

Long-term effects of fire and fire-return interval on population structure and growth of longleaf pine (*Pinus palustris*)

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Abstract: We investigated the effect of fire and fire frequency on stand structure and longleaf pine (*Pinus palustris* P. Mill.) growth and population demography in an experimental research area in a southwest Florida sandhill community. Data were collected from replicated plots that had prescribed fire-return intervals of 1, 2, 5, or 7 years or were left unburned. Experimental treatment burns have been ongoing since 1976. Plots were sampled to estimate species distribution, stand structure, and longleaf pine density in four developmental stage classes: grass, bolting, small tree, and large tree. Tree-ring growth measurements in combination with burn history were used to evaluate the effects of fire and fire-return interval on basal area increment growth. Fire-return interval impacted stand structure and longleaf pine population structure. Our results suggest that recruitment from the bolting stage to later stages may become adversely affected with very frequent fires (e.g., every 1 or 2 years). Although adult tree productivity was negatively impacted during fire years, tree growth during years between fire events was resilient such that growth did not differ significantly among fire-return intervals. Our study shows that the longleaf pine population as a whole is strongly regulated by fire and fire-return interval plays a key role in structuring this population.

Résumé : Nous avons étudié l'effet des feux et de leur fréquence sur la structure de peuplement, la croissance et la démographie de la population de pin des marais (*Pinus palustris* P. Mill.) dans une zone de recherche expérimentale dans une communauté de grues du Canada du sud-ouest de la Floride. Les données ont été collectées dans des parcelles répétées où l'intervalle entre les brûlages dirigés était de 1, 2, 5 ou 7 ans ou qui n'étaient pas brûlées. Les traitements expérimentaux de brûlage ont été appliqués depuis 1976. Les parcelles ont été échantillonnées pour estimer la distribution des espèces, la structure de peuplement et la densité du pin des marais dans quatre classes de stade de développement : stade herbacé, montée à graines, petits arbres et gros arbres. Des mesures de croissance des cernes annuels combinées à l'historique des brûlages ont été utilisées pour évaluer les effets du feu et de l'intervalle entre les feux sur l'accroissement en surface terrière. L'intervalle entre les feux a eu un impact sur la structure du peuplement et celle de la population de pin des marais. Nos résultats indiquent que les feux très fréquents (p. ex. chaque 1 ou 2 ans) peuvent avoir un impact négatif sur le recrutement à partir du stade de montée à graines jusqu'aux stades ultérieurs. Même si la productivité des arbres adultes était négativement affectée les années durant lesquelles il y avait un feu, la croissance des arbres pendant les années entre les feux était résiliente de telle sorte que la croissance n'était pas significativement différente entre les différents intervalles entre les feux. Notre étude montre que, dans l'ensemble, la population de pin des marais est fortement contrôlée par le feu et que l'intervalle entre les feux joue un rôle important dans la structuration de cette population.

[Traduit par la Rédaction]

Introduction

Communities dominated by longleaf pine (*Pinus palustris* P. Mill.) in the southeastern United States depend on fire to maintain their characteristic structure and species composition. Although the role of fire in maintaining these communities has been recognized for more than a century (Pinchot 1899; Andrews 1917), prescribing fire as a land management tool is a relatively recent practice, for example, since the 1940s (Platt et al. 1988; Hartnett and Krofta 1989; Boyer 1990; Myers 1990; Fowler and Konopik 2007). In many lo-

calities, fire exclusion is still practiced, in part due to the challenges faced in implementing a fire management regime on landscapes long unburned, such as the possibility of unintended catastrophic mortality of overstory longleaf pine (Varner et al. 2005; Campbell et al. 2008); unintentional fire exclusion can also result from other human actions such as road building. Yet, the ecological benefits of restoring longleaf pine communities with fire are clear, as these communities contribute a disproportional amount to global species diversity (Walker and Peet 1984; Myers et al. 2000; Mitchell et al. 2006).

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There has been considerable interest in investigating the consequences of different fire-return intervals, season of fire, and fire behavior and intensity in longleaf pine communities, motivated in part by a desire to explicate the forces shaping ecological communities and in part by a desire to improve and even optimize wildland management practices. One influential idea as to how to optimize management of these systems has been to restore historical fire regimes (Platt and Rathbun 1993; Beckage et al. 2005). The historical fire-return interval in longleaf pine communities is thought to be relatively short (i.e., 7 years or less) (Platt 1999) and serves to maintain the understory species richness, limit hardwood growth and fuel accumulation, and create a favorable microclimate for longleaf pine seedling germination (Glitzenstein et al. 1995; Beckage and Stout 2000; McGuire et al. 2001; Glitzenstein et al. 2003; Brockway et al. 2005). Another widely held notion is that the optimum fire-return interval is one that maximizes species richness or diversity in the understory community (Glitzenstein et al. 2003). Most studies exploring the issue of optimum fire frequency do so with the rationale that the frequency eliciting the strongest positive response in some community-level variable such as species richness is the frequency under which the community presumably adapted (see Beckage et al. 2005) and therefore the goal for management. Using this rationale, many studies focus on the understory response and have found that burning as frequently as fuels will allow (e.g., annually) results in the greatest understory species richness (Glitzenstein et al. 2003). Lastly, an emerging approach is that the optimum fire-return interval is one that restores the structure and function of the system while also allowing landowners to capitalize on multiple ecosystem services, such as recreation, biodiversity, and timber production (Mitchell et al. 2006).

There are few data on the effects of fire-return intervals on pine populations themselves, however. In particular, it is not clear how very frequent (every year or two) burning affects pine population growth and demography. For example, while annual burning might well create favorable microsites for longleaf pine seedling recruitment, the long-term effects of annual burning on the growth and population structure of longleaf pine may not be desirable. Fire has also been shown to decrease the productivity of longleaf pine trees (Boyer 2000; Haywood and Grelen 2000). Whether fires occurring every year, when fuel accumulation is minimal, affect growth more or less negatively than fires occurring less frequently is poorly quantified, however. Also unknown is how long fire in a current year may affect growth in subsequent years.

