Dems et al. Fire Ecology (2021) 17:10
https://doi.org/10.1186/s42408-021-00093-5

Fire Ecology

FIELD NOTE Open Access

Prescribed fire alters structure and composition of a mid-Atlantic oak forest up to eight years after burning

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Abstract

Background: Prescribed fire in Eastern deciduous forests has been understudied relative to other regions in the United States. In Pennsylvania, USA, prescribed fire use has increased more than five-fold since 2009, yet forest response has not been extensively studied. Due to variations in forest composition and the feedback between vegetation and fire, Pennsylvania deciduous forests may burn and respond differently than forests across the eastern US. We measured changes in forest structure and composition up to eight years after prescribed fire in a hardwood forest of the Ridge and Valley region of the Appalachian Mountains in central Pennsylvania.

Results: Within five years post fire, tree seedling density increased more than 72% while sapling density decreased by 90%, midstory density decreased by 46%, and overstory response varied. Following one burn in the mixed-oak unit, overstory tree density decreased by 12%. In the aspen–oak unit, where pre-fire harvesting and two burns occurred, overstory tree density increased by 25%. Not all tree species responded similarly and post-fire shifts in species relative abundance occurred in sapling and seedling size classes. Abundance of red maple and cherry species decreased, whereas abundance of sassafras, quaking aspen, black oak, and hickory species increased.

Conclusions: Forest composition plays a key role in the vegetation–fire relationship and localized studies are necessary to measure forest response to prescribed fire. Compositional shifts in tree species were most pronounced in the aspen–oak unit where pre-fire overstory thinning and two prescribed fires were applied and significant structural changes occurred in all stands after just one burn. Increases in fire-tolerant tree species combined with reductions in fire-intolerant species highlight the role of prescribed fire in meeting management objectives such as altering forest structure and composition to improve game habitat in mid-Atlantic hardwood forests.

Keywords: *Acer*, fire management, hardwood forest, post-fire tree mortality, *Quercus*, Ridge and Valley

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Resumen

Antecedentes: Las quemas prescriptas en los bosques deciduos del Este, han sido poco estudiadas en relación a otras regiones en los Estados Unidos. En Pensilvania, EEUU, las quemas prescriptas se han incrementado más de cinco veces desde 2009, aunque sus respuestas en los bosques no han sido extensivamente estudiadas. Debido a variaciones en la composición del bosque y a la retroalimentación entre fuego y vegetación, los bosques deciduos de Pensilvania pueden quemarse y responder demanera diferente que otros bosques a través del Este de los EEUU. Medimos cambios en la composición y estructura del bosque hasta ocho años después de una quema prescripta en un bosque de la región del valle de las montañas Ridge en los Apalaches del centro de Pensilvania.

Resultados: Dentro de los cinco años post incendio, la densidad de plántulas se incrementó más del 72%, la densidad de brinzales (árboles jóvenes) decreció en un 90%, la densidad del sotobosque de media altura decreció en un 46% y la respuesta del dosel superior fue variable. Después de una quema en la unidad de roble-álamo, la densidad del dosel superior decreció en un 12%. En la unidad de roble-álamo, donde se realizó una corta pre fuego y luego dos quemas, la densidad del doselsuperior se incrementó en un 25%. No todas las especies respondieron de manera similar y desviaciones en la abundancia relativa de especies ocurrieron en tamaños y clases de edad de plántulas y brinzales. La abundancia del arce rojo y de especies de cerezo decrecieron, mientras que aumentó la abundancia de especies como el sasafrás, álamo temblón, roble negro y nogal americano.

Conclusiones: La composición del boque juega un rol clave en la relación fuego-vegetación, y estudios localizados son necesarios para medir la respuesta del bosque a lasquemas prescriptas. Las desviaciones en la composición de especies fueron más pronunciadas en la unidad de roble-álamo, donde un raleo pre fuego del dosel superior y dos quemas prescriptas fueron aplicadas, ocurriendo cambios estructurales significativos en todos los rodales con solo una quema. El incremento de especies de árboles tolerantes al fuego combinado con la reducción de especies intolerantes alfuego, destaca el rol de las quemas prescriptas en la consecución de objetivos de manejo, como la alteración de la estructura del bosque y su composición para mejorar el hábitat para la fauna en los bosques Atlánticos de madera dura de los EEUU.

Background

Prescribed fires are planned disturbances used to influence forest structure and composition with varying effects across regions (Ryan et al. 2013). Prescribed fire is relatively understudied in the eastern deciduous forests of the United States (Stambaugh et al. 2015; Varner et al. 2016), yet fire is increasingly used for management purposes. For example, the State of Pennsylvania passed the Prescribed Burning Practices Act in 2009, reducing the legal barriers placed on the use of prescribed fire within the state (Pennsylvania General Assembly 2009). This policy change supports the desires of multiple land agencies to use prescribed fire to promote specific forest compositions for ecological and economic benefit (Brose et al. 2008; Pennsylvania General Assembly 2009). In the seven years following the legislation, the annual number of prescribed fires in Pennsylvania increased from 56 to 222, and area burned increased from 1107 to 7532 ha (PA DCNR 2015; National Interagency Fire Center 2017), many hectares burning only once due to the barriers forest managers face when planning and implementing prescribed fires (Smithwick et al. 2020). This influx of prescribed fire is introducing disturbance to areas that have been fire free for about 80 years (Klimkos 2017), and localized forest response has not been extensively studied.

