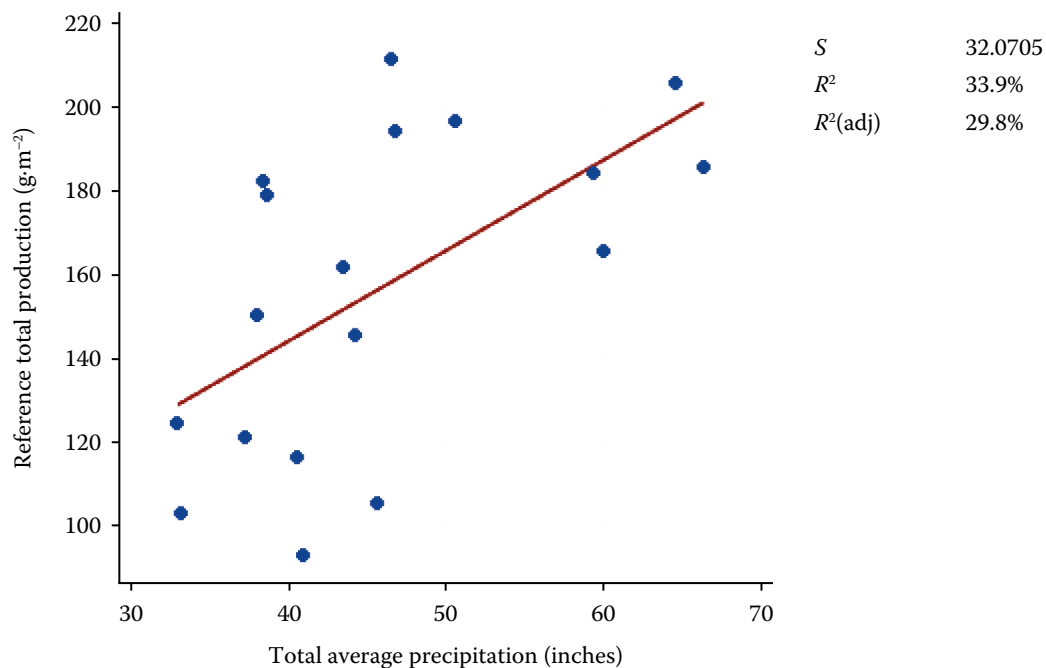


Figure 11. Regression between reference sites and total precipitation

Statistically significant regression ($P = 0.011$) was found; S – standard error of the estimate; R^2 – coefficient of determination; $R^2(\text{adj})$ – adjusted coefficient of determination