In this study, we ask the following: how do fire and fire frequency affect longleaf pine growth at the population and individual levels? We hypothesized that population structure would differ among the different fire-return interval treatments. Specifically, we hypothesized that frequent fires (every 1–2 years) create a more open-structured stand (more hardwood sprouts compared with hardwood trees) and more germination microsites and thus greater longleaf pine population numbers in the young growth stages (i.e., grass stage) compared with plots with less frequent fires. For individual longleaf pine tree growth, we hypothesized that fire events would negatively affect growth in the year of the fire. We

also explored resiliency by determining, on average, how long the hypothesized negative effect of fire on longleaf growth persisted. Our results come from an ongoing experiment on fire frequency in a Florida sandhill that began in 1976; as a result, our study plots have been through more repeated burn–no burn cycles, of greater variation in length, than in other studies elucidating the effect of fire frequency on longleaf pine communities.

Methods

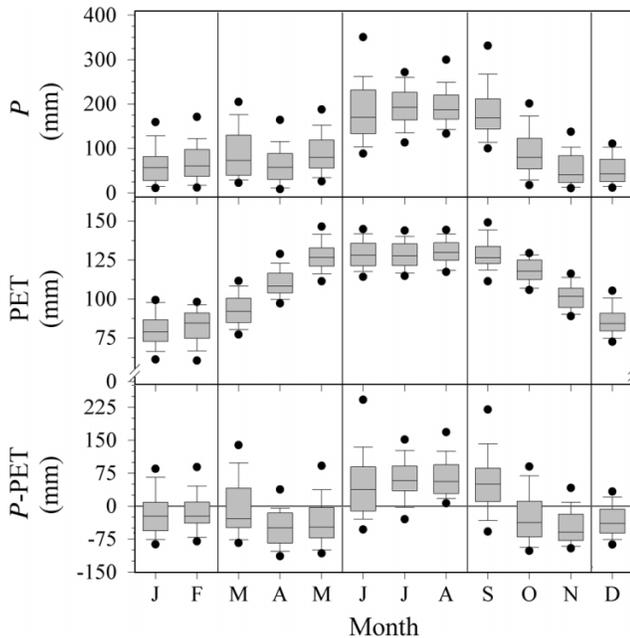
Study system and site

The study site is located in the University of South Florida's Ecological Research Area in Tampa, Florida (27°57'N, 82°32'W). Climate in the area is classified as humid subtropical with mild winter temperatures (long-term mean 17.5 °C) and hot summer temperatures (long-term mean 27.3 °C). Precipitation events occur year-round (long-term mean 1314 mm·year⁻¹); however, 57% of the annual precipitation occurs during June–September and precipitation deficits in relation to potential evapotranspiration regularly occur in all other months (Fig. 1).

The 200 ha Ecological Research Area borders the Hillsborough River and ranges in elevation from 7 to 18 m. The xeric sandhill communities are found at the highest elevations and occur on excessively well-drained, deep, sand-textured soils with little horizon development predominately in the entisol order. Soil types are primarily Candler and Pomello fine sands. Dominant tree species in this community are longleaf pine and xeric oak species (*Quercus laevis* Walt., *Quercus incana* Bartr., and *Quercus geminata* Small). Dominant subcanopy tree and shrub species are saw palmetto (*Serenoa repens* (Bartr.) Small), sparkleberry and deerberry (*Vaccinium* spp.), and winged sumac (*Rhus copalimum* L.). Dominant grass and herbaceous species are wiregrass (*Aristida stricta* Michx.), broomsedges (*Andropogon* spp.), and dog fennel (*Eupatorium compositifolium* Walt.) (Schmidt 2005). Prior to acquisition in 1956 by the University, the Ecological Research Area was primarily used for pasture and as a source of turpentine and timber. The present condition of the xeric sandhill communities in the Ecological Research Area is typical of second-growth longleaf stands, with a mean tree age of 45 years but ranging up to 100 years (described below).

Within the sandhill community type, 10 plots of approximately 1 ha were established on similar soils (see above) and randomly assigned ($n = 2$ replicates, east and west) to a prescribed fire-return interval of 1, 2, 5, or 7 year (treatment plots) or unburned. All prescribed fire treatments occurred during late spring and summer months (mid-May through early August), with treatments beginning in 1976. In general, most burns occurred as scheduled; however, during some years, no burning took place for various reasons (e.g., 1994, 1995, and 1997) (see Fig. 2). These events mainly affected the 1- and 2-year fire-return interval treatments, resulting in actual mean intervals of 1.5 and 3 years. Despite these irregularities, we retained the treatment names; however, the 1- and 2-year treatments should be thought of generally as “more frequent” and 5- and 7-year treatments of as “less frequent” fire-return intervals.

Fig. 1. Average monthly abiotic data: precipitation (P) (1895–1998), potential evapotranspiration (PET) (1948–1996), and P -PET. Vertical dividing lines denote seasons. Boxes show the median (line) and 25th and 75th percentiles (box ends), the box whiskers are the 10th and 90th percentiles, and the 5th and 95th percentiles are denoted as points.



Effects of fire-return interval on stand and longleaf pine population structure

To characterize the community and size structure of the longleaf pine population in each plot, we subsampled whole plots by randomly placing a minimum of 51 quadrats measuring 2 m × 10 m in each plot. This design allowed us to sample between 6% and 15% of the area of each whole plot. Within each quadrat, we identified and counted all nonherbaceous species. All individuals that were at least 1.5 m tall had diameter measurements taken at this height. For the cabbage palm (*Sabal palmetto* (Walt.) Lodd. ex J.A. & J.H. Schultes) and saw palmetto individuals, we also measured the percent ground cover. For longleaf pines, we categorized each individual into one of four developmental stage classes: grass (apical meristem at or below ground surface), bolting (height <1.5 m), small tree (height >1.5 m and diameter <5 cm), or large tree (diameter >5 cm). We also measured the height of all bolting-stage individuals. For all other tree species, we categorized each individual into either the sprout–sapling stage (height <1.5 m) or tree stage (height ≥1.5 m). We surveyed all plots in the spring of 2000.

To determine if significant differences in the population stage structure existed among plots with differing fire-return intervals, we used a loglinear model to analyze the counts of individuals in the subplots. Loglinear models are appropriate for count data and are a particular case of generalized linear model (McCullagh and Nelder 1989). We modeled the counts as a function of the fire-return interval, stage class, and their interaction (while adjusting for the area sampled) using analysis of deviance (a generalization of analysis of variance; McCullagh and Nelder 1989) (PROC GENMOD, SAS Institute Inc., Cary, North Carolina). We conducted

pairwise comparisons of interaction terms, e.g., the density of grass-stage plants was compared between all pairs of fire-return intervals. To make these comparisons, we calculated the differences between expected values for interval pairs (e.g., the difference between the least-square means of grass-stage density in the 5- and 7-year intervals). We used Wald χ^2 tests, with $\chi^2 = \theta^2/\text{var}(\theta)$ and 1 df, where θ is the difference between the expected values for interval pairs. We used the Type III approach to the analysis of deviance for the loglinear model.