Over the past century, Eastern oak (*Quercus* spp.) forests experienced a shift in species abundance with increases in fire-intolerant species such as red maple (*Acer rubrum* L.) and limited regeneration of fire-tolerant oak (Abrams 2003; Nowacki and Abrams 2008). Reduced oak dominance is a management concern due to declines in wildlife habitat quality (Brose et al. 2008; Dey 2014), timber market stability (Brose et al. 2008), nutrient cycling (Alexander and Arthur 2010; Alexander and Arthur 2014), and understory plant diversity (Hutchinson et al. 2005). While multiple interacting factors are driving this forest change (McEwan et al. 2011), research indicates that humans played a significant role in altering the type and extent of forest disturbance (Drummond and Loveland 2010) to include landscape-scale forest clearing and homogenization of forest age (Dey 2014) as well as decreasing fire frequency (Stambaugh et al. 2018; Abrams and Nowacki 2019). Both indigenous peoples and European settlers set fires, but early twentieth century policy required all fires to be suppressed, which abruptly curbed human ignitions (Donovan and Brown 2007; Marschall et al. 2016; Lafon et al. 2017). Prescribed fire is considered a tool to reinstate disturbance in Eastern forests (Brose 2014), an idea that stems from a historical relationship between frequent fire and oak dominance (Nowacki and Abrams 2008).

One way prescribed fire alters forests is by killing trees and promoting new germination and growth. Most post-fire tree death occurs in smaller-diameter trees due to the combination of mild burn conditions (Schwilk et al. 2009) and increased fire resistance as trees get larger (Brando et al. 2012). Following prescribed fire, top-killed or injured trees of certain species use below-ground energy stores to re-sprout (Huddle and Pallardy 1999; Blankenship and Arthur 2006), and fire promotes seedling germination by consuming surface fuels, which reduces litter and duff depth (Graham and McCarthy 2006; Arthur et al. 2012; Arthur et al. 2017). Additionally, fire promotes seedling growth with temporary increases in light availability due to canopy thinning (Alexander et al. 2008). However, the extent of tree death and regrowth is dependent on time of year (Huddle and Pallardy 1999; Knapp et al. 2009), number and frequency of fires (Keyser et al. 2017), direct and indirect fire effects (Hood et al. 2018), pre-fire management (Albrecht and McCarthy 2006; Schwilk et al. 2009), landscape position (Iverson et al. 2008; Arthur et al. 2015), and tree species (Fan et al. 2011; Keyser et al. 2018). Species in Eastern forests have traits that influence their response to fire (Fan et al. 2011; Keeley et al. 2011; Pausas 2015). For example, many oak species have thicker bark, more flammable leaf litter, and greater below-ground energy stores than red maple, effectively increasing their survival and promoting fire where they are dominant (Abrams 2003; Kreye et al. 2013). Variation in species composition contributes to a feedback by which vegetation influences flammability and fire effects, and fire effects influence future vegetation (Nowacki and Abrams 2008; Mitchell et al. 2009; Tiribelli et al. 2018).

In this study, we ask how prescribed fire affects mid-Atlantic deciduous forests over time. To answer this, we measured changes in forest structure (abundance in tree size classes) and composition in the Ridge and Valley Region of the Appalachian Mountains in central Pennsylvania up to eight years after prescribed fire. We hypothesized that (H1) following one or two dormant-season prescribed fires, there would be a pulse of seedling and sprout recruitment, but a reduction of living sapling and canopy trees; and that (H2) the relative abundance of fire-tolerant tree species would increase following prescribed fire due to higher survival and regeneration relative to fire-intolerant trees. Our results expand existing knowledge of Eastern deciduous forest response to prescribed fire for multiple tree species in mixed-deciduous forests of the mid-Atlantic.

Methods

Study site

Fire effects were studied on Pennsylvania State Game Lands 176 (SGL176) in the Ridge and Valley Physiographic Province of central Pennsylvania (40.7° N, 77.9° W). SGL176 has a humid continental climate with 80 to 100 cm of annual precipitation and averages 9.4 °C throughout the year (calculated from State College data, ~7 km away; The Pennsylvania State Climatologist 2019). SGL176 is about 400 m above sea level and located in a valley floor "frost pocket," where cold air pools as it sinks from surrounding ridges (O'Neil 2006). Soils are well drained, acidic sandy loams (USDA Web Soil Survey 2019) and land use has varied over the past 200 years, including eras of iron ore mining and charcoal production (O'Neil 2006; Abrams and Johnson 2014), as well as extensive logging and human-caused fires from these activities.

To measure prescribed fire effects in SGL176, we sampled vegetation before and after burning (between 2009 and 2018). All fires were ignited by hand in spring before leaf out, conducted by the Pennsylvania Game Commission (PGC) under pre-established prescription parameters (Additional file 1), and intended to improve wildlife habitat. Forests in this area had not burned since 1939 (Klimkos 2017). Prescribed fire was applied in two units, identified here as mixed-oak and aspen–oak based on pre-fire overstory dominance (Fig. 1). The mixed-oak unit totaled 108 ha and was burned in three sections during 2010 to promote mixed oak–hickory (*Carya* Nutt. spp.) stands by reducing maple (*Acer* L. spp.), birch (*Betula* spp.), and aspen (*Populus* L. spp.) regeneration. The aspen–oak unit was 28 ha and burned in both 2014 and 2017 to restore scrub oak (*Quercus ilicifolia* Wangenh.)–pitch pine (*Pinus rigida* P. Mill) communities. Before prescribed fire use, the aspen–oak unit was actively managed for ruffed grouse (*Bonasa umbellus* Linnaeus, 1766) habitat using checkerboard mowing and overstory tree removal (alternating one-hectare squares; Palmer 2000). To identify forest changes related to prescribed fire versus those already occurring in the forest, we compared data from the two burn units to data from unburned forests in SGL176 using monitoring data from the PGC's Continuous Forest Inventory (CFI). CFI plots occur throughout PGC lands, were located in ≥20-year-old forests, and provided comparable metrics. SGL176 had three CFI plots for comparison.

