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Yellow pine regeneration as a function of fire severity and post-burn stand structure in the southern Appalachian Mountains

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ABSTRACT

We used pre- and post-burn fire effects data from six prescribed burns to examine post-burn threshold effects of stand structure (understory density, overstory density, shrub cover, duff depth, and total fuel load) on the regeneration of yellow pine (*Pinus* subgenus *Diploxylon*) seedlings and cover of herbaceous vegetation in six prescribed-fire management units located within western Great Smoky Mountains National Park (GSMNP) in east Tennessee, USA. We also evaluated the utility of the Keetch–Byram Drought Index (KBDI) as a predictor of post-burn stand and fuel conditions by comparing post-burn stand variables for different ranges of KBDI (23–78; more wet, and 328–368; more dry). We found that yellow pine seedlings were effectively absent in post-burn forests until overstory density was reduced over 40%, understory density was reduced over 80%, and post-burn shrub cover was 10% or less. We also observed that a reduction in total fuels of 60% and a post-burn duff layer depth of less than four cm were required for successful regeneration of yellow pine. Total herbaceous species cover exhibited near identical responses with increased cover following an 80% reduction in understory density and a post-burn duff depth of less than 4 cm. We observed strong positive relationships between high KBDI values and burn severity, changes in forest structure, reductions in fuels, and post-burn yellow pine reproduction. We observed continuous recruitment of yellow pine seedlings 5 years after fire in high KBDI burns while low KBDI burns showed little change in yellow pine density through time. An intense outbreak of the southern pine beetle (SPB; *Dendroctonus frontalis*) occurred within 2 years of our high KBDI burns and reduced shading resulting from overstory mortality likely enhanced the survival of yellow pine seedlings. The results of this study provide targets for the application of prescribed fire to restore yellow pine in the southern Appalachians. Continued research and monitoring will help determine how prescribed fire can best be applied in combination with other disturbance agents such as SPB to perpetuate yellow pine forests.

1. Introduction

Although hazardous fuel reduction has been the dominant focus of prescribed fire programs over the past two decades in North America, Australia, and Europe (Fernandes and Botelho, 2003), the importance of restoration has increased with the recognition of fire as a critical ecosystem process. Within the conceptual framework of ecological restoration, prescribed fire has been used to sustain endangered plant populations (Pendergrass et al., 1999; Lesica, 1999), maintain wildlife habitat (Plentovich et al., 1998; Dees et al., 2001), and preserve declining vegetation communities (Glitzenstein et al., 1995; Covington et al., 1997). In North America, restoration efforts have frequently required the reintroduction of fire to biotic communities that have experienced nearly a century of fire suppression (Harmon, 1982; Baker, 1994; Covington, 2000). In many cases, managers have sought to reestablish pre-European fire regimes (Keeley, 2006), an endeavor that possesses obvious merit, but is likewise difficult as a result of drastic changes that have occurred throughout the forests of North America. Years of fire suppression have changed the structure of many forests, human populations have increased within an expanded wildland urban interface (Radeloff et al., 2005), and invasive species have entered species pools (Keeley et al., 2005; Kuppinger et al., 2010). These factors have altered fuel loading and burn prescriptions, which in turn have altered fire behavior and effects. Under such conditions, restoring fire-dependent communities requires a clear understanding of how contemporary composition, structure, and regeneration dynamics will respond to the restoration of fire.

In the southern United States, xeric yellow pine forests (dominated by *Pinus* subgenus *Diploxylon*) have experienced severe

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decline due to the combined impacts of fire exclusion and heavy overstory mortality resulting from periodic outbreaks of the southern pine beetle (SPB; *Dendroctonus frontalis*, a native insect). With fire suppression in the southern Appalachian Mountains, overstory density has increased, understories have filled in with less fire tolerant hardwood species, and thick layers of leaf litter have accumulated, preventing yellow pine species from regenerating (Harrod et al., 1998; Williams, 1998; Brose and Waldrop, 2010). Consequently, when SPB kills the overstory, these stands undergo accelerated succession towards dominance by less fire tolerant hardwood species.

Similar to other forest regions, the use of prescribed fire has increased across the southern Appalachian Mountains over the last two decades. For example, annual prescribed burning in Great Smoky Mountains National Park (GSMNP) have increased from 4 ha in 1996 to over 800 ha in 2008. Management objectives for these burns have expanded from fuel reductions along the park boundary to landscape-scale burns that focus on reducing stand density and regenerating fire dependent species. Within the region, prescribed burns are frequently conducted to restore and maintain yellow pine forests that are in decline due to fire suppression. The regeneration of yellow pine is a critical measure of the restoration success of these burns since it is the first step in insuring the long-term persistence of pine-dominated communities. Studies have shown that prescribed and wildfire on xeric sites in the southern Appalachians shifts vegetation composition away from mesophytic species (Arthur et al., 1998), decreases stand density (Welch et al., 2000), increases herbaceous-layer cover and species richness (Harrod et al., 2000), and reduces the thickness of duff layers (Waldrop and Brose, 1999; Waldrop et al., 2010), allowing yellow pine seedlings to establish (Waldrop and Brose, 1999). Because of the logistical difficulty of sampling prescribed burns, existing studies have focused on a few sites (Arthur et al., 1998; Elliott et al., 1999; Waldrop and Brose, 1999; Welch et al., 2000) or conducted small experimental burns (Waldrop et al., 2010). Consequently, studies that have examined multiple operational burns across a forested landscape are lacking. Therefore, relationships between initial burn conditions, burn severity, post-burn stand structure, and yellow pine regeneration across a prescribed burning program have not been studied in detail.

The successful implementation of prescribed fire as a restoration tool depends upon the ability to predict what effects burning will have on forest composition, structure, and processes under a range of moisture and stand conditions. Prediction of these effects is critical to understanding the environmental conditions, seasonality, and number of burns needed to achieve management objectives. The Keetch–Byram Drought Index (KBDI) quantifies drought based upon precipitation and upper horizon soil moisture analyzed in a water budget model (Keetch and Byram, 1968) and is widely used in wildfire monitoring and prediction (Heim, 2002; Chan et al., 2004). While the potential uses of this index to rate fire danger (Melton, 1989; Chan et al., 2004) and predict fire intensity (Sparks et al., 2002) have been examined, its utility for predicting fire effects within restoration burns has received little study.

The Fire Effects Monitoring Program in GSMNP has collected data within prescribed burns for over a decade with the goal of better understanding the relationship between fire and the composition, structure, and function of fire-dependent ecosystems. The restoration and maintenance of yellow pine forests have been a major focus of this program. In this study, we use fire effects data from six prescribed burns to address three critical questions concerning the perpetuation of this threatened forest type: (1) are there threshold effects on stand structure (understory density, overstory density, shrub cover, duff depth, and total fuel load) that must be achieved with prescribed burning to facilitate the regeneration of yellow pine seedlings? (2) do changes to stand structure that favor the regeneration of yellow pine also promote the cover of herbaceous species? and (3) how do pre-burn moisture conditions and drought severity as represented by KBDI influence the effects of fire on stand structure and pine regeneration?

2. Methods

2.1. Study area

The study area was composed of six prescribed-fire management units located within western Great Smoky Mountains National Park (GSMNP) in east Tennessee, USA (Fig. 1). The area lies near the boundary of the Blue Ridge and Ridge and Valley physiographic provinces, and is topographically distinct from the high mountains of the Great Smoky Range (Southworth et al., 2005). This landscape is characterized by narrow, highly dissected ridges of relatively low elevation (260–670 m) that largely follow a southwest-to-northeast orientation. Loamy soils are shallow, highly weathered, and rocky (USDA NRCS, 2009) and overlay meta sandstone, siltstone and shale bedrock (Southworth et al., 2005). The mean annual temperature of nearby Gatlinburg, TN is 13 °C, and the mean annual precipitation is 143 cm.