Effects of fire-return interval on tree growth

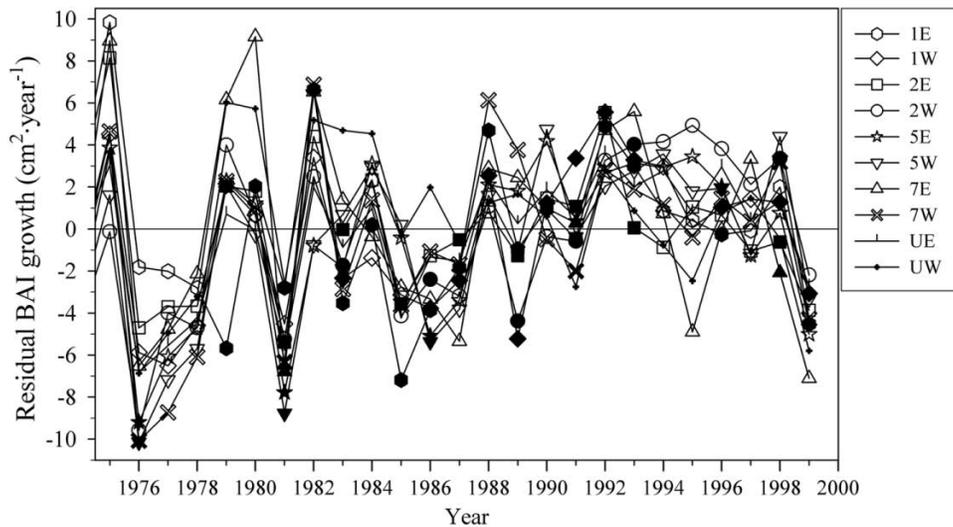
To determine the effect of fire and fire-return interval on growth, we used tree-ring growth measurements on trees in treatment and unburned plots coupled with the long-term burn history record. We targeted the 17 largest trees in each plot for tree-ring sampling. We assumed that the likelihood of obtaining at least a 24-year tree-ring record from these individuals was higher than if we had sampled smaller diameter trees. In 2000, we extracted two increment cores per tree at least 90° apart at breast height (1.34 m above the ground surface) using an increment borer (Haglöf Inc., Långsele, Sweden). After collection, cores were dried, mounted, and surfaced (Stokes and Smiley 1968) and cross-dated visually (Schweingruber et al. 1990; Yamaguchi 1991); quality control of visual cross-dating was checked with the COFECHA software program (Holmes 1983; Grissino-Mayer et al. 1997). Cores were measured to the nearest 0.001 mm under a 40× stereoscope (Olympus SZ-4045) (Japan) with a linear-encoded (Acu-Rite Inc., Jamestown, New York) measurement stage using the Velmex system (Bloomfield, New York). From tree-ring width measurements, we estimated annual basal area increment (BAI), assuming that the cross-sectional area of the stem approximated the area of a circle. BAI series from an individual tree were averaged; then, series from all trees in each plot were averaged into a BAI site chronology. We tested for significant differences in mean BAI among fire-return interval treatments during 1976–1999 using a single-factor, completely randomized design with two replicates (PROC ANOVA, SAS software) and performed a post hoc mean separation using Duncan's NMR test.

Because the long-term growth trend in BAI was Gaussian shaped for all plots, we factored out this trend by fitting a three-parameter Gaussian curve to each BAI plot series. For each site, the residuals from the curve fit (see Fig. 2) were then used as the dependent variable in all further analyses.

To assess the effect of fire on growth during fire years, we calculated the mean residual BAI during fire years and nonfire years for each treatment plot. We restricted our analysis to the period spanning 1976–1999, which corresponded to the period of prescribed burning treatments. We performed two t tests with eight replicates testing the hypotheses that residual BAI growth during fire and nonfire years was not significantly different from zero or below average (PROC TTEST, SAS software).

To assess the effect of fire-return interval on growth during fire and nonfire years, we calculated the difference between residual BAI of treatment plots in fire years and the mean residual BAI of unburned plots in those same years. Similarly, to assess the effect of fire-return interval on

Fig. 2. Residual annual basal area increment (BAI) growth of large trees ($n = 17$) in each plot during the 1976–1999 study period. The burn schedule began in 1976. The solid symbols denote years when plots were burned.



growth during nonfire years, we calculated the mean difference between residual BAI of treatment plots in nonfire years and the mean residual BAI of unburned plots in those same years. These two variables can be interpreted as the effect that fire-return interval had on growth during fire and nonfire years, independent of climate effects. Negative differences indicate negative effects of fire-return interval and positive differences indicate positive effects. The magnitude of the difference also indicates the strength of the effect, with larger numbers having a larger effect on growth than smaller numbers. We tested for significant differences among fire-return interval treatments using a single-factor, completely randomized design with two replicates (PROC ANOVA, SAS software) and performed a post hoc mean separation using Duncan's NMR test.

To address the question of how long fire in a current year affected growth in subsequent years, we used the difference between residual BAI of treatment and unburned plots in the 5- and 7-year treatments only. We tested for significant differences in the difference in residual BAI among the 5 years comprising the year of the fire and the 4 years following the fire. We used a single-factor, randomized block design with four replicates (PROC GLM, SAS software) where each plot was the blocking factor and accounted for nonindependence in repeated measures of BAI within the plot, and time since burn was the single treatment factor with five levels ($j = 0, 1, \dots, 4$ years). We performed a post hoc mean separation using a simple t test to not only separate the levels of treatment but also to test the hypothesis that the mean value of each treatment level was not significantly different from zero. All statistical tests were performed at the $\alpha = 0.05$ level (two-tailed).