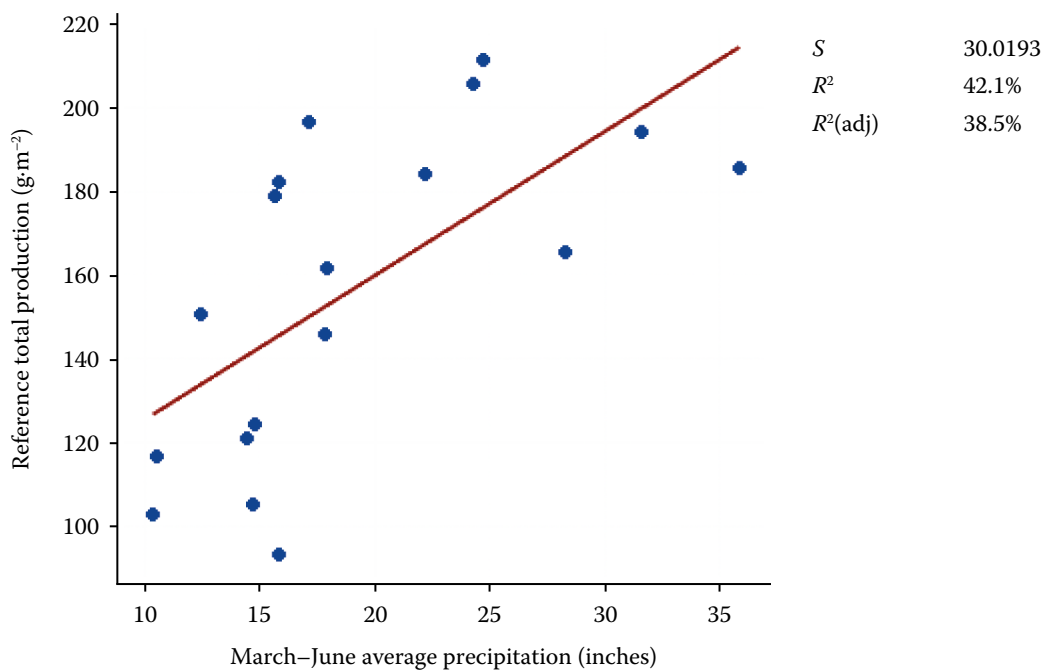


Figure 12. Regression between reference sites and March–June precipitation
Statistically significant regression ($P = 0.004$) was found; S – standard error of the estimate; R^2 – coefficient of determination; $R^2(\text{adj})$ – adjusted coefficient of determination

For average March–May: Statistically significant regression was not observed between average March–May temperature and productivity across any of the three woodland sites. However, a statistically significant regression (Figure 13) was observed between March–May average precipitation and the

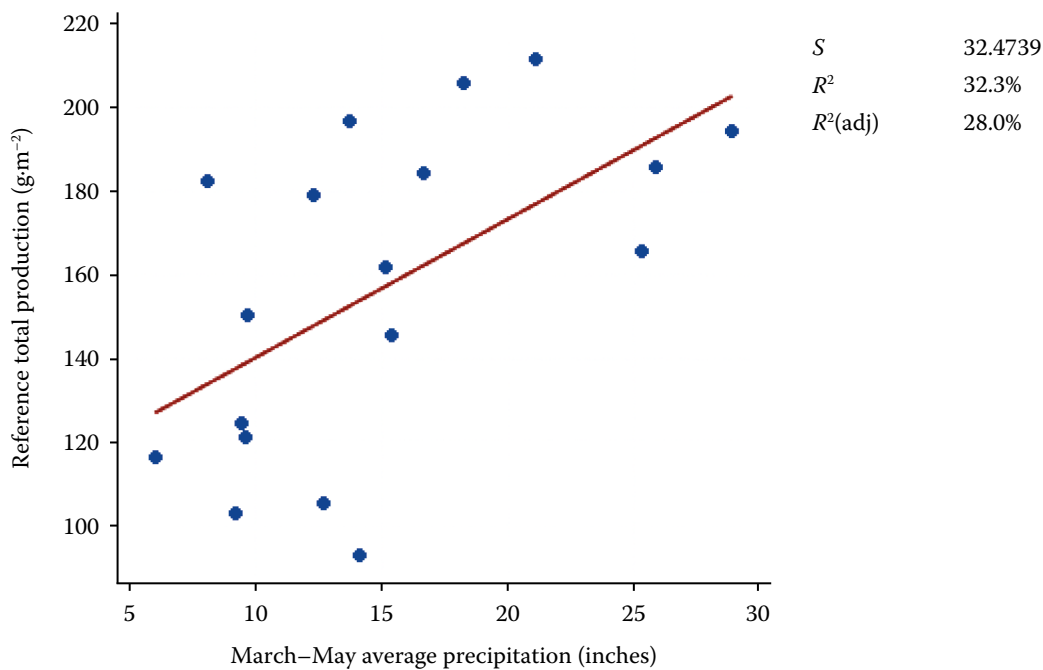


Figure 13. Regression between reference sites and March–May precipitation
Statistically significant regression ($P = 0.014$) was found; S – standard error of the estimate; R^2 – coefficient of determination; $R^2(\text{adj})$ – adjusted coefficient of determination