Vegetation in the study area varies along a topographic-moisture gradient, with pine (*Pinus*) and oak (*Quercus*) forests occupying ridgetops and exposed slopes. These xeric forests cover over 33,000 ha in GSMNP (Jenkins, 2007), making them one of the most common forest types in the Park. Oak-hickory (*Quercus-Carya*) forests occupy semi-protected slopes within the study area, while mixed hardwood/conifer forests dominate the highly protected slopes and valleys.

Our study focused on the effects of prescribed fire in a single association within xeric pine forests: Appalachian Low-Elevation Mixed Pine/Hillside Blueberry Forest (White et al. 2003). *Pinus rigida* (pitch pine) dominates these forests, followed by two other yellow pine species; *P. virginiana* (Virginia pine) and *P. echinata* (shortleaf pine). Seed dispersal is similar for these three species, most cones open within 2–3 months of maturity and the majority of seeds disperse less than 50 m from the parent (Carter and Snow, 1990; Lawson, 1990; Little and Garrett, 1990). None of these species have truly serotinous cones, although some cones on *P. rigida* trees may remain closed until opened by heat from a fire. Seeds of all three yellow pine species require reduced litter depth and shading to successfully germinate and establish seedlings. Both *P. rigidia* and *P. echinata* are able to resprout when top killed, which makes them ideally suited to survive under a regime of frequent fire. *P. virginiana* does not possess this trait and typically established after the cessation of fire in these forests.

Other common overstory species in the study area include *Pinus strobus* (white pine), and xeric site oaks (*Quercus prinus* – chestnut oak, and *Q. coccinea* – scarlet oak). Subcanopies in these forests are strongly dominated by shade-tolerant canopy species including *Nyssa sylvatica* (black gum), *P. strobus*, *Acer rubrum* (red maple), and *Tsuga canadensis* (eastern hemlock), and the subcanopy species *Oxydendrum arboretum* (sourwood). The shrub layer is typically well developed and ranges from moderate density of tall shrubs (primarily *Kalmia latifolia* – mountain laurel) to high density of low shrubs (*Vaccinium* spp. – blueberry and *Gaylussacia* spp. – huckleberry). Few herbaceous species occur and none occur in any abundance (White et al., 2003).

The xeric forests within the study area have experienced recurrent fires for hundreds of years, and there is evidence that fires have occurred within the region for thousands of years (Harmon, 1982; Fesenmyer and Christensen, 2010; Delcourt and Delcourt, 1998). Though the scale and impacts of pre-European fire regimes are poorly understood, lightning and Native American populations

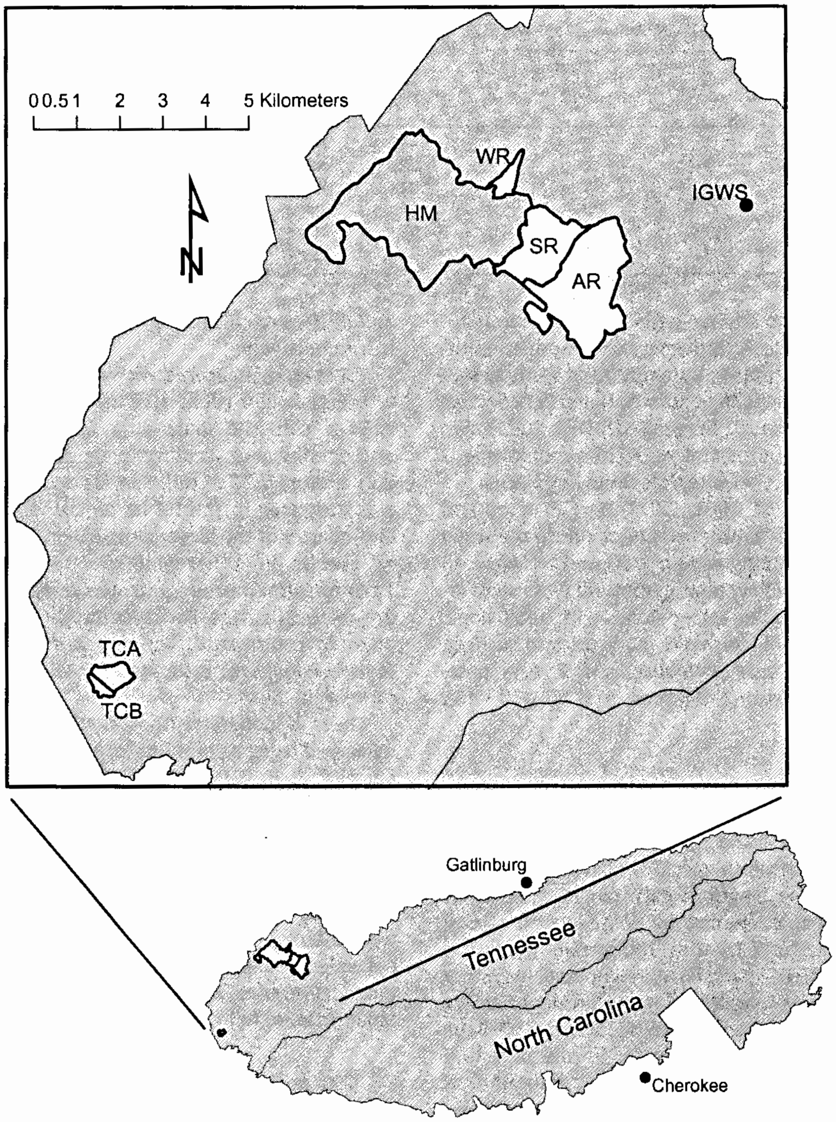

Fig. 1. Locations of the six burn units within western Great Smoky Mountains National Park. The location of the Indian Grave Weather Station (IGWS) is also shown. AR, Arbutus Ridge; HM, Hatcher Mountain; SR, Stony Ridge; TCA, Tabcat Creek A; TCB, Tabcat Creek B; and WR, Wedge Ridge.

both served as potential ignition sources prior to European settlement, which began in the late 18th century. Disturbances associated with European settlement included small-scale agriculture and logging, grazing, land clearing, and fire (Pyle, 1988). The mean fire return interval in xeric forest within the study area for the years between 1856 and 1940 was 12.7 years (Harmon 1982). Fire was effectively removed as a landscape-level disturbance following establishment of the National Park in 1934 and the implementation of a policy of full fire suppression.

2.2. Prescribed burns

The six prescribed burns were conducted between March and October over an eight year period (1997–2005) and ranged in size from 25 to 939 ha (Table 1). Values for temperature, relative humidity and winds were collected at an automated weather station in the west end of the Park (Indian Grave RAWS) located within 18.7 km of the farthest burn unit (Fig. 1). The Keetch–Byram drought index (KBDI; Keetch and Byram, 1968) uses daily temperature, daily precipitation, antecedent precipitation, and annual precipitation to produce a value between 0 (no drought) and 800 (extreme drought) to describe moisture conditions in surface soil and duff. KBDI values for the primary burning day of each prescribed fire were calculated from daily weather observations taken at the Indian Grave weather station within the study area. To compare conditions for each prescribed burn to annual cycles of soil moisture and fuel availability, bimonthly averages for KBDI were calculated from 20 years of weather data collected from this weather station. Inspection of similar data from other fire weather stations and the original Keetch and Byram (1968) publication confirmed that the overall trend in annual KBDI values during the 8 years of burning in our study was consistent with general trends observed throughout the southern Appalachians.

2.3. Study design

The Fire Effects Monitoring Program of GSMNP was initiated in 1997 to document the response of vegetation communities to

Table 1
Characteristics of prescribed burns conducted at GSMNP between 1997 and 2005. RH, relative humidity (24 h high/low), KBDI, Keetch–Byram Drought Index.