Results

Effects of fire-return interval on stand and longleaf pine population structure

Fire-return interval significantly impacted stand structure and composition (Table 1), supporting our first hypothesis. Stands were relatively open with low basal area. As ex-

pected, frequent fires (every 1–2 years) were associated with more open structured stands with lower tree densities (fire return interval effect $\chi^2 = 142.10$, $P < 0.0001$) than those found in the less frequently burned plots. Although total basal area tended to increase with increasing fire-return interval, this was not statistically significant ($F_{[4,5]} = 4.03$, $P = 0.08$). Oak species were more dense than any other tree species in all fire-return interval plots; however, the structure of the oak community differed among fire-return intervals (significant interaction $\chi^2 = 290.71$, $P < 0.0001$). Oak individuals encountered were more likely to be in the sprout or sapling stage than the tree stage; however, the likelihood of encountering an oak in the tree stage increased with length between fires (Fig. 3).

Fire-return interval also significantly impacted longleaf pine population stage structure (Fig. 4), again supporting our first hypothesis. Longleaf pine individuals were distributed unevenly among developmental stages (stage class effect $\chi^2 = 681.14$, $P < 0.0001$). In addition, some fire-return intervals had higher counts of longleaf pines than others (fire-return interval effect $\chi^2 = 79.67$, $P < 0.0001$); however, the distribution of individuals among stage classes was not the same for all fire-return intervals (significant interaction $\chi^2 = 352.26$, $P < 0.0001$).

Differences in grass-stage longleaf pine density among all fire-return intervals were statistically significant ($P < 0.01$). The largest disparity in grass-stage density, roughly an order of magnitude, was found between the 1-, 2-, and 5-year intervals on the one hand and the 7-year and unburned plots on the other. Indeed, a longleaf individual picked at random out of the 1-, 2-, and 5-year plots would be a grass-stage plant 85% of the time. It is also worth noting that while densities of grass-stage plants in 7-year and unburned plots were lower than in plots more frequently burned, they were nevertheless substantial (e.g., roughly 15% of that found in 1-, 2-, and 5-year plots).

Within the bolting stage, a more subtle pattern of variation in longleaf pine density emerged: we found significantly more bolting plants in the unburned plots than in any burn plots ($P < 0.01$). There were also significantly more

Table 1. Species distribution and stand structure of woody tree species, palms, and palmettos.

	Fire-return interval plot									
	1E	1W	2E	2W	5E	5W	7E	7W	UE	UW
Tree density (stems-ha⁻¹)										
<i>Diospyros virginiana</i>	0	50	10	0	0	30	20	0	20	50
<i>Pinus elliotii</i>	0	20	0	0	10	0	0	30	30	10
<i>Pinus palustris</i>	90	40	70	140	270	110	100	190	360	200
<i>Prunus seritona</i>	0	0	0	0	0	0	0	0	10	10
<i>Quercus incana</i>	90	30	0	0	10	0	60	10	50	0
<i>Quercus laevis</i>	90	220	190	250	460	440	340	410	750	610
<i>Quercus virginiana</i>	280	120	50	0	40	0	80	580	200	250
Total density (least-square mean)	517d		355e		684c		913b		1265a	
Sprout or sapling density (stems-ha⁻¹)										
<i>Diospyros virginiana</i>	820	1030	2740	1240	100	600	3260	380	410	850
<i>Pinus elliotii</i>	0	0	0	0	50	20	0	30	40	120
<i>Pinus palustris</i>	1250	446	600	1808	2385	5324	186	346	588	627
<i>Prunus seritona</i>	0	0	0	0	0	0	59	0	10	10
<i>Quercus incana</i>	650	450	130	70	40	90	60	150	510	20
<i>Quercus laevis</i>	1900	1820	3330	4580	4560	4400	1460	3090	1000	230
<i>Quercus virginiana</i>	1660	3610	1030	720	2710	2390	2320	1970	1600	960
Basal area or percent cover (m²-ha⁻¹)										
<i>Diospyros virginiana</i>	0.00	0.03	0.00	0.00	0.00	0.01	0.00	0.00	2.53	0.13
<i>Pinus elliotii</i>	0.00	0.33	0.00	0.00	0.09	0.00	0.00	0.40	0.05	0.40
<i>Pinus palustris</i>	2.13	2.89	4.98	6.75	3.85	7.05	5.86	4.78	3.80	2.19
<i>Prunus seritona</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.02
<i>Quercus incana</i>	0.21	0.05	0.00	0.00	0.01	0.00	1.60	0.50	0.35	0.00
<i>Quercus laevis</i>	0.30	1.01	2.13	2.08	0.62	0.62	3.81	1.49	4.40	4.32
<i>Quercus virginiana</i>	3.36	1.64	0.03	0.00	0.41	0.00	0.40	6.16	3.50	1.81
<i>Sabal palmetto</i>	4.30	0.00	16.70	0.00	4.60	0.30	14.40	0.00	0.60	43.70
<i>Serenoa repens</i>	280.50	428.80	215.20	256.90	441.90	272.30	442.70	675.90	985.10	247.60
Total basal area	6.00	5.94	7.14	8.83	4.97	7.68	11.67	13.33	14.63	8.87

Note: E, east; W, west; U, unburned. Tree density included individuals ≥ 1.5 m tall. Sprout or sapling density included shorter individuals. Longleaf pine sprout and sapling totals include grass-stage and bolting-stage classes and tree totals include small and large trees. Total tree densities among fire return intervals not sharing the same letter were significantly different at $P < 0.05$.

bolting plants in the 1-year than in the 2-year plots ($\chi^2 = 3.88$, $P = 0.05$); no other comparisons of bolting plant densities were statistically significant. Height of the bolting longleaf pines tended to be greater in the longer fire-return interval plots (5 and 7-year and unburned plots) compared with the shorter fire-return interval plots (22 ± 7 versus 50 ± 9 cm, respectively) (Fig. 5); however, this was not statistically significant.

Density of small longleaf pine trees appeared to increase with decreasing fire frequency. We found no small longleaf pine trees in our subsamples of the 1- and 2-year plots. The differences between 5- and 7-year intervals in small longleaf pine tree densities were not significant ($\chi^2 = 0.47$, $P = 0.49$), but the unburned plots had significantly more small trees than either the 5- or 7-year plots ($\chi^2 = 8.00$, $P = 0.005$ and $\chi^2 = 5.27$, $P = 0.02$, respectively). Densities of large longleaf pine trees differed significantly only between the 1- and 5-year and the 1-year and unburned plots ($\chi^2 = 7.66$, $P = 0.006$ and $\chi^2 = 7.83$, $P = 0.005$, respectively). Because there were so few small longleaf pine trees in the frequently burned plots, but relatively minor differences in the large longleaf pine tree densities among fire-return intervals, the average diameter of trees tended to decline with increas-

ing time between fires, although this was not statistically significant ($F_{[4,5]} = 2.06$, $P = 0.22$) (Fig. 5).