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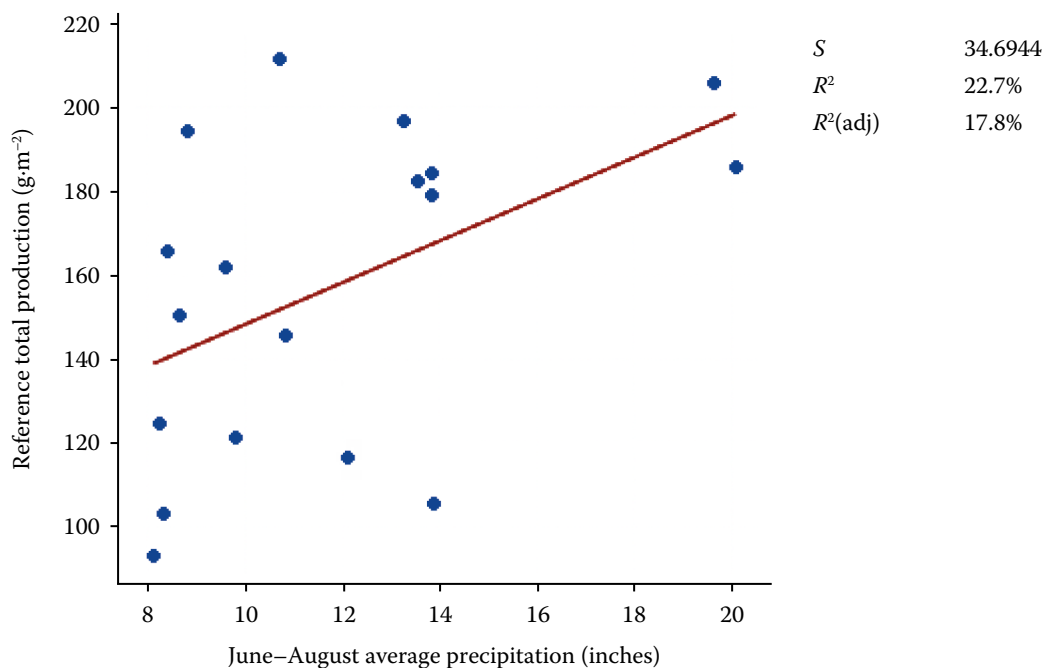


Figure 14. Regression between reference sites and June–August precipitation

Statistically significant regression ($P = 0.046$) was found; S – standard error of the estimate; R^2 – coefficient of determination; $R^2(\text{adj})$ – adjusted coefficient of determination

reference site ($P = 0.014$). Statistically significant regression was not observed between March–May average precipitation and burnt sites or control sites.

For average June–September: Statistically significant regression was not observed between average June–September temperature and productivity across any of the three woodland sites. Similarly, statistically significant regression was not observed between average precipitation and productivity in June–September across any of the three woodland sites.

For average June–August temperature: Statistically significant regression was not observed between average June–August temperature and productivity across any of the three woodland sites. However, a statistically significant regression (Figure 14) was observed between June–August average precipitation and reference site ($P = 0.046$). Statistically significant regression was not observed between June–August average precipitation and burnt sites or control sites.

CONCLUSION

The study offers valuable insights into the intricate dynamics of woodland productivity and the interplay between fire, species composition, and climatic factors. It reveals that while closed degraded woodlands initially exhibit higher leaf production, recent

fires have led to a reduction in overall output. However, post-fire, oak leaf production increases on burnt sites, suggesting the importance of periodic fires in promoting oak habitat restoration by suppressing shade-tolerant species and favouring oak growth. However, the burnt sites also favour the shade-intolerant species sassafras, which highlights the need for further research on oak management and restoration. The reference sites do not contain the sassafras, but the leaf production is relatively low compared to the burnt or control.

Furthermore, the study emphasises the complexity of the relationship between primary productivity and climatic factors, with precipitation emerging as a significant predictor of production in reference woodlands. This underscores the need to consider multiple variables, including leaf phenology, soil conditions, and decomposition rates, to develop accurate predictive models for woodland productivity across different burn histories.

In conclusion, the findings underscore the importance of a comprehensive understanding of the factors influencing woodland productivity to guide effective management and restoration efforts. By integrating knowledge of fire ecology, species dynamics, and climatic variability, we can develop informed strategies that promote ecosystem resilience, biodiversity, and

long-term sustainability in woodlands. These insights are invaluable for guiding future research and conservation initiatives aimed at preserving and restoring these critical ecosystems.

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Received: January 26, 2024

Accepted: April 26, 2024

Published online: August 14, 2024