Site name	Burn start date	Burning days	Days since last rain	size (ha)	Ignition technique	High/low temp. (°C)	High/Low RK (%)	Wind speed	KBDI
Arbutus Ridge	03/10/03	3	3	422	Hand	23/2	63/26	1–5	25
Hatcher Mountain	04/11/05	2	2	939	Aerial	27/12	64/35	1–4	76
Stony Ridge	04/23/01	2	7	214	Aerial	28/12	100/30	1–5	66
Tabcat Creek A	08/04/97	7	5	39	Hand	31/15	100/42	1–3	368
Tabcat Creek B	04/03/03	1	2	52	Hand	24/14	80/38	1–6	23
Wedge Ridge	10/30/98	2	21	25	Hand	24/12	93/51	1–3	328

prescribed burning and provide science-based feedback for adaptive management to increase the effectiveness of prescribed burning in the Park. This program employs a standardized study design and field methodology used across the entire National Park Service to monitor the effects of prescribed burns (USDI NPS, 2003). Fire behavior is monitored during burns and vegetation monitoring is conducted prior to burns and at set intervals following burns.

Between May 1997 and June 2002, 24 0.1 ha (20 m × 50 m) plots were established in the six prescribed burns within the study area. A restricted random sampling design was used to locate all plots in forests dominated by yellow pine species. All plots were located on ridgetops and SE-W facing upper slopes with <45% slope. Measurements of vegetation and fuels were made prior to burning, immediately after burning, 1 year post-burn, and 2 years post-burn. A subset of plots were resampled 5 years post burn ($n = 18$).

2.4. Field sampling

Fire behavior was monitored and recorded during each burn, though it was not possible to observe specific behavior such as fire type, rate-of-spread and flame length at each plot. Fire behavior ranged from creeping fires characterized by flame lengths <0.6 m to head fires with flame lengths of 1.5–3 m (NPS unpublished data; R. Klein, personal observation). Bark char height and overstory crown scorch reflect the flame length during the primary flaming front, which can be used to characterize fireline intensity (DeBano et al., 1998). Though the use of bark char height and overstory crown scorch to estimate fireline intensity has some limitations (Cain, 1984) this technique has been widely used to estimate relative fire intensity (Waldrop and Brose, 1999; Pomp et al., 2008). Comparisons of pre- and post-burn biomass, particularly of litter and duff, provide a widely used quantitative measure of substrate burn severity (DeBano et al., 1998; USDI NPS, 2003).

Dead and down woody fuels, litter, and duff were sampled along four randomly oriented 15.2 m transects in each plot. Dead and down woody fuels were sampled using the planar intersect method described by Brown (1974). Fine woody debris (detached twigs and sticks) were tallied by fuel/size class: 1-h fuels (0–0.62 cm diameter) and 10-h fuels (0.62–2.54 cm) were tallied along the first 1.83 m of the transect and 100-h fuels (2.54–7.62 cm) were tallied along the first 3.66 m. Coarse woody debris (logs; 1000-h fuels, >7.62 cm) were tallied along the entire transect, classified as decayed or sound, and measured to the nearest 1.27 cm (diameter at intersect). Depths of litter and duff layers were measured to the nearest 0.25 cm at 10 points along each transect.

Fuel loading calculations were based on Brown et al. (1982) and Brown (1974). Non-slash (naturally fallen material) composite values were used to calculate quadratic mean diameter, non-horizontal correction (adjusted weight estimates for logs that are not flat on the ground), and specific gravity of 1, 10, and 100-h fuels. One thousand hour fuels were assigned a specific gravity of 0.40 or 0.30 for sound and rotten particles, respectively. Loading of litter and duff were calculated using bulk densities of 35.3 and 70.6 g/m^3, respectively.

Trees were measured within three classes based upon diameter at breast height (dbh; 1.37 m). The overstory included all stems >15 cm dbh, the understory included all stems $\geqslant$2.5 cm and $\leqslant$15 cm dbh, and seedlings were defined as woody stems <2.5 cm dbh and/or <1.37 m tall. Species and dbh were recorded for each overstory tree in the 0.1 ha plot, and for all understory trees in one-quarter of the larger plot (250 m^2). Tree seedlings were tallied by species in a nested 50 m^2 subplot. Within approximately 1 month after burning, all overstory trees were reassessed for fire-related damage. Bark char height was measured as the highest point of continuous char on each overstory bole, and percent crown scorch was estimated for all trees that had foliage at the time of the burn.

Cover of understory herbs, shrubs, subshrubs, and vines was measured using a point intercept method along two 50 m transects per plot. Every 30 cm along each transect (332 points per plot), a 0.635 cm diameter pole was dropped plumb to the ground and each species touching the pole was recorded. No species was recorded more than once per point, and strikes from leaves, twigs and stems attached to trees >2m tall were not counted. Species counts for each plot were calculated by adding all species that were intercepted along either transect within each plot, and may not reflect the total number of species present within plots. Yellow pine seedling density was calculated on a per hectare basis. Species nomenclature follows Kartesz (1999).

2.5. Data preparation and analysis

We used a combination of simple linear and non-linear regression techniques to evaluate the influence of post-burn changes in stand structure and fuels (overstory density, overstory density change, understory density, understory density change, total fuels, total fuel change, post-burn duff depth, and post-fire shrub cover) on the seedling density of yellow pine species (stems/ha) and the post-fire cover (%) of herbaceous-layer vegetation. Because it is difficult to separate yellow pine from *P. strobus* seedlings in the first year following a burn, we used seedling density data collected two years post-burn in our regression analyses. Non-linear regression was also used to examine the relationship between post-fire stand density change (overstory and understory; %) and changes in total fuel load (%). Square root and natural log transformations were employed in linear regression analyses to homogenize variances when necessary. We used non-linear regression when transformation of variables did not provide an adequate fit to the data. The regression assumption of constant variance was assessed with plots of studentized residuals versus fitted values (Neter et al., 1996). We used residual plots and standard techniques to screen for and evaluate the influence of potential outliers (Neter et al., 1996). Prior to regression analyses, relationships among variables were examined with Pearson product moment correlation analysis (Zar, 1996). Because correlation coefficients revealed strong correlations among explanatory variables (Table 2) resulting in

Table 2

Pearson correlation coefficients of a drought index (kBDI), first order fire effects, and short term vegetative response for 24 yellow pine plots in GSMNP. Plots were burned in management-ignited prescribed fires between 1997 and 2005.

	KBDI	PCS	BCH	LLC	PBDD	TFLC	ODC	UDC	YPSD	PBHC	PBSC
PCS	0.483										
BCH	0.481	0.777**									
LLC	ns	ns	ns								
PBDD	−0.715**	−0.555*	−0.540*	0.552*							
TFLC	−0.837**	−0.602*	−0.481	ns	0.764**						
ODC	−0.861**	−0.699**	−0.580*	ns	0.653**	0.793**					
UDC	−0.778**	−0.564*	−0.622*	ns	0.709**	0.653**	0.801**				
YPSD	0.788**	0.507	0.522	ns	−0.593*	−0.736**	−0.874**	−0.758**			
PBHC	0.809**	0.470	0.505	ns	−0.599*	−0.690**	−0.826**	−0.750**	0.946**		
PBSC	−0.642**	−0.486	ns	0.600*	0.892**	0.694**	0.595*	0.589*	−0.573*	−0.611*	
TPSR	0.695**	0.480	0.644**	−0.498	−0.626*	−0.504	−0.540*	−0.580*	0.518	0.665**	−0.628*

KBDI, Keetch–Byrum Drought Index; PCS, percent crown scorch; BCH, bark char height; LLC, litter load change; PBDD, Post-burn duff depth; TFLC, total fuel load change; ODC, overstory density change; UDC, understory density change; YPSD, post-burn yellow pine seedling density; PBHC, post-burn herbaceous cover; PBSC, post-burn shrub cover; TPSR, total post-burn species richness. Only coefficients with $p < 0.05$ are shown. ns, non-significant.