Pre-fire tree species composition for the burn units and unburned plots are provided in Table 1, and initial tree density and basal area measures are presented in Fig. 2. Ground cover in the study area consisted of scattered fern (including *Pteridium aquilinum* [L.] Kuhn, *Dryopteris carthusiana* [Vill.] H.P. Fuchs, and *Dennstaedtia punctilobula* [Michx.] T. Moore) and lowbush blueberry (*Vaccinium* L. spp.) patches. Clusters of invasive privet (*Ligustrum obtusifolium* Siebold & Zucc.), bush honeysuckles (including *Lonicera maackii* [Rupr.] Herder, *Lonicera tatarica* L., and *Lonicera* × *bella* Zabel), and Japanese barberry (*Berberis thunbergii* DC) were scattered throughout the forest, and extensive deer browse created understory conditions such that

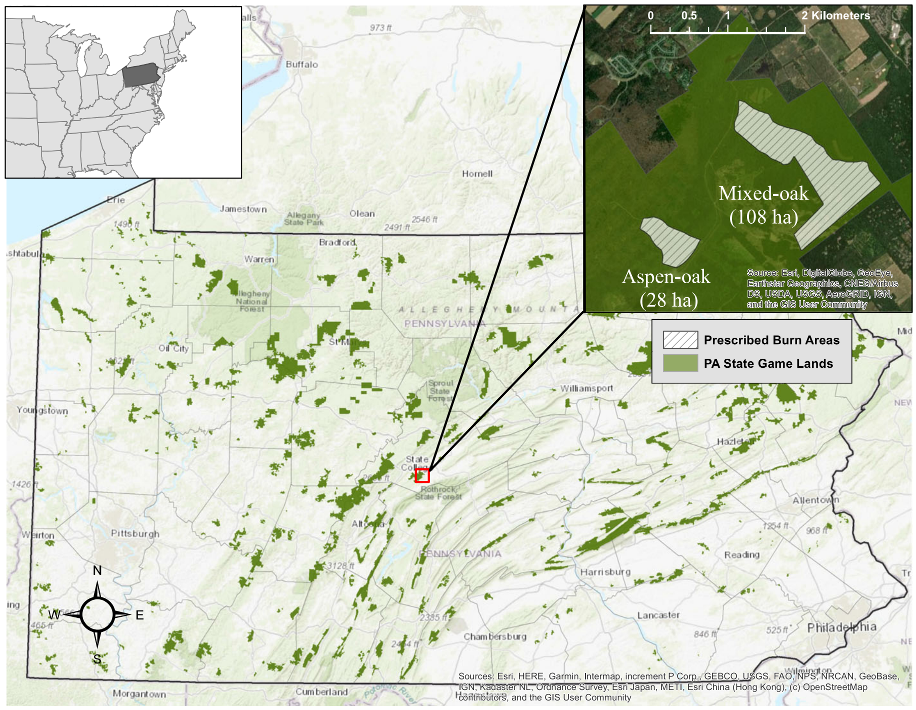

Fig. 1 Map of study area within State Game Lands 176, in central Pennsylvania, USA, where we measured changes in forest structure and composition after prescribed fire, between 2009 and 2018

hardwood leaf litter was the primary ground cover. In addition, the aspen–oak unit had a large shrub component of scrub oak and dwarf chestnut oak (*Quercus prinoides* Willd.).

Field measurements

Within the burned units, field measurements began the summer prior to the initial burn and the same protocols were repeated at various intervals for five to eight years after fire (mixed-oak unit measured in 2009, 2010, 2015, and 2018; aspen–oak unit measured in 2013, 2015, and 2018). All measurements were completed between 1 May and 31 August to capture growing season vegetation. Nested fixed area plots (12.6 m radius for overstory and midstory; 4 m for saplings; four 1.3 m for seedlings) were established within each burn unit using a systematic sampling design (mixed-oak, n = 44; aspen–oak, n = 10 [five of which were mowed or thinned pre fire]). Plots were located at least 60 m from unit boundaries and the number of plots in each burn unit was determined by unit size.

To measure forest structure and composition change over time, all living trees >5 cm tall were identified to species (to genus by some observers) and their diameter at breast height (DBH) recorded with 0.1 cm accuracy. When seedling trees (seedlings, sprouts, and suckers ≤2.54 cm DBH) were growing from the same base, only the three largest were recorded. Unburned forest plots were measured twice, in 2009 and 2014, using the PGC's CFI protocols (Bureau of Wildlife Habitat Management 2013) and slightly larger vegetation plots (16.1 m radius for overstory and midstory; 8 m for saplings; 1.3 m for seedlings) than those in the burn units.

Data analysis

Forest structure

To quantify changes in forest structure, we used linear mixed-effects models (Bates et al. 2015; R Core Team 2018) to compare living tree stem density and basal area across years. We treated year as a categorical fixed effect, independent variable and modeled mean values at the plot level. To account for the variation across plots, we included plot as a random effect and, when present, nested subplots within each plot (seedling measurements). A few plots could not be relocated during at least one year of data collection so our analysis only includes plots measured at all time points (mixed-oak, n = 40; aspen–oak, n = 7; unburned, n = 3). A small portion of the mixed-oak unit (<10%) was affected by an aspen harvest prior to burning; however, there were too few plots (n = 2) included in the harvested area to analyze them separately. Yearly differences of each response variable were analyzed with Tukey pairwise comparisons using least-squares means (Lenth 2016). All statistical tests were considered significant at α = 0.05.