The density distribution among longleaf pine stages tended to be more bimodal or uneven in the shorter fire-return interval plots and more even in the longer fire-return interval and unburned plots. For example, all stage classes in the 7-year plots, aside from the grass stage, had statistically similar plant densities in them. In contrast, each stage class had a distinctly different density of plants in the 1-year plots.

Effects of fire and fire-return interval on tree growth

Fire was associated with below-average tree growth in all treatment plots, supporting our second hypothesis (Fig. 6). Across all fire-return intervals, tree growth during fire years was significantly less than average ($t = -5.86$, $P < 0.01$), while mean growth during all nonfire years was not significantly different from the overall average ($t = 0.34$, $P = 0.74$). Thus, during fire years, tree growth was significantly reduced.

Adjusting for climate effects, growth during fire years depended on the fire frequency (Fig. 7). During fire years, fire-return interval significantly affected residual BAI in treat-

Fig. 3. Density (log scale) of all oak species in the fire-return interval (1, 2, 5, and 7 years) treatment and unburned (U) plots as a function of stage class (sprouts and trees). Bars are the least-square mean estimates of density for the east and west replicate plots; error bars are 1 SE. Within each stage class, different letters among fire-return intervals denote significant differences ($\alpha = 0.05$).

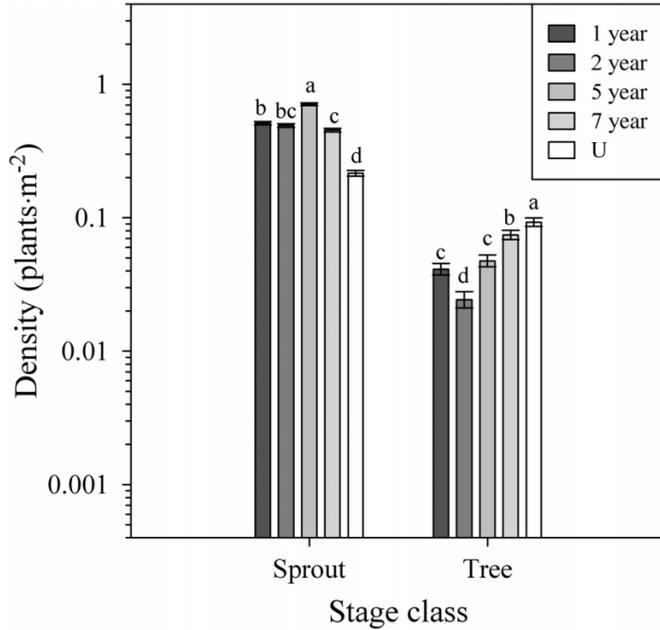


Fig. 4. Density (log scale) of longleaf pine (*Pinus palustris*) individuals in the fire-return interval (1, 2, 5, and 7 years) treatment and unburned (U) plots as a function of stage class (grass, bolting, and small and large tree). Bars are the least-square mean estimates of density for the east and west replicate plots; error bars are 1 SE. Within each stage class, different letters among fire-return intervals denote significant differences ($\alpha = 0.05$).

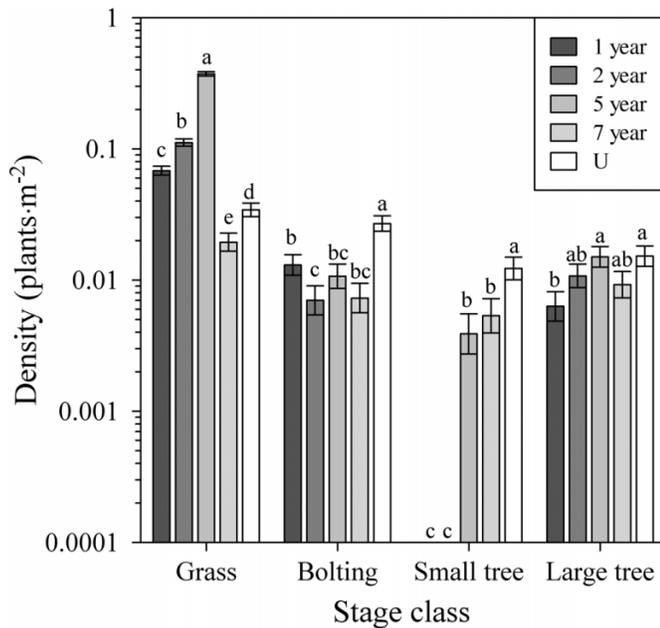


Fig. 5. Average height of all bolting stage longleaf pines (*Pinus palustris*) (upper panel) and average diameter at breast height (DBH) of all small and large trees (lower panel) surveyed in the 51 quadrats in each replicate plot ($n = 2$). Error bars are 1 SE.

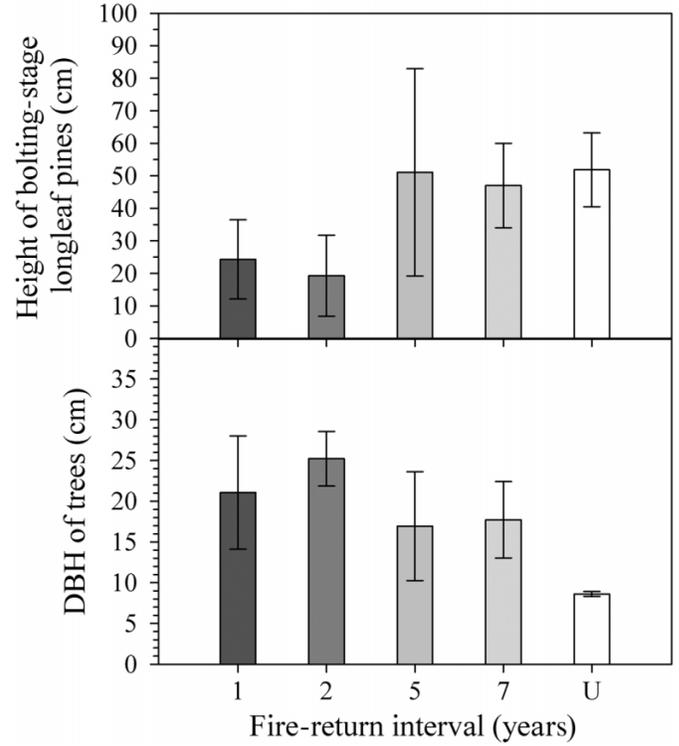


Fig. 6. Effect of fire on growth of large trees in treatment plots (excluding the unburned plots). Bars denote the mean across eight treatment plots of the residual basal area increment in all fire years and nonfire years; error bars are 1 SE. Asterisk denotes a significant departure from zero ($\alpha = 0.05$); ns, not significant.