* $p < 0.01$.

** $p < 0.001$.

multicollinearity (Chatterjee et al., 2000), multiple linear regression analysis was not used.

To evaluate the utility of KBDI as a predictor of post fire stand and fuel conditions, we compared post-fire and stand variables for different classes of KBDI. Because our data violated assumptions of normality and equal variance, we used Mann–Whitney rank sum tests. Analyses were performed for overstory density change, understory density change, post-fire duff depth, and total fuel load change between two range classes of KBDI (23–78; more wet, and 328–368; more dry). To examine changes in yellow pine density in high and low KBDI burns, we performed one-way repeated measures ANOVA to compare changes in yellow pine density pre-burn, 2 years post-burn and 5 years post-burn in high and low KBDI burns. We used the Kolmogorov–Smirnov test to confirm normality ($p = 0.534$) and the Levene median test to confirm equal variances ($p = 0.227$) in our data. When ANOVA revealed significant differences, we used the Holm–Sidak multiple comparisons test for post hoc comparisons ($\alpha = 0.05$). For this analysis, we used the subset of plots that were resampled five years post burn ($n = 6$ for high KBDI and $n = 12$ for low KBDI plots).

3. Results

3.1. Fire intensity and severity

Mean values for percent evergreen crown scorch and bark char height indicate that the six burns we sampled displayed a range of fire intensities (Table 3). Generally, these indirect measures of intensity were greater following burns that occurred later in the season (Tabcat A and Wedge Ridge, August and October) than burns that occurred earlier in the season (March and April). Similar differences between early and late season burns were observed for indicators of burn severity. Fuel load reductions varied from 11% (Arbutus Ridge, a March burn) to 70% (Wedge Ridge, an October burn), largely due to variability in duff reduction, which comprised over 71% of the average total fuel load prior to burning (Table 3). Post-burn duff depths were also lower in the two late season burns. Both char height and percent crown scorch were significantly correlated with measures of post-fire change in structure, fuels, and vegetation (Table 2).

3.2. Fire effects on vegetation composition and structure

There were major differences in overstory density change between the late season burn sites (Tabcat A and Wedge; 49% and 68% reductions, respectively), and the remaining early season burn sites, which all experienced <12% reductions (Table 4). The large overstory reductions at the late season burn sites were driven by proportionally greater losses of yellow pines, *P. virginiana* in particular. Prior to burning, woody understories were dominated by five species (in order of decreasing density) *N. sylvatica, P. strobus, P. virginiana, A. rubrum, and O. arboretum* that comprised 79% of stems across all plots. Across all burns, mean understory tree density was reduced by 60% within 2 years following burning. Again, there were substantial differences in density change between sites, with the two late season burns experiencing >85% mortality, and the early season burns experiencing <60% mortality.

Similar differences between early and late season burns were evident for shrub and herbaceous species cover (Table 4). Shrub cover was reduced 2–58% across the early season burns vs. 82–85% following the late season burns. Average herbaceous cover in late season burns increased 6–15-fold two years after burning, while the early season burns showed essentially no change. Similarly, species richness of the late season burns experienced a 40–50% increase, while the early season burns experienced no change, or in one case, an average decrease. While we observed

Table 3

Mean values (pre-burn/post-burn) of evergreen crown scorch (ECS, %), bark char height (BCH, m), fine woody debris (FWD, Mg/ha), coarse woody debris (CWD Mg/ha), litter load (LL, Mg/ha), duff load (Mg/ha), post-fire duff depth (PDD, cm), and total fuel (Mg/ha) by prescribed burn unit.

Site	Number of plots	ECS	BCH	FWD	CWD	LL	Duff Load	PDD	Total Fuel
Arbutus Ridge	4	1	0.4	5.8/5.6	7.6/12.1	15.2/7.6	133.5/118.7	11.2	162.0/143.8
Hatcher Mountain	6	3	0.7	6.0/6.7	6.0/10.3	18.4/2.9	67.4/64.1	6.1	98.1/84.0
Stony Ridge	3	13	0.8	8.3/6.7	11.4/17.9	18.1/3.8	78.4/65.0	6.1	116.3/93.4
Tabcat Creek A	4	34	1.9	9.0/4.3	8.1/7.4	12.1/2.7	57.6/14.8	1.4	86.2/29.1
Tabcat Creek B	3	28	1.3	3.8/2.5	11.6/2.7	13.9/1.8	46.4/41.4	3.9	75.7/48.4
Wedge Ridge	4	42	1.1	6.7/3.6	10.8/6.0	17.5/4.7	92.7/24.2	2.3	127.7/38.6

Post-burn fuels were measured within one year post-burn, except for Arbutus Ridge, which was measured two years post-burn.

Table 4
Pre- and post-burn overstory and understory structure and species composition (mean ± 1 SE).

	Pre/post burn	Arbutus $n = 4$	Hatcher $n = 6$	Stony $n = 3$	Tabcat A $n = 4$	Tabcat B $n = 3$	Wedge $n = 4$	Total n=24
Overstory								
Total basal area ($\text{m}^2\ \text{ha}^{-1}$)	Pre-burn	31.4 ± 5.2	22.3 ± 3.4	30.5 ± 1.3	18.3 ± 1.3	22.6 ± 2.1	27.3 ± 2.9	25.0 ± 1.6
	Post-burn	30.5 ± 5.6	24.0 ± 3.7	26.1 ± 2.5	12.6 ± 1.5	22.1 ± 2.6	9.8 ± 1.0	20.8 ± 2.0
Total density (stems ha^{-1})	Pre-burn	483 ± 69	393 ± 60	487 ± 43	403 ± 38	427 ± 55	555 + 58	453 ± 25
	Post-burn	478 ± 74	407 ± 65	427 ± 37	205±21	410 ± 69	178 ± 34	350 ± 30
Yellow pine density (stems ha^{-1})	Pre-burn	243 ± 51	130 ± 53	210 ± 60	310 ± 44	323 ± 122	398 ± 60	258 ± 30
	Post-burn	240 ± 50	130 ± 53	167 ± 69	155 ± 20	317 ± 128	103 ± 19	176 ± 26
P. virginiana density (stems ha^{-1})	Pre-burn	123 ± 46	52 ± 14	150 ± 40	203 ± 47	217 ± 96	290 ± 69	161 ± 25
	Post-burn	123 ± 46	53 ± 14	130 ± 50	65 ± 16	210 ± 103	70 ± 23	99 ± 18
Quercus spp. density (stems ha^{-1})	Pre-burn	48 ± 19	112 ± 26	90 ± 31	80 ± 22	53 ± 30	38 ± 5	73 ± 10
	Post-burn	48 ± 15	107 ± 25	77 ± 22	40 ± 4	50 ± 26	25 ± 3	61 ± 10
Other species density (stems ha^{-1})	Pre-burn	233 ± 50	152 ± 43	187 ± 54	13 ± 5	50 ± 40	120 ± 18	128 ± 21
	Post-burn	230 ± 50	168 ± 42	183 ± 52	10 ± 7	40 ± 34	50 ± 12	119 ± 22
Understory								
Total understory basal area($\text{m}^2\ \text{ha}^{-1}$)	Pre-burn	6.0 ± 0.5	7.1 ± 0.6	6.9 ± 1.7	10.1 ± 2.1	9.4 ± 1.1	9.1 ± 2.0	8.0 ± 0.6
	Post-burn	5.7 ± 0.5	4.8 ± 0.8	4.8 ± 1.6	1.5 ± 0.9	7.3 ± 1.2	1.5 ± 0.7	4.2 ± 0.5
Total understory density (stems ha^{-1})	Pre-burn	1150 ± 237	1560 ± 144	1493 ± 497	1980 ± 241	2187 ± 150	1710 ± 343	1657 ± 116
	Post-burn	950 ± 179	800 ± 182	640 ± 197	270 ± 158	1240 ± 189	140 ± 35	662 ± 98
Yellow pine seedling density (stems ha^{-1})	Pre-burn	0 ± 0	267 ± 176	0 ± 0	1350 ± 1100	0 ± 0	300 ± 191	357 ± 204
	Post-burn	250 ± 250	0 ± 0	333 ± 333	4400 ± 2174	67 ± 67	5550 ± 732	750 ± 590
Tree seedling cover (%)	Pre-burn	5 ± 1	13 ± 2	7 ± 1	3 ± 2	17 ± 4	6 ± 2	8 ± 1
	Post-burn	3 ± 1	11 ± 3	13 ± 1	11 ± 2	5 ± 1	26 ± 5	12 ± 2
Shrub cover (%)	Pre-burn	70 ± 13	38 ± 10	47 ± 5	51 ± 13	33 ± 10	26 ± 6	44 ± 5
	Post-burn	56 ± 10	27 ± 6	46 ± 7	9 ± 2	14 ± 4	4 ± 2	26 ± 5
Kalmia latifolia cover (%)	Pre-burn	18 ± 11	16 ± 10	0 ± 0	29 ± 15	1 ± 1	0 ± 0	12 ± 4
	Post-burn	14 ± 8	11 ± 8	1 ± 1	5 ± 3	1 ± 1	0 ± 0	6 ± 3
Exotic species cover (%)	Pre-burn	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
	Post-burn	0 ± 0	0 ± 0	0 ± 0	1 ± 1	0 ± 0	1 ± 1	1 ± 1
Herbaceous species cover (%)	Pre-burn	1 ± 1	6 ± 2	1 ± 1	4 ± 1	2 ± 1	2 ± 1	3 ± 1
	Post-burn	1 ± 1	7 ± 3	1 ± 1	24 ± 9	1 ± 1	30 ± 4	11 ± 3
Herbaceous-layer species richness	Pre-burn	11 ± 2	20 ± 2	15 ± 1	18 ± 3	24 ± 3	14 ± 1	17 ± 1
	Post-burn	12 ± 1	19 ± 2	14 ± 1	25 ± 2	16 ± 2	21 ± 2	18 ± 1