Table 1 Pre-fire tree species composition by tree size class within State Game Lands 176, Pennsylvania, USA, where we measured post-fire changes in forest structure and composition between 2009 and 2018

		Pre-fire composition (% of total trees)			
		Seedlings	**Saplings**	**Midstory**	**Overstory**
		>5.08 cm tall, <2.54 cm DBH	**2.54-10.15 cm DBH**	**10.16-19.99 cm DBH**	**>19.99 cm DBH**
Unburned (measured 2009)					
Bigtooth aspen	*Populus grandidentata* Michx.	-	-	22.2	27.4
Birch	*Betula* spp.	-	-	1.9	-
Black oak	*Quercus velutina* Lam.	5.6	-	-	8.3
Cherry	*Prunus* L. spp.	-	-	3.7	-
Dogwood	*Cornus* L. spp.	-	4.2	-	-
Hickory	*Carya* spp.	3.7	-	3.9	2.8
Northern red oak	*Quercus rubra* L.	5.7	-	-	13.2
Red maple	*Acer rubrum* L.	73.7	70.8	50.9	11.5
Sassafras	*Sassafras albidum* (Nutt.) Nees	-	-	4.2	2.8
Serviceberry	*Amelanchier* Medik. spp.	0.4	12.5	-	-
White oak	*Quercus alba* L.	11.0	8.3	13.2	34.0
Mixed-oak (measured 2009)					
American chestnut	*Castanea dentata* (Marsh.) Borkh.	0.1	-	-	-
Bigtooth aspen	*Populus grandidentata*	0.4	0.7	2.9	14.3
Birch	*Betula* spp.	0.4	-	0.7	0.5
Blackgum	*Nyssa sylvatica* Marshall	0.3	0.7	-	-
Black oak	*Quercus velutina*	3.9	4.9	2.0	10.7
Cherry	*Prunus* spp.	3.4	0.7	0.9	0.6
Chestnut oak	*Quercus montana* Willd.	11.5	6.5	4.4	11.9
Dogwood	*Cornus* spp.	0.1	-	-	-
Eastern white pine	*Pinus strobus* L.	-	-	0.9	-
Hickory	*Carya* spp.	2.9	0.4	23.9	5.6
Northern red oak	*Quercus rubra*	9.0	2.9	-	2.7
Pitch pine	*Pinus rigida* MIll.	-	-	0.3	0.9
Red maple	*Acer rubrum*	46.4	71.2	33.8	15.9
Sassafras	*Sassafras albidum*	14.0	3.1	21.8	2.4
Scarlet oak	*Quercus coccinea* Muenchh.	0.4	1.6	1.5	10.7
Serviceberry	*Amelanchier* spp.	0.1	-	-	-
Striped maple	*Acer pensylvanicum* L.	0.1	-	-	-
Sugar maple	*Acer saccharum* Marshall	-	-	0.6	-
White oak	*Quercus alba*	7.1	6.0	7.4	23.8
Aspen–oak (measured 2013)					
Bigtooth aspen	*Populus grandidentata*	-	4.8	12.4	37.2
Black oak	*Quercus velutina*	0.3	7.1	0.8	2.4
Cherry	*Prunus* spp.	22.4	26.6	54.1	26.3
Dogwood	*Cornus* spp.	1.4	1.3	-	-
Hawthorn	*Crataegus* Tourn. ex L. spp.	0.2	-	-	-
Hickory	*Carya* spp.	0.6	1.8	-	-

Table 1 Pre-fire tree species composition by tree size class within State Game Lands 176, Pennsylvania, USA, where we measured post-fire changes in forest structure and composition between 2009 and 2018 *(Continued)*

		Pre-fire composition (% of total trees)			
		Seedlings	**Saplings**	**Midstory**	**Overstory**
		>5.08 cm tall, <2.54 cm DBH	**2.54-10.15 cm DBH**	**10.16-19.99 cm DBH**	**>19.99 cm DBH**
Northern red oak	*Quercus rubra*	1.0	0.4	-	-
Pitch pine	*Pinus rigida*	-	-	-	5.6
Quaking aspen	*Populus tremuloides* Michx.	-	-	4.8	-
Red maple	*Acer rubrum*	70.7	18.3	7.8	-
Scarlet oak	*Quercus coccinea*	0.2	19.0	2.6	9.5
Serviceberry	*Amelanchier* spp.	1.6	-	-	-
Spruce	*Picea* Mill. spp.	-	1.8	-	-
White oak	*Quercus alba*	1.4	19.8	17.5	19.0

Changes in live stem density and basal area were modeled separately within each forest type (mixed-oak, aspen–oak, unburned) and tree size class (seedlings, saplings, midstory, overstory). Tree size classes were designated based on sampling protocols and review of similar studies. Seedlings were <2.54 cm DBH, >5.08 cm tall, and had at least two leaves not bearing cotyledons; saplings were 2.54 to 10.15 cm DBH; midstory trees were 10.16 to 19.99 cm DBH; and overstory trees were stems ≥20 cm DBH. Seedling stem diameter was not measured and therefore seedling basal area was not calculated. Sapling trees were grouped in 2.54 cm DBH size classes and basal area was calculated using the median diameter of stems in each class. Stem density and basal area measures were log transformed, to satisfy assumptions of