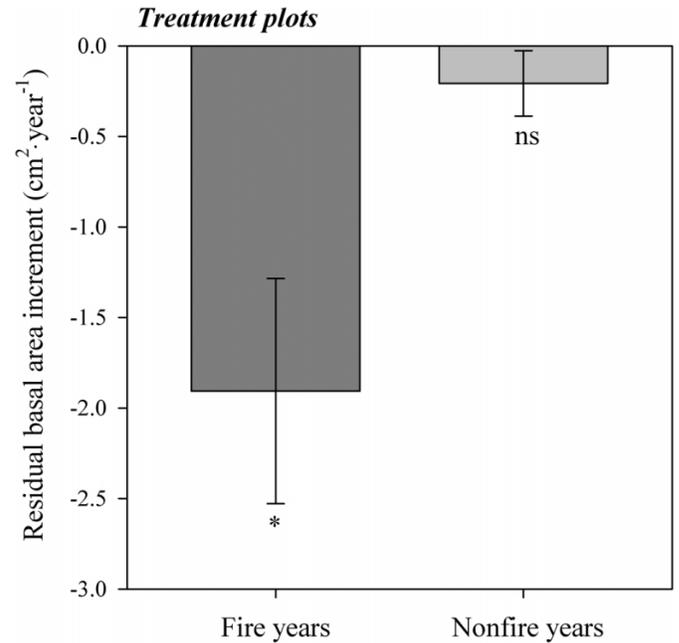
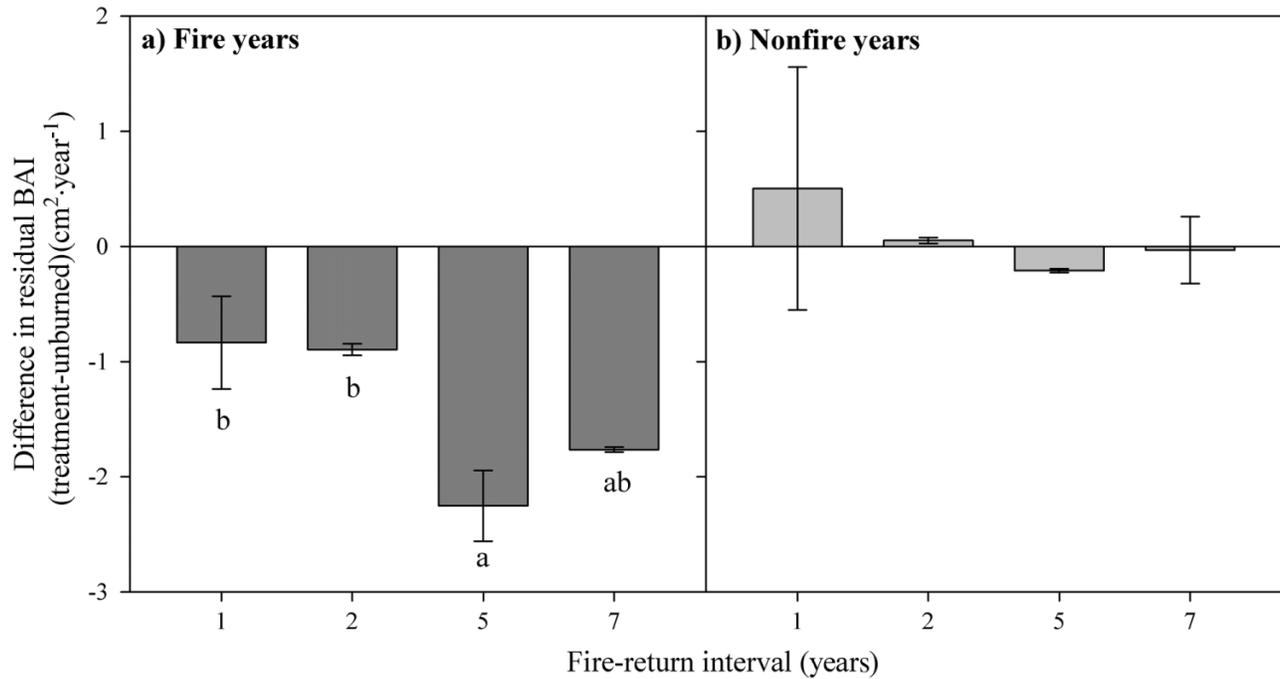


Fig. 7. Difference in residual basal area increment (BAI) between treatment and unburned trees during (a) fire years and (b) nonfire years. Bars denote the mean of two replicate plots; error bars are 1 SE. Different letters denote significant differences at $\alpha = 0.05$ if main effects were significant in the full model.



ment plots compared with unburned plots ($F_{[3,4]} = 7.34$, $P = 0.04$). Fire events in the longer fire-return intervals (5–7 years) affected growth more negatively than in the shorter ones (1–2 years). In contrast, during nonfire years, fire-return interval did not explain a significant amount of variation in residual BAI in treatment plots compared with unburned plots ($F_{[3,4]} = 0.31$, $P = 0.82$).

For the 5- and 7-year fire-return interval treatments, we found a pattern indicating recovery after fire during those nonburn years (time effect $F_{[4,12]} = 4.97$, $P = 0.01$) (Fig. 8). In these longer fire-return interval plots, the negative impact of fire on BAI was apparent not only during the year the fire occurred but also for 1 year after the fire. By the second year after the fire, residual BAI was not significantly different from that in the unburned plots.