$n = 23$ for pre-burn understory data, $n = 24$ for post-burn understory and pre- and post-burn overstory data.

only modest post-fire invasion of non-native plants (*Paulownia tomentosa* – princess tree and *Tussilago farfara* – coltsfoot), these highly aggressive species were not detected prior to burning and were only found following more severe late-season burns (Table 4).

Prior to burning, we encountered few yellow pine seedlings across the six sites we sampled (Table 4). The high pre-burn average at Tabcat A resulted from the occurrence of a large number of *P. virginiana* seedlings within a single plot. Two years following burning, the overall mean number of yellow pine seedlings in our plots increased nearly 500%. This overall increase was driven exclusively by large increases in pine seedlings density within late season burn plots, which had a combined average of 4975 yellow pine seedlings/hectare within 2 years following the burns. The density of yellow pine seedlings was correlated with increased crown scorch and char height and displayed strong negative correlations with changes in total fuel, overstory density, and understory density (Table 2).

3.3. Yellow pine regeneration response to thresholds of forest structural change

Yellow pine regeneration displayed strong relationships to changes in fuels and forest structure. Regression analysis revealed a strong relationship ($R^2 = 0.78$; $p < 0.001$) between seedling density and total fuel load change with a rapid increase in seedling density occurring when total fuel load reduction exceeded 60% (Fig. 2a). A similar curvilinear relationship was observed between yellow pine seedling density (YPSD) and total fuel load [TFL; $\text{YPSD} = 20753.3 * \exp(-0.051 * \text{TFL})$, $R^2 = 0.60$, $p < 0.001$] with a rapid increase in seeding density occurring when total fuel load was reduced to 50 Mg/ha or less (data not shown). A similar relationship was also observed between seedling density and post-fire duff depth, with greatly increased seedling densities occurring for duff depths of 4 cm or less (Fig. 2b).

Regressions of individual plot values of overstory and understory density changes against the percent total fuel load change revealed that significant amounts of variation in tree mortality can be explained by the substrate severity of the burn, as measured by the percent change in total fuel load (Fig. 3). Changes in both understory and overstory density were segregated into two groups: greater than 60% fuel reduction and less than 60% fuel reduction, suggesting that for the range of fire severity observed, minimal mortality occurred until burns were severe enough create greater than 60% reduction in total fuels.

Changes in the overstory, understory, and shrub layers were also correlated with yellow pine seedling density (Fig. 4). Seedling density increased with reductions in overstory density, with increasing yellow pine regeneration occurring at overstory reductions greater than 40% (Fig. 4a). Similarly, we observed increased yellow pine regeneration when overstory density (OD) was less than 250 stems ha^{-1} [$\text{sqrt(YPSD)} = 123.27 - 5.413 * \text{sqrt(OD)}$; $R^2 = 0.46$, $p < 0.001$; data not shown]. Yellow pine regeneration was also strongly related to understory density, with seedling density rapidly increasing at understory reductions greater than 80% (Fig. 3b). A similar relationship was evident between yellow pine seedling density and understory density [$\text{YPSD} = 8601.95 * \exp(-0.00517 * \text{UD})$; $R^2 = 0.87$, $p < 0.001$] with increased seeding density occurring when understory density was reduced to 250 stems ha^{-1} or less (data not shown). Our results further show that shrub cover strongly influences yellow pine regeneration (Fig. 4c). We observed greatly increased yellow pine regeneration

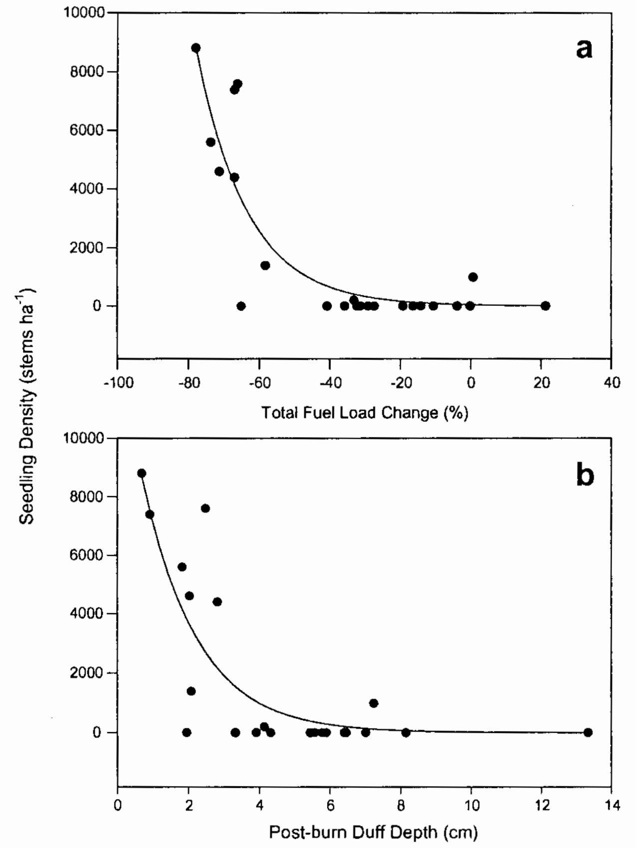

Fig. 2. Yellow pine seedlings density (YPSD) as a function of total fuel load change (TFLC) and post-burn duff depth (PBDD). $\text{YPSD} = 41.815 * \exp(-0.068 * \text{TFLC})$; $F = 74.55$, $R^2 = 0.78$, $p < 0.001$. $\text{YPSD} = 13628.45 * \exp(-0.138 * \text{PBDD})$; $F = 49.01$, $R^2 = 0.70$, $p < 0.001$.