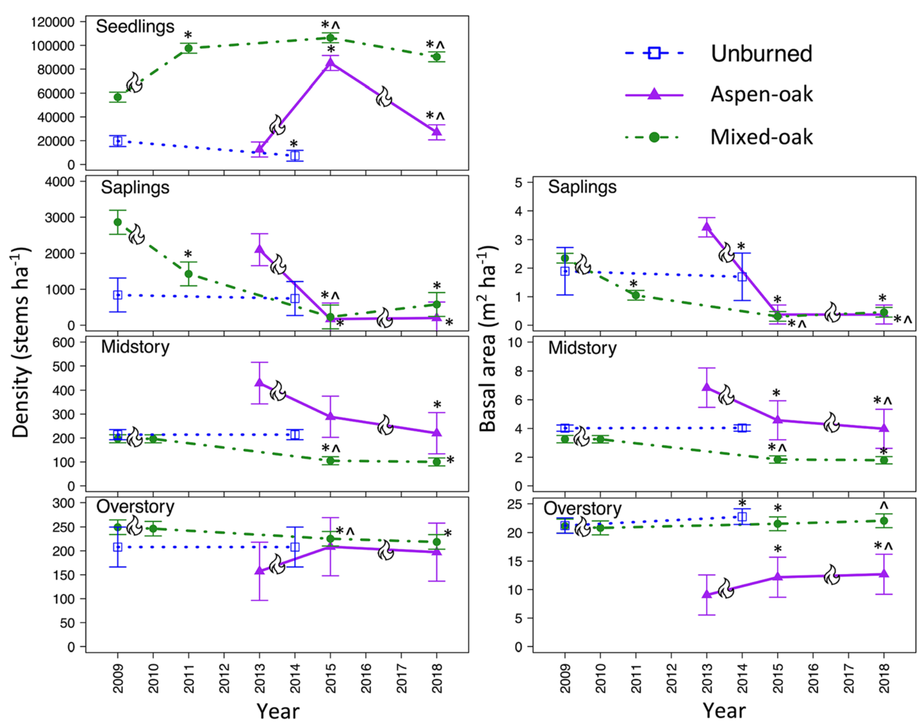

Fig. 2 Absolute density (stems ha^{-1}) and basal area (m^2 ha^{-1}) in the unburned, aspen–oak, and mixed-oak units of State Game Lands 176, Pennsylvania, USA, where we measured post-fire changes in forest structure and composition between 2009 and 2018. Fire symbol indicates the years that prescribed fire occurred in each unit. Yearly differences were determined using linear-mixed effects models and Tukey pairwise comparisons. Asterisk (*) indicates that the mean is significantly different from the initial measurement. Caret (^) indicates that the mean is significantly different than the previous measurement. Error bars represent standard error of the mean. Statistics were tested on log transformed data and graphs show untransformed data. Note *y*-axis numbers vary by tree size class

homoscedasticity and normality, for statistical analysis. To account for zero values, due to the absence of trees at some size classes and some years, $\log(x + 1)$ was used.

Forest composition

To evaluate change in species abundance following prescribed fire, the relative density of each species within each size class was calculated by sampling year. To determine shifts in individual species abundance, initial relative densities of each species in each plot were subtracted from those of the most recent collection. Plot-level differences were averaged to calculate mean and standard error over the management unit. In half of the burned plots, there were no living sapling trees post fire and these plots were removed from the sapling portion of forest composition analysis as relative abundance cannot be calculated when no trees are present. To explore change in species groups over time, most trees were grouped by species, but genus level classification was used for hickories (*Carya* spp.; a combination of *Carya glabra* P. Mill and *Carya tometosa* Nutt.), cherries (*Prunus* spp.; mostly *Prunus serotina* Ehrh. and some *Prunus pensylvanica* L.f.), birch (*Betula* spp.; primarily *Betula lenta* L. with small numbers of *Betula papyrifera* Marshall), dogwood (*Cornus* spp.; a mixture of *Cornus amomum* Mill., *Cornus racemosa* Lam., and *Cornus florida* L.), and serviceberry (*Amelanchier* spp.; largely *Amelanchier arborea* Michx.), since some field observers only identified to the genus level. Species-specific shifts were deemed notable when one standard error of the mean change in relative density did not include zero.

Results

Forest structure

The largest structural changes following prescribed fire were observed in the seedling and sapling layers with less pronounced shifts in the midstory and overstory (Fig. 2). Following a single prescribed fire (year 2010 in mixed-oak and 2014 in aspen–oak), both burn units showed large increases in seedling density two years post fire. Seedling density in the aspen–oak unit increased by more than six-fold between 2013 and 2015 ($P < 0.0001$) and mixed-oak unit seedling density increased by 72% between 2009 and 2011 ($P < 0.0001$). In both units, mean post-fire seedling densities were between 78 000 and 102 000 stems ha^{-1}. The cohort of post-fire seedling regeneration remained over the course of eight years in the single burn mixed-oak unit. However, a second fire in the aspen–oak unit significantly reduced seedling density ($P < 0.0001$), but seedling density remained more than 100% greater than before any fire.

Prior to prescribed fire, there were more sapling stems in both the aspen–oak (2103 stems ha^{-1}) and mixed-oak (2862 stems ha^{-1}) units than on the unburned inventory sites (840 stems ha^{-1}). However, within two growing seasons post fire, both burned units had fewer saplings than the unburned sites and between 50 and 92% fewer saplings than were initially present (Fig. 2). Sapling density in unburned plots did not change over the measurement period (between 2009 and 2014; $P = 0.29$). In addition to post-fire reductions in sapling density, following one prescribed fire, sapling basal area in both burned units dropped 87 to 89% (below 0.4 m^2 ha^{-1}), while the unburned sites remained at 1.7 m^2 ha^{-1} during the same years.

Living midstory stem density did not change on the unburned sites but decreased in both burned units (Fig. 2). Midstory stem densities in the burned units were not statistically different from pre-fire measurements prior to the fifth growing season, at which point midstory stem density in both burned units decreased by 46 to 48% ($P < 0.05$). Further reductions in midstory stem density occurred in the mixed-oak unit between years five and eight; however, these changes were minor and statistically insignificant ($P = 0.98$). Midstory basal area responded similarly and decreased following prescribed fire ($P < 0.001$) by a total of 45% in the mixed-oak unit and 42% in the aspen–oak unit.

Overstory structural change varied by burn unit (Fig. 2). Between the initial and final measurements, overstory stem density remained the same on the unburned sites (208 stems ha^{-1}); slightly but insignificantly increased, through successional ingrowth, in the aspen–oak unit (from 157 to 197 stems ha^{-1}, $P = 0.25$); and decreased in the mixed-oak unit within six years post burn (from 249 to 218 stems ha^{-1}, $P < 0.01$). At the same time, overstory basal area had minor increases on unburned sites (from 21.2 to 22.8 m^2 ha^{-1}, $P > 0.05$) and in the mixed-oak unit (from 21.1 to 22.1 m^2 ha^{-1}, $P = 0.74$) but, following two fires, increased by 40% in the aspen–oak unit (9.0 to 12.7 m^2 ha^{-1}, $P < 0.001$).