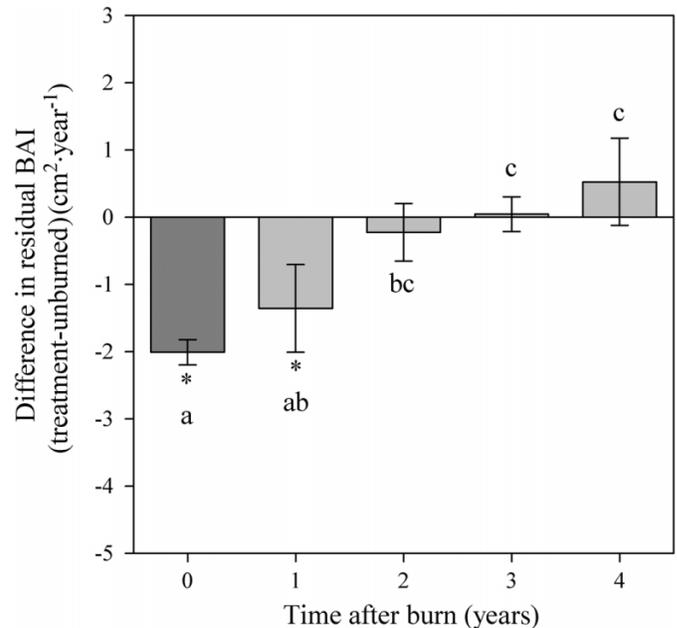
These analyses indicate a negative effect of fire on tree growth, and this effect is more negative for longer fire-return intervals. Given our result that growth recovery after fire occurred within a year, we asked whether the greater number of recovered growth years compensated for the increased negative impact of fire under longer fire-return intervals. A post hoc ANOVA analyzing mean BAI (across all 24 years) as a function of fire-return interval showed that mean levels of tree growth across all study years (1976–1999) did not differ among fire-return interval treatments including the unburned plots ($F_{[4,5]} = 2.54$, $P = 0.16$) and BAI averaged 16.87 ± 0.82 (SE) cm²·year⁻¹.

Discussion

Fire effects on population structure

Longleaf pine population structure depends strongly on fire frequency, either directly through the effect of fire or indirectly through changes in stand structure and fire behavior.

Fig. 8. Relationship between difference in residual basal area increment (BAI) between 5- and 7-year fire-return interval treatment trees and unburned trees and time since last burn. Bars denote the mean of four replicate plots; error bars are 1 SE. Different letters denote significant differences among years and asterisks denote means that are significantly different from zero ($\alpha = 0.05$).



Under short (1–2 years) fire-return intervals, the population structure was bimodal, with numerous large adults and numerous grass-stage and juvenile plants but almost no small trees. Frequent fires decrease the frequency and density of hardwood tree competitors and foster relatively open land-

scapes with numerous canopy gaps, which, in turn, increase space and resources for longleaf pine recruitment (Battaglia et al. 2002; Palik et al. 2003; Rodríguez-Trejo et al. 2003). In addition, frequent fires decrease fuel loads and thus decrease fire intensity (Hiers et al. 2009). Our data clearly show that frequent fires were associated with significantly more longleaf pine grass-stage individuals. What is less clear, however, is the mechanism governing the bimodal structure. One hypothesis is that fires returning every 1–2 years increase juvenile mortality enough to halt the recruitment of juveniles into larger size classes. An alternative hypothesis is that dispersal into open patches causes a lag in increases of adult density. Although these hypotheses are not mutually exclusive, we argue below that there is evidence in favor of the former hypothesis but none in favor of the latter.

The low densities of small trees in the frequently burned plots suggest that there was little recruitment from the bolting stage into the next larger size class and, correspondingly, little to no recruitment from the small-tree stage into the large-tree stage. In support of this point, the average diameter of all of the trees surveyed (encompassing both small and large trees) tended to decrease with increasing length between fires. In other words, the average diameter at breast height of all trees in the 5-year and 7-year and unburned plots was lower because there were more small trees compared with the 1- and 2-year plots. We do not know the ages of these particular trees, but because diameter and age are correlated (Platt and Rathbun 1993), this result implies that, on average, trees in the less frequently burned plots were younger than those in the plots more frequently burned. Additional support for this inference comes from our dendrochronological work: the variance in year of establishment (assessed at breast height) increased with increasing interval between fires (data not shown). Furthermore, the height of the bolting-stage longleaf pines in the 1- and 2-year plots was less than half the height of those found in the other plots, and the greatest density of bolting-stage longleaf pines was found in the unburned plots. The likely high postfire mortality rates of bolting-stage longleaf pines could be limiting recruitment into the tree stage class in these plots. Other studies have shown that mortality rates of grass-stage and juvenile longleaf pines after fire are high, e.g., 80% (Boyer 1974; Platt et al. 1988; Grace and Platt 1995), and specifically, after fire, grass-stage mortality rates are higher than the mortality rates of small and large longleaf pine trees (Platt et al. 1988). However, grass-stage longleaf pines can readily resprout, whereas once height growth is initiated (i.e., bolting stage), resprouting is not observed (Boyer 1974; Brockway et al. 2006). If mortality rates this high occur for long sequences of years, juvenile survival will be a rare event indeed. For example, if only 20% of juveniles survive fires (Grace and Platt 1995) for 5 years in a row, the fraction surviving will be $0.2^5 = 0.0003$. Whether burning at 1- or 2-year intervals, other studies have found similar mortality and recruitment rates between these two frequencies (Glitzenstein et al. 1995). The similarity in population structure between our 1- and 2-year plots also agrees with this finding.

The other hypothesis explaining the bimodal population structure in the 1- and 2-year plots is that recruitment into

large open spaces might be limited by seed dispersal. If the open spaces created by fires in the 1- and 2-year plots are greater than the average dispersal distances from adult trees, then long time lags between increases in adult density could result. The mean seed dispersal distance for longleaf pine is about 20–40 m (Platt et al. 1988); if large gaps (>40 m in radius) existed in the 1- and 2-year plots, then long time lags between increases in adult density could result (Platt et al. 1988). This hypothesis, then, predicts that adult trees are at low density, $<0.0008 \text{ plant}\cdot\text{m}^{-2}$ (i.e., one adult plant in an area with radius of 20 m) in our 1- and 2-year plots. This was not the case, however. In our 1- and 2-year plots, we had a minimum adult density five times as great as this, $0.004 \text{ plant}\cdot\text{m}^{-2}$, suggesting that dispersal into gaps was not limiting recruitment into or causing a time lag in small tree density.