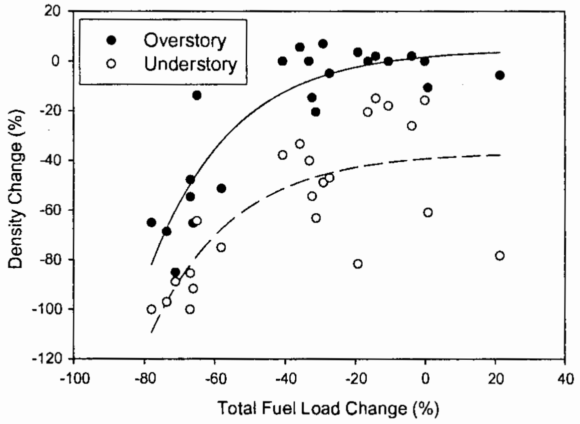

Fig. 3. Overstory (ODC) and understory density change (UDC) as functions of total fuel load change (TFLC). $\text{ODC} = 3.050 * (1 - \exp(-0.0429 * \text{TFLC})) + 1.611$; $F = 41.15$, $R^2 = 0.80$, $p < 0.001$. $\text{UDC} = 2.544 * (1 - \exp(-0.043 * \text{TFLC}))\ -39.264$; $F = 14.05$, $R^2 = 0.58$, $p < 0.001$.

at post-burn shrub covers less than 10%, but very low seedling densities on plots with post-fire shrub cover greater than 10%.

3.4. Herbaceous species cover in response to structural changes

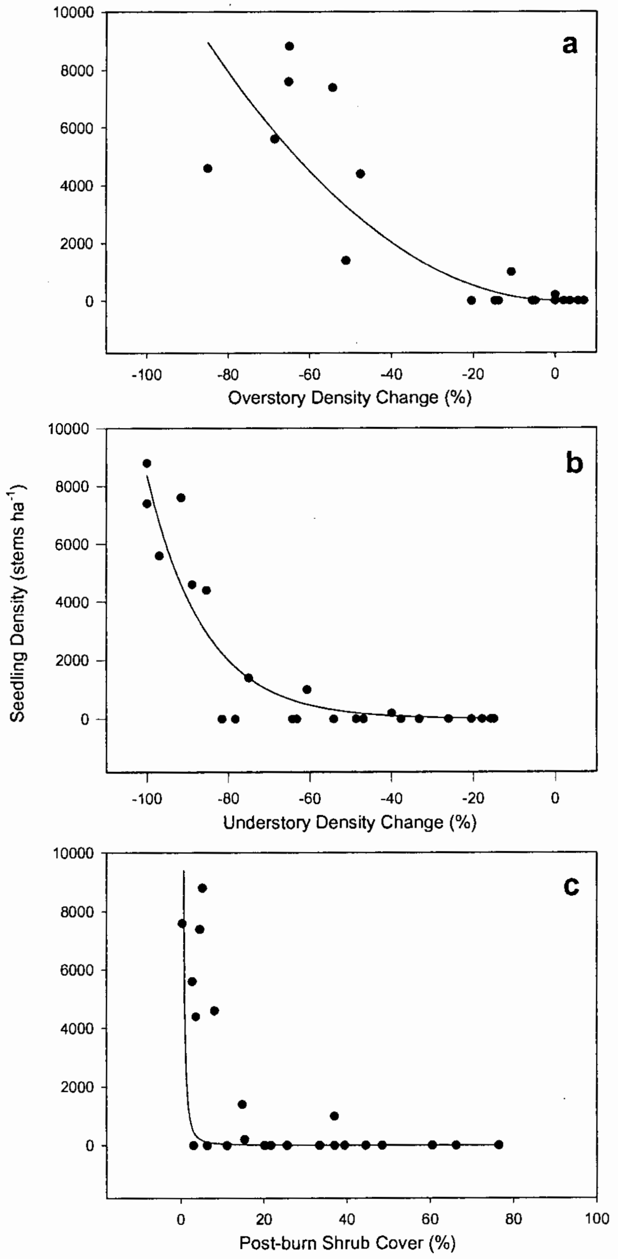

Fig. 4. Yellow pine seedlings density (YPSD) as a function of overstory density change (ODC), understory density change (UDC), and post-burn shrub cover (PBSC). $\text{Sqrt(YPSD)} = 1.038 - (1.099 * \text{ODC})$; $F = 110.54$, $R^2 = 0.84$, $p < 0.001$. $\text{YPSD} = 6.491 * \exp(-0.0716 * \text{UDC})$; $F = 150.19$, $R^2 = 0.88$, $p < 0.001$. $\ln(\text{YPSD}) = 8.316 - (1.953 * \ln(\text{PBSC}))$; $F = 15.09$, $R^2 = 0.42$, $p < 0.001$.

Total herbaceous cover displayed relationships to changes in fuels and stand structure similar to those of yellow pine seedling density. Herbaceous cover displayed strong correlations with post-burn duff depth, total fuel load change, overstory density change, and understory density change. Also, the cover of herbaceous species was highly correlated ($R = 0.946$) with the post-burn density of yellow pine seedlings (Table 2). Regression analysis revealed that the relationship between post-burn herbaceous cover and understory density change was very similar to that of yellow pine seedling density and understory density change. Like yellow pine regeneration, post-burn herbaceous cover (PBHC) increased at understory density reductions greater than 80% [$\text{PBHC} = 0.188 * \exp(-0.0538 * \text{UDC}$; $R^2 = 0.81$, $p < 0.001$, data not shown]. Also similar to yellow pine seedling density, the cover of herbaceous species increased rapidly at post-fire duff depths below 4 cm [PBHC = 59.238 ∗ exp(−1.271 ∗ PBDD); $R^2 = 0.64$, $p < 0.001$, data not shown].

3.5. KBDI, fire effects, and yellow pine regeneration

We observed very strong relationships between KBDI, fire severity, and the effects of fire on forest structure. Burns conducted under higher KBDI conditions resulted in greater reductions in duff depth, total fuel load, overstory density and understory density. KBDI was more highly correlated to many fire severity and effect variables than crown scorch or char height (Table 2), potentially due to the less subjective nature of KBDI measurements. KBDI was higher during late season burns than during early season burns, suggesting that observed differences between burn seasons may be attributable to differences in soil moisture conditions.

Seasonality varied between burns, with four burns occurring throughout the late winter/early spring fire season and two occurring in the late growing season/fall (Table 1). There were notable differences in KBDI among burns, with the higher values for late growing season burns indicative of lower soil and duff moisture. KBDI was strongly negatively correlated with percent change of total fuel loading (Table 2), meaning that as KBDI increased, total fuel loading was reduced more by fire. Burns conducted under high KBDI conditions exhibited significantly greater reductions in duff depth, total fuels, understory density, and overstory density (Fig. 5).

Burning under high KBDI conditions (328–368; more dry) resulted in greater yellow pine regeneration compared to low KBDI conditions (23–78, more wet; Fig. 6). We observed continuous recruitment of yellow pine seedlings 2 and 5 years post-burn in high KBDI burns while low KBDI burns showed little change in yellow pine density through time. In high KBDI burns, yellow pine seedling density was significantly greater 2 years (3933 ± 1137 stems ha^{-1}, $p = 0.035$) and five years post-burn (11,100 ± 3051 stems ha^{-1}, $p = 0.003$) than pre-burn (200 ± 137 stems ha^{-1}).