Forest composition

The magnitude of tree species compositional change varied by size class and burn unit. The aspen–oak unit had the largest changes in relative density and most compositional change occurred in the seedling and sapling strata (Fig. 3). After two prescribed fires, red maple (*Acer rubrum* L.) seedling relative density decreased by 49% and black oak (*Quercus velutina* Lam.) increased by 29%, becoming the dominant seedling species. Other seedling shifts in the aspen–oak unit included slight increases in northern red oak (*Quercus rubra* L.; +9%), white oak (*Quercus alba* L.; +11%), and quaking aspen (*Populus tremuloides* Michx.; +19%) following prescribed fire; and decreases in cherry (−18%). The top four most abundant pre-fire seedlings were red maple, cherry, serviceberry, and white oak. After two fires, the top four were black oak, red maple, quaking

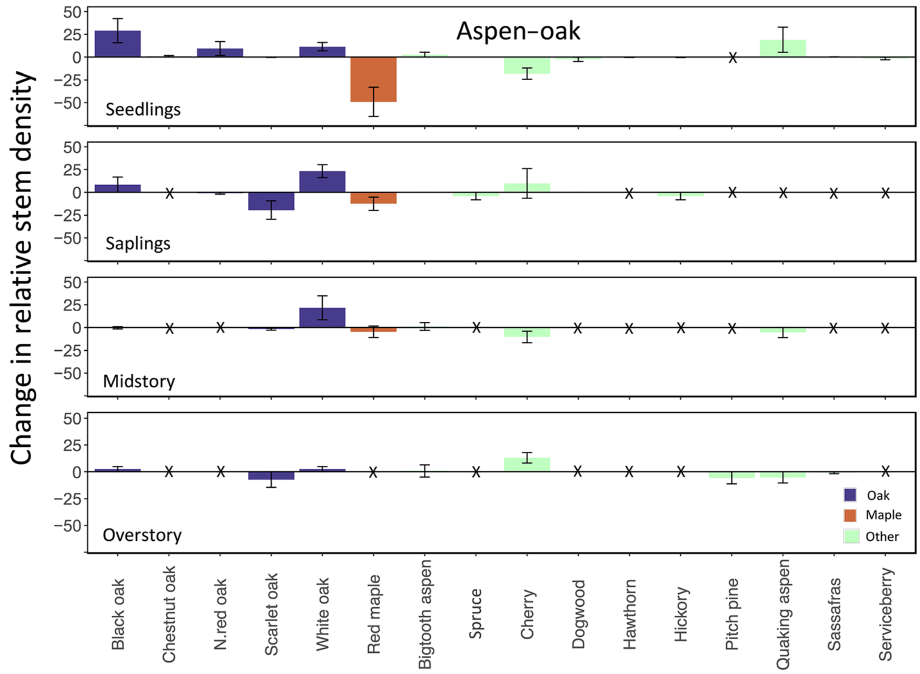

Fig. 3 Change in relative stem density between 2013 and 2018 (five growing seasons after initial prescribed fire) in the aspen–oak unit of State Game Lands 176, Pennsylvania, USA, where we measured changes in forest structure and composition after prescribed fire. Error bars represent standard error of the mean. "X" indicates that a given species was not present within a specific tree size class. N. red oak = northern red oak

aspen, and white oak. At the sapling level, white oak had the largest increase in relative density (+23%) and was the most abundant sapling in the aspen–oak unit after two fires. Additional increases occurred for black oak (+8%) and, after two fires, cherry was the only other tree present in the sapling layer. There were minor changes in relative density of midstory and overstory trees and there were no changes in the top four species in these size classes over the sample period. The most abundant midstory tree in the aspen–oak unit was cherry, followed by white oak, bigtooth aspen (*Populus grandidentata* Michx.), and red maple. The overstory was dominated by bigtooth aspen followed by a mix of cherry, scarlet oak (*Quercus coccinea* Muenchh.), and white oak.

In comparison to the aspen–oak unit, seedling abundance by species in the mixed-oak unit barely changed (Fig. 4). Both before prescribed fire and eight years post fire, the three most abundant seedling species were red maple, chestnut oak (*Quercus montana* Willd.), and serviceberry. No species had a relative density change more than 9% at the seedling level. Sapling dominance in the mixed-oak unit shifted from red maple to sassafras (*Sassafras albidum* [Nutt.] Nees) between 2009 and 2018. Although red maple saplings were still the second most abundant species, they dropped in relative abundance by 41% and sassafras increased by 35%. Minor increases in sapling abundance occurred for black oak (+6%) and hickory (+10%) with decreases measured in chestnut oak (−2%), scarlet oak (−3%), and white oak (−5%). Similar to the aspen–oak unit, the midstory and overstory trees in the mixed-oak unit showed little change in relative abundance. Both before and eight years after fire, the midstory was dominated by red maple, hickory, sassafras, and white oak. White oak dominated the overstory pre fire but was second to red maple post fire. Bigtooth aspen remained the third most abundant overstory tree and chestnut oak was replaced by black oak as the fourth most abundant.

On the unburned sites (Fig. 5), red maple and white oak seedling abundance decreased over six growing seasons but not by large amounts (<9%). Red maple remained as the most dominant seedling species over time. Sapling, midstory, and overstory tree relative density did not notably change in unburned plots over time.