In contrast, a more even population structure existed in plots less frequently burned (5- and 7-year plots). Although direct evidence of historic fire frequency in longleaf pine communities is generally lacking, one recent study has provided a quantitative determination of the historic fire frequency in one longleaf pine savanna (Huffman 2006). In that study, longleaf pine annual xylem growth rings dated for fire events during 1679–1868 showed that 95% of all fires dated returned within 6 years and 72% of all fires dated were 1–3 years in frequency.

Our data suggest that young longleaf pines in the bolting stage, when repeatedly burned (every 1 or 2 years), have a low recruitment into the next size class. This agrees with early observations that saplings that have already initiated height growth are extremely vulnerable to fire (Heyward 1939; Wahlenberg 1946), more so than grass-stage seedlings. Although frequent fire disturbance has been interpreted as a process that serves to “spatially buffer” the longleaf pine population against both declines in population density and increases in extinction risk (Platt et al. 1988), our results suggest that persistent 1- to 2-year fire-return intervals may affect the population structure and reduce population growth rates more than 5- to 7-year burns. Other variables, such as fire behavior and intensity, are indirectly affected by fire-return interval through accumulation of fuels, fuel quality, and stand structure. Hence, these variables cannot be decoupled from fire frequency and may also strongly influence population structure and growth of longleaf pine.

Fire and fire-return interval effects on secondary growth

We found that fire negatively impacted secondary growth of adult longleaf pines during fire years. Although systems dominated by longleaf pine are naturally fire-disturbed systems, and species comprising this community likely evolved under this disturbance pressure, it is clear that on short time scales, the effect of fire on the growth of individual longleaf pines is a negative one. Other studies have also shown that productivity of individual longleaf pine trees decreases when managed with fire (Boyer 2000; Haywood and Grelen 2000), possibly because fires can damage the crown and cambium (Huffman 2006). At the population level, fire can also have a negative effect; fire is the second leading cause of tree mortality, lightning strikes being the primary cause (Palik and Pederson 1996; Outcalt 2008). Over time scales

spanning multiple years or decades, fire did not negatively impact individual adult tree growth in a significant way, as we found no significant differences in mean growth among treatments. Fire suppresses growth of hardwood species, reducing competition for light, water, and nutrients, and thus has a positive effect on longleaf production over longer time scales.

During fire years, longer fire-return intervals (e.g., 5–7 years) had a more negative impact on growth of adult longleaf pine than shorter fire-return intervals (e.g., 1–2 years). Several scenarios (which are not mutually exclusive) could explain this result. With longer fire-return intervals, more fuels could have accumulated, thus increasing fire intensity and enhancing the likelihood of cambial, leaf, or root damage. Conversely, lower fire intensities can arise in scenarios of frequent fires that impart a high degree of fire patchiness due to lower fuel accumulation between burns. For example, Glitzenstein et al. (1995) found that a longer fire-return interval allowed more fuel to accumulate, resulting in a more intense fire and thus more negatively affected diameter growth of longleaf pines (>20 cm) compared with a shorter fire-return interval. Alternatively, in our study, the trees in the 5- and 7-year plots could have taken longer to resume secondary growth, to a level proportional to climate immediately after the fire events, than trees in the 1- and 2-year plots. If more intense fires in the 5- and 7-year plots led to tissue damage, and subsequent carbon was allocated to leaf or fine root growth instead of secondary xylem growth, this pattern would have resulted.

In the longer fire-return interval plots, growth in the year following a fire event was also negatively affected, but growth returned to average levels during the time between fire events. This suggests that negative effects are ameliorated during the time between fires. If stored carbon reserves in structural tissues were mobilized to supply carbon to other tissues playing more active roles in nutrient or carbon uptake (i.e., fine roots and leaves), then recovery from fire events could occur relatively quickly. Guo et al. (2004) found that 2 months after canopy scorching in longleaf pine, total nonstructural carbohydrates showed the largest decrease in structural roots, while terminal fine roots showed no decrease in total nonstructural carbohydrates. They also hypothesized that in systems adapted to frequent disturbance, carbon reserves in structural tissues, such as coarse roots and stem tissue (Kozłowski and Pallardy 1996; Newell et al. 2002), metabolically buffer other tissues. Both stored carbon reserves (Varner et al. 2009) and a rooting morphology that may allow access to groundwater (Ford et al. 2008) may confer higher rates of growth in otherwise arduous conditions. These also could explain the resiliency in productivity of this species after fire and shed light on the relatively poor climate–growth correlations that others have found for longleaf pine (West et al. 1993; Foster and Brooks 2001).

Conclusions

Longleaf pine as a species displays individual and population characteristics that are buffered against severe disruption from fire, both spatially and temporally. While there is a common perception in the ecological literature that longleaf pine is fire dependent, in the very narrow sense that they would go extinct without fire, our study shows that the

longleaf population is strongly regulated by fire and fire-return interval plays a key role in structuring this population. With fires occurring very frequently, e.g., every 1 or 2 years, population structure becomes significantly different from that in 5- and 7-year and unburned plots, with recruitment from the grass and bolting stages into the tree stage potentially being the most negatively affected. Adult tree growth is also reduced in fire years. Interestingly, trees are resilient in growth during years between fire events such that average growth did not differ significantly among fire-return interval treatments in this study. Further research along the geographic range of longleaf pine is needed to reveal whether the effect of fire and fire-return interval on individual and population stage structure is generally true and over what range of fire intervals. Such studies can also shed light on the extent to which results from our site, near the southern edge of the range for longleaf pine, are general.

Although numerous studies show generally positive effects of burning at short fire-return intervals on the understory community in longleaf-dominated woodlands, our study is the only long-term, replicated experiment to elucidate the cumulative effects of fire and fire-return interval on population structure and growth of longleaf pine itself. Clearly, while prescribed fire is an essential management tool in the preservation and restoration of these communities, it is possible that prescribing a frequent and relatively static burn schedule could yield unintended structural and functional consequences. We suggest that further studies of the demography and growth of longleaf pine, in addition to their intrinsic interest, may inform management programs about the effects of fire on both understory and tree populations. In restoration management situations, a dynamic burn schedule, for example, burning initially at 1- and 2-year intervals followed by longer, more-variable fire-return intervals, would serve to initially open the landscape, promote seedling establishment, and confer to those seedlings a greater chance of surviving into adulthood, which would ultimately increase the longleaf pine population compared with a static 1- to 2-year fire-return interval.

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