4. Discussion

Post-fire structural changes facilitate the reproduction of yellow pine species by altering understory light and seedbed conditions (Zobel, 1969). Our results suggest that post-fire regeneration of yellow pine species is greatest when distinct thresholds of structural change are achieved. We found that yellow pine seedlings were effectively absent in post-burn forests until overstory density was reduced over 40% and understory density was reduced over 80%. Further, a very clear threshold of regeneration success was identified when post-fire shrub cover was 10% or less. Waldrop and Brose (1999), identified a similar response of pine reproduction to prescribed burning with the greatest density of post-burn pine seedlings occurring in stands that experienced 85% mortality of trees and shrubs over 2.5 cm dbh. However, many tree and shrub species, including the often dominant *K. latifolia*, sprout prolifically after fire and may eventually reestablish in the understory and shade the forest floor without continued burning (Elliott et al., 1999; Welch et al., 2000). The rather sharp threshold of regeneration success we observed when post-burn shrub cover was less than 10% suggests that shrubs may compete more directly with

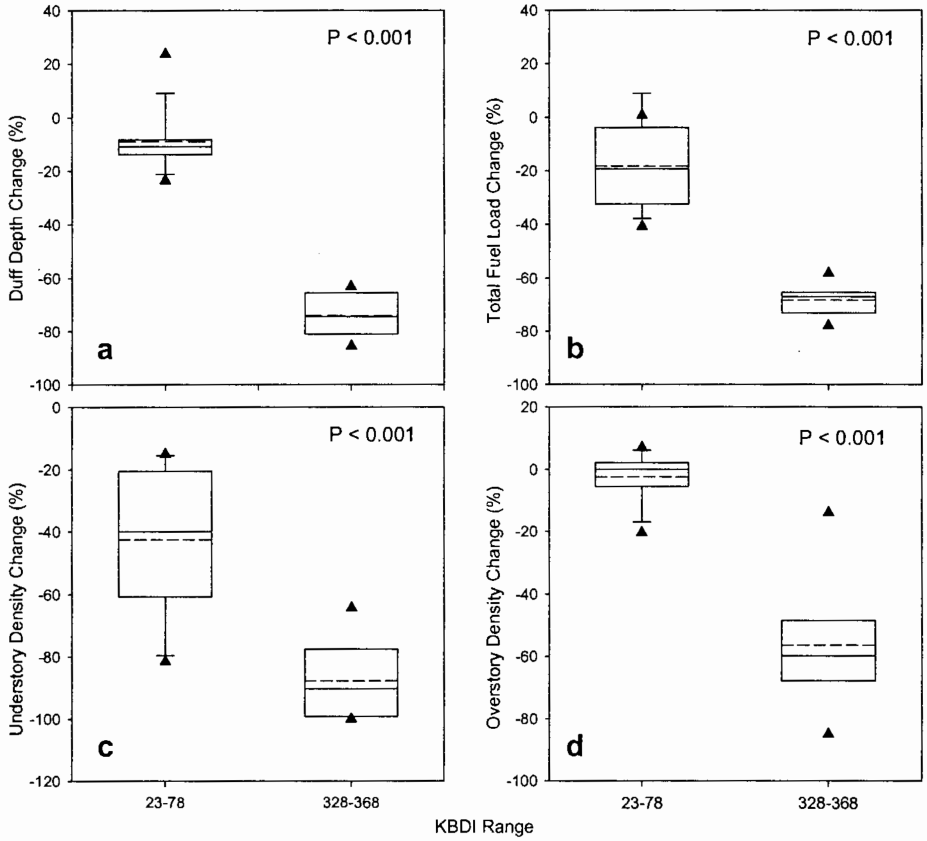

Fig. 5. Duff depth change, total fuel load change, understory density change, and overstory density change for two ranges of KBDI (Keetch–Byram Drought Index): 23–78 (wet conditions, $n = 15$) and 328–368 (dry conditions, $n = 8$). Plots show means (dashed horizontal lines), medians (solid horizontal lines), 25th and 75th percentiles (box ends), and 10th and 90th percentiles (whiskers). Minimum and maximum values are also shown (▲). Whiskers are not shown for the 328–368 KBDI range because a minimum of 9 plots are required to calculate the 10th and 90th percentiles.

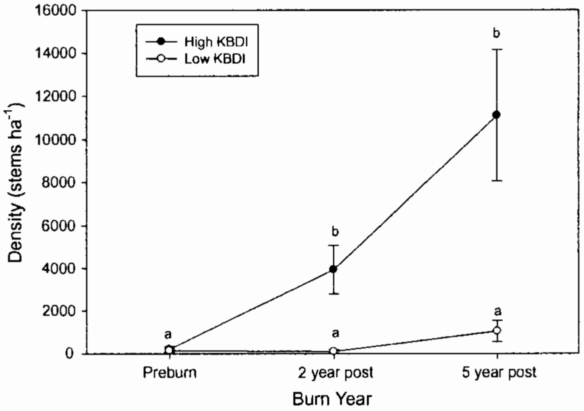

Fig. 6. Pre-burn, two years post-burn, and 5-years post-burn yellow pine seedling densities (mean ± 1 SE) in burns that occurred under high and low KBDI conditions. Means superscripted by different letters within a KBDI category (high and low) were significantly different ($p < 0.05$) according to a one-way repeated measures ANOVA with Holm–Sidak multiple comparisons tests. High KBDI $n = 6$, low KBDI $n = 12$.

pine seedlings for available sunlight than the more diffuse pine overstory. We also observed that a reduction in total fuels of 60% and a post-burn duff layer depth of less than 4 cm were required for successful regeneration of yellow pine. Similarly, Waldrop and Brose (1999) tallied the greatest density of pine seedlings stands with a mean post-burn duff depth of 3.8 cm because the roots of 95% of pine seedlings were able to penetrate the duff layer and reach the mineral soil. Similarly, Williams and Johnson (1992) did not observe yellow pine seedlings at litter and duff depths greater than 4 cm.

Understanding the relationship between fire characteristics, such as severity and intensity, and effects on vegetation, such as structural change, pine seedling establishment, and herbaceous species cover, is critical to the application of prescribed fire as a management tool to maintain yellow pine forests. Much of the research on pine regeneration following fire has centered on *Pinus pungens* (Table Mountain pine), a serotinous species endemic to the central and southern Appalachian Mountains that often grows in association with *P. rigida*. Based upon observations of seedlings establishing on mineral soil under a fire-killed overstory, Zobel (1969) emphasized the need for a severe fire to perpetuate *P. pungens*. However, fire history studies of oak-pine forests in the central and southern Appalachians have revealed a low to moderate intensity fire regime with return intervals of three to 12 years prior to the mid-20th century. (Harmon, 1982; Sutherland et al., 1995; Armbrister, 2002; Aldrich et al., 2010; Feathers, 2010). This fire regime largely consisted of non-catastrophic surface fires occurring in conjunction with other types of canopy disturbance (Brose and Waldrop, 2006).