Discussion

Following prescribed fires, these Eastern mixed-oak and aspen–oak forests experienced shifts in species composition and changes in size-class structure resulting from post-fire mortality and forest regrowth. Large post-fire reductions of saplings (80 to 91%) and midstory trees (46%) substantially decreased the density of smaller-diameter stems. Prescribed fire effectively removed stems <10 cm DBH likely due to their thinner bark and lower crown heights, which made them more susceptible to

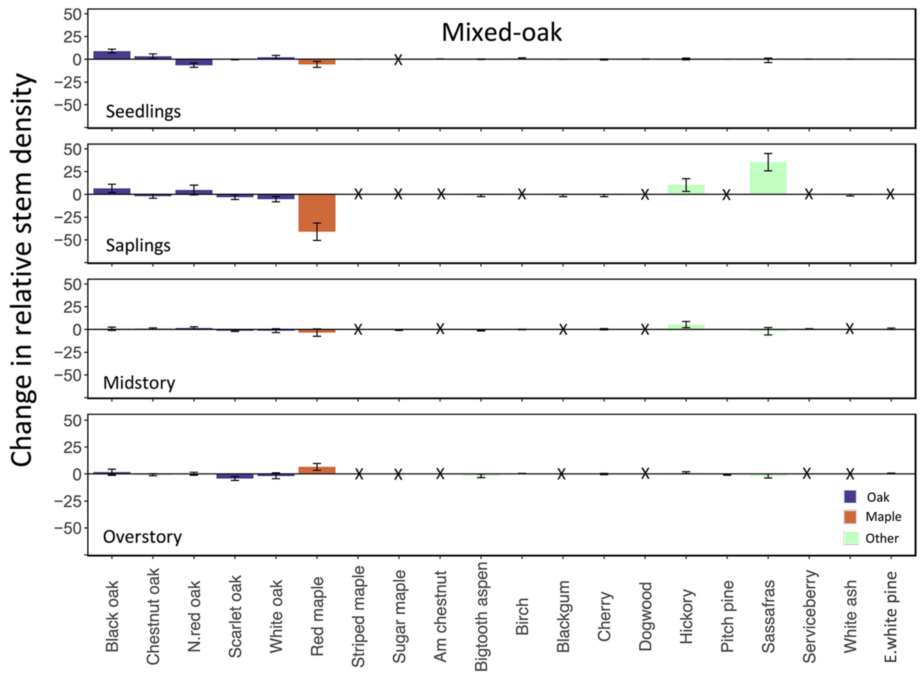

Fig. 4 Change in relative density between 2009 and 2018 (eight years after prescribed fire) in the mixed-oak unit of State Game Lands 176, Pennsylvania, USA, where we measured changes in forest structure and composition after prescribed fire. Error bars represent standard error of the mean. "X" indicates that a given species was not present within a specific tree size class. N. red oak = northern red oak; E. white pine = eastern white pine

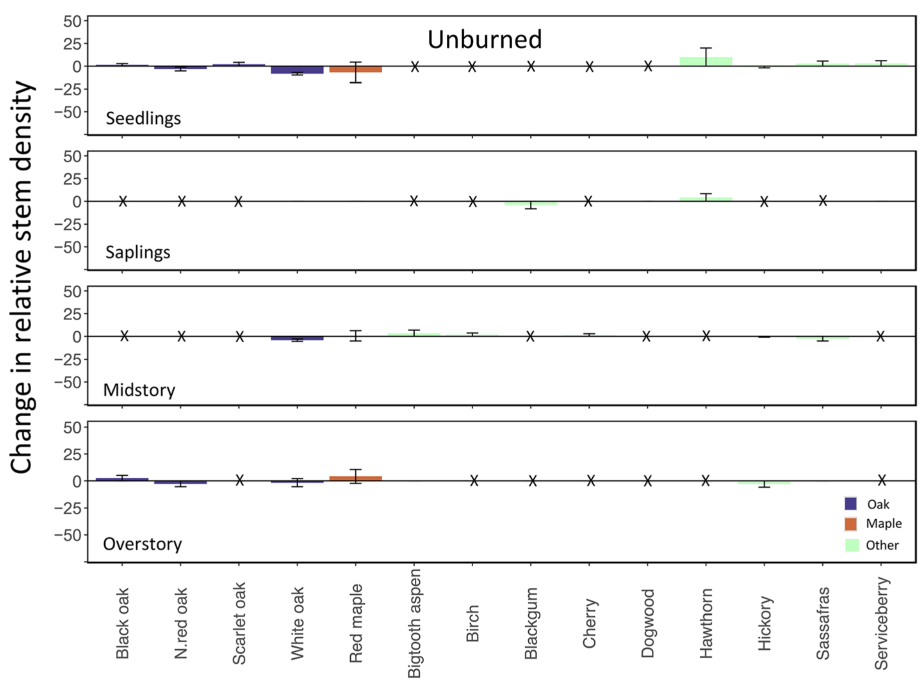

Fig. 5 Change in relative density between 2009 and 2014 in the unburned forests of State Game Lands 176, Pennsylvania, USA, where we measured changes in forest structure and composition after prescribed fire. Error bars represent standard error of the mean. "X" indicates that a given species was not present within a specific tree size class. N. red oak = northern red oak

fire damage than larger-diameter trees. Seedling density increased potentially due to basal sprouting from belowground energy stores (Blankenship and Arthur 2006), temporarily increased sunlight on the forest floor (Chiang et al. 2005), and a modified seed bed due to litter and duff consumption (Arthur et al. 2017). Our findings are consistent with prescribed fire studies in other Eastern deciduous forests (Peterson and Reich 2001; Schwilk et al. 2009; Hutchinson et al. 2012; Arthur et al. 2015; Knapp et al. 2015) that show that single, low-severity burns lead to similar structural changes across regions, but compositional changes require repeat burns or pre-fire management (Brose et al. 2013). However, in contrast to similar studies (Franklin et al. 2003; Blankenship and Arthur 2006), we found that, after a single prescribed fire, overstory stem density decreased (by 12% in the mixed-oak unit) over eight years. At the same time, overstory basal area increased, likely as a result of reduced competition and increased post-fire resource availability. The bulk of structural changes occurred between two and five years post fire; however, response varied among tree species.

Species compositional changes were greatest in the aspen–oak unit that experienced a combination of pre-fire thinning and repeat burning. Among tree seedlings and saplings, the relative abundance of maple decreased and the abundance of oak increased after prescribed fire. However, the response of individual species was nuanced; for example, in both mixed-oak and aspen–oak units, black oak increased or maintained abundance across all size classes, whereas saplings and overstory stems of scarlet oak, a species with thinner bark (Chamberlain and Meyer 1950; Spalt and Reifsnyder 1962), decreased. White oak responded differently between the two units with clear increases at all size classes in the aspen–oak unit and steady or decreasing abundance in the mixed-oak unit. Both northern red oak and chestnut oak abundance remained constant regardless of size class and burn unit. Interspecific variation in post-fire response is due to multiple direct and indirect fire effects (Hood et al. 2018) such as timing of burn and tree regeneration stage (Arthur et al. 2012), forest floor light availability (Dillaway et al. 2007), and differences in tree bark thickness (Spalt and Reifsnyder 1962; Miles and Smith 2009; Hammond et al. 2015). In general, trees with thinner bark are more vulnerable to fire (Pellegrini et al. 2017). However, large-diameter, thin-barked trees such as maple can withstand low-severity prescribed fire (Keyser et al. 2018), and in the mixed-oak unit, overstory red maple trees increased in relative abundance following one prescribed fire.

Although maple and oak made up a large component of the forests in this study, a suite of other species and genera were present. Of these, sassafras, hickory, quaking aspen, and cherry had notable changes in relative abundance in at least one size class. Sassafras abundance increased in the mixed-oak sapling layer eight years after fire and went from the fifth most abundant to the first most abundant species. Sassafras's high growth rate and opportunistic regeneration post fire (Iverson et al. 1999) account for this compositional change. Additionally, hickory saplings increased in the mixed-oak unit and became the fourth most abundant species in the sapling size class, supporting the prescribed fire objective to promote hickory at various stages of succession in the mixed-oak unit.

Within the aspen–oak unit, quaking aspen, a species with root suckers stimulated by fire (Iverson et al. 1999), increased relative abundance in the seedling category one year after the second burn; however, the biggest non-oak, non-maple changes were found in cherry (*Prunus* sp.) trees. After two fires and five years, overstory cherry trees increased in abundance while cherry seedlings declined. Although cherry trees, like maple, are considered pyrophobic (Nowacki and Abrams 2015) or fire-intolerant, the two genera differ in their shade tolerance (Knott et al. 2019), with maple growing better in shade than cherry. Any post-fire increases in forest floor light availability were likely temporary due to rapid growth of forest shrubs (Chiang et al. 2005) and living overstory trees, effectively limiting cherry regeneration and highlighting how fire and shade tolerance interact to influence post-fire vegetation growth over time.

Forests in this study are managed to "protect wildlife and their habitats" (Pennsylvania Game Commission 2020) with prescribed fire objectives focused on maintaining overstory oak trees and top-killing young maple, birch, and aspen. Overstory oak increased 27% in the aspen–oak unit but decreased 24%, primarily among scarlet oaks, in the mixed-oak unit over eight years, partially achieving PGC burn objectives for overstory oak survival. Red maple seedlings and saplings decreased in relative abundance, birch and bigtooth aspen did not change, and quaking aspen seedling abundance increased where overstory aspen were dominant. Although the burn objectives were not met in full, post-fire reductions in red maple seedling and sapling trees were measured over eight years while red maple remained the dominant species on unburned plots. Species-specific responses to prescribed fire indicate a potential trajectory of compositional changes to be maintained through additional monitoring, treatments, and management.

Overall forest composition plays a key role in vegetation–fire relationships, and localized studies, like ours, are necessary to measure the extent of forest heterogeneity following prescribed fire disturbance. The degree of compositional change following prescribed fire is determined by multiple interacting factors (Chazdon 2008; Stroud 2012; Chapman and McEwan 2016) and the aspen–oak forest, where pre-fire overstory thinning and two prescribed fires were used, had more pronounced compositional shifts than the single burn, mixed-oak forest. However, significant structural changes occurred in both forests after just one burn. Prescribed fire goals focused on changing forest structure can be achieved in varied mid-Atlantic oak forest types, while goals focused on compositional shifts should vary based on forest type, management history, and opportunity to apply multiple burns.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s42408-021-00093-5.

Additional file 1. Prescribed fire information for five burns conducted between 2010 and 2017 within State Game Lands 176, Pennsylvania, USA. Our study measured forest structure and composition change for up to eight years after these prescribed fires. Asterisk (*) indicates information gathered from The Pennsylvania State Climatologist and collected in State College, Pennsylvania. Caret (^) indicates information visually measured post fire. NR stands for not recorded. All other information was collected by fire managers in the field.

Acknowledgements

The authors would like to thank the staff of the Pennsylvania Game Commission, namely P. Lupo, B. Stone, B. Jones, J. Wakefield, and E. Erdman, for use of the Continuous Forest Inventory data, access to field sites, and ease of partnership. We thank C. Lauvaux, E. Maynard-Bean, L. Onofrio, and S. Perkins for assisting with data collection over multiple years, as well as L. and E. Ryan for creating maps of our study area. Funding for this project was provided by the Joint Fire Science Program (Project: 16-1-02-5) and USDA National Institute of Food and Agriculture Federal Appropriations under Project PEN04658 and Accession number 1016433.

Authors' contributions

CLD: data collection, statistical analyses, interpretation of data, manuscript preparation and editing. AHT: study design, data collection, interpretation of data, manuscript editing. EAHS: study design, interpretation of data, manuscript editing. JK: interpretation of data, manuscript editing. MWK: study design, data collection, interpretation of data, manuscript preparation and editing. All authors read and approved the final manuscript.

Funding

This project was funded by the Joint Fire Science Program (Project: 16-1-02-5) and USDA National Institute of Food and Agriculture Federal Appropriations under Project PEN04658 and Accession number 1016433.

Availability of data and materials

The datasets used or analyzed during the current study are available from the corresponding author on reasonable request.

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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Received: 5 November 2020 Accepted: 4 February 2021
Published online: 23 April 2021

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