Waldrop and Brose (1999) suggested that fires of medium–high intensity may offer the best option to regenerate Table Mountain pine stands. High intensity fire may result in low seedling density and stocking, potentially as a result of moisture stress on exposed mineral soil (Waldrop et al., 2003) and reduced post-fire formation of mycorrhizal root tips (Ellis et al., 2002). According to Waldrop and Brose (1999), medium–high intensity burns produced a mean bark char height of 6.6 m and reduced overstory basal area by 93%. By comparison, the two most intense burns in our study (Tabcat A and Wedge Ridge) produced char heights of 1.9 and 1.1 m and reduced overstory basal area by 31% and 64%, respectively. These values of char height and basal area reduction are roughly comparable to the medium–low intensity burns described by Waldrop and Brose (1999). However, the fire studied by Waldrop and Brose (1999) was characterized by low substrate severity and largely intact post-burn duff layers on moderate intensity plots, compared to the 74% reduction in mean duff load we observed following our moderate severity (high KBDI) burns. Waldrop and Brose (1999) observed the greatest density and stocking of pine seedlings (22,551 seedlings ha^{-1}) following medium–low intensity fire 1 year after burning. The authors, however, suggested that these stands did not experience sufficient overstory mortality to increase insolation enough for seedlings to survive in adequate numbers and insure continued pine dominance. Following our moderate severity burns, we observed a mean density of 4975 seedlings per hectare 2 years post-burn and a mean density 11,100 seedlings per hectare 5 years post-burn (Fig. 5). Harrod et al. (2000) observed a similar increase in yellow pine seedling density 7 years following wildfire in pine-oak forests, but Elliott et al. (2009) observed decreased density 10 years following a prescribed burn in a degraded pine-hardwood forest. In addition to the severity of the initial fire, post-fire competition and the year-to-year availability of yellow pine seeds may influence the continued post-fire recruitment of seedlings.

While we observed continued recruitment of yellow pine seedlings five years after burning, other studies have shown that shading in these stands will eventually increase due to canopy closure, increased stand density, and the re-expansion of the shrub layer (Harrod et al., 1998; Harrod and White, 1999). These developmental changes reduce the likelihood that pine regeneration will reach the canopy on sites that did not experience high overstory and understory mortality (Waldrop and Brose, 1999). While repeated burning may reverse or slow these changes, disturbances other than fire may also affect overstory tree survival and density in these forests (Brose and Waldrop, 2006). Mortality from southern pine beetle, a native insect, represents a cyclic disturbance that occurs every 6–12 years and lasts for 2–4 years in the southern Appalachians. Accounts of this insect date back to 1750 with descriptions of mortality across large tracts of pine timber (Price et al., 1978). The long-term sustained coexistence of yellow pine species and the SPB suggests that fire and SPB mortality historically interacted to perpetuate yellow pine forests. In contemporary forests, dead trees resulting from SPB infestations create heavy fuel loads that may result in more intense fires that kill more trees and reduce stand density (Kuykendall, 1978; Knebel and Wentworth, 2007). However, Schowalter et al. (1981) suggested that upland pine forests prior to fire suppression were not susceptible to heavy SPB outbreaks because low stand density resulted in reduced tree stress, likely due to reduced competition (Coulson, 1979) and reduced effectiveness of pheromone communication by the SPB (Fares et al., 1980; Thistle et al., 2004). Under these conditions, the role of SPB may have been more akin to the second stage of a silvicultural shelterwood harvest. The frequent low intensity fire regime endemic to southern upland pine forests may have increased advanced regeneration of yellow pine seedlings by creating necessary seedbed conditions and preserving mature seed trees. Subsequent mortality of scattered and small groups of overstory trees may have provided light conditions needed for this advanced regeneration to grow into the canopy.

In the southern Appalachians, a heavy SPB outbreak occurred in 1999–2002, 1–2 years following our two high KBDI burns (Tabcat Creek A and Wedge Ridge). Although we did not separate trees that were killed by SPB from trees that may have declined and died following the burns, five years post-burning we observed heavy mortality of overstory yellow pine (76%) in our high KBDI burns following this outbreak (GSMNP Fire Effects Monitoring Program, unpublished data). During this same outbreak, Elliott and Vose (2005) observed similar mortality of yellow pines in 2001–2002 in stands that did not burn (79% mortality for *P. echinata* and 47% for *P. virginiana*). This suggests that the increased yellow pine regeneration we observed five years post-burn on our high KBDI plots may have resulted from the combined effects of burning and SPB-driven reductions in overstory density following the burns.

Our study found that burning when KBDI ranged from 328 to 368 resulted in greater fire severity (reduction in overstory density, understory density, total fuels, and duff depth) and increased yellow pine reproduction. Moreover, these KBDI values are typical of annual soil moisture minimums during late summer and early fall in the southern Appalachians (Keetch and Byram, 1968; unpublished GSMNP weather data). However, the distribution of KBDI for our burns was bimodal with four burns ranging from 23 to 76 and two burns ranging from 328 to 268. More information is needed about burns conducted in the interval of KBDI between these two ranges. While KBDI has been largely unreported in studies of prescribed burning in the southern Appalachians, Waldrop and Brose (1999) reported uniformly low substrate severity regardless of intensity level following a prescribed burn conducted in a *P. pungens* stand with a KBDI of 110. The ability to predict severity based upon KBDI, combined with an understanding of how KBDI varies seasonally, may allow managers to better coordinate the timing of burns with varied intensity levels and frequency to achieve restoration objectives. However, the relationship between KBDI, seasonality, and fire severity may vary by region, fuel loading, and *Pinus* community type. In a *Pinus* flatwoods of central Florida, Outcalt and Foltz (2004) reported that a high KBDI was correlated with greater scorch height, but not with tree mortality. In *P. echinata* grasslands of west-central Arkansas, Sparks et al. (2002) found that KBDI did not provide a good index of fire behavior or intensity on drought-prone sandy loam soils. Average duff depth in these communities (0.9 ± 0.2 cm; USDA Forest Service unpublished data) is much less than the depth we observed on our plots prior to burning (7.5 ± 0.6 cm), and this lack of duff may combine with a lack of 1-h time lag fuels (Sparks et al. 2002) to produce low substrate severity regardless of KBDI.

The historic fire regime of the central and southern Appalachians consisted largely of frequent burns of low to moderate intensity (Harmon, 1982; Sutherland et al., 1995; Aldrich et al., 2010). Most fires of the late 19th and early 20th century burned during the dormant seasons with burns occurring in the spring and, with less frequency, the fall (Harmon, 1981; Lafon et al., 2005; Hoss et al., 2008). Trees within pine stands that have been sampled in the central and southern Appalachians mostly originated during the late 1800s and early 1900s under this regime (Sutherland et al., 1995; Armbrister, 2002; Brose and Waldrop, 2006; Aldrich et al., 2010). Severe burns did occur during this time period, but were a smaller component of the fire regime, and may have been most common on remote montane sites that were more reliant on lightning than humans for ignition. Cohen et al. (2007) found that lightning fires in GSMNP were more likely to occur during the growing season, persisted for durations lasting up to 38 days, and produced periodic bursts of high intensity behavior.

While our study and others have shown that a single prescribed burn of sufficient severity and/or intensity can effectively regenerate yellow pine species, it may be operationally impractical for many fire management programs to burn under these conditions. In addition, the exclusive use of greater severity fires could produce greater cover of reinitiating even-aged pine forest than likely occurred historically and favor the establishment of early-successional invasive species (Kuppinger et al., 2010). Wide-scale use of greater severity burns might also produce seed source limitations due to mortality of residual overstory trees combined with the reduced abundance of pine stands on the contemporary landscape as a result of successive outbreaks of the SPB. Further, high severity burns may extend into surrounding oak forests and kill mature trees, hindering concurrent management objectives to restore and maintain oak forests. For these reasons, prescribed burning in GSMNP, by necessity and design, is focused on using repeated low-moderate severity and low-moderate intensity fires to restore forest structure, regenerate yellow pine seedlings, and promote herbaceous-layer species diversity. The results of this study provide some targets for long-term restoration of yellow pine in the southern Appalachians, particularly with regard to tree density, shrub cover, and duff depth. Continued research and monitoring of forest structure, fuels, stand development, and species composition following repeated prescribed burns will help determine how repeated burns of varying intensity and severity levels can best be applied in combination with other disturbance agents, such as SPB, to perpetuate yellow pine forests.

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