Interactions among prescribed fire, herbivore pressure and shortleaf pine (Pinus echinata) regeneration following southern pine beetle (Dendroctonus frontalis) mortality

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Abstract

We monitored natural and artificially regenerating shortleaf pine (Pinus echinata) seedlings and their associated herbivores in forests stands that suffered extensive overstory mortality due to the southern pine beetle (Dendroctonus frontalis). Seedling performance was evaluated based on survival and absolute and relative growth rates. Trapping stations were established to monitor the abundance and seasonal activity of pine regeneration insects. Seedlings were regularly inspected for the frequency and severity of herbivore pressure. Seedling performance, insect abundance and activity, and herbivore pressure were compared between stands treated with prescribed fire and untreated controls.

Survival and absolute growth rates were greatest for naturally regenerating seedlings. Naturally regenerating seedlings grew more vigorously in the burned areas, but prescribed fire did not influence the growth of planted seedlings. Relative height growth comparisons indicated the growth potential of planted seedlings was not significantly different from that of the natural seedlings. Herbivore pressure was greater on natural regeneration, possibly due to superior seedling health and vigor. Pine weevil (Hylobius pales and Pissodes nemorensis) and Nantucket pine tip moth (Rhyacionia frustrana) abundance and herbivore pressure did not differ between the burned and unburned stands, but there was a significant interaction between sampling date and prescribed fire on their seasonal activity. Conifer sawfly (Hymenoptera: Diprionidae) abundance and activity was effectively suppressed by prescribed fire treatments. Pine webworm (Tetralopha robustella) infestations occurred with greater frequency and severity on seedlings growing in burned areas. Mammalian herbivory was minimal. Herbivore-induced seedling mortality was low, and herbivory did not reduce seedling growth. Growth of naturally regenerating shortleaf pine seedlings was greater in burned plots.

Keywords: Seedling growth; Herbivory; Pine weevils; Conifer sawflies; Tip moths; Regeneration insects

1. Introduction

Biotic and abiotic disturbances cause extensive changes in forest canopy structure and composition. Intermittent disturbances create canopy gaps that encourage regeneration and growth, and also maintain a mosaic of species and age classes within a forest (Batista and Platt, 2003). A suite of disturbance forces, including herbivory, pathogens, human use, weather events, climate change, and fire, has affected the formation, maintenance, and function of forests throughout eastern North America (Abrams, 1992). These changes influence stand succession (Blair and Brunett, 1976; Batista and Platt, 2003), herbaceous and woody plant diversity, the abundance and diversity of vertebrates and invertebrates (Sousa, 1984), and can result in complete restructuring of habitats (Foster et al., 1998).

The southern pine beetle (SPB) (Dendroctonus frontalis Zimmermann, Coleoptera: Curculionidae subfam. Scolytinae) is a significant biotic disturbance agent that causes extensive pine mortality, furthering the decline of pine forests in the southeastern United States. It is a native insect that prefers over-mature, stressed loblolly (Pinus taeda L.), shortleaf (Pinus echinata Mill.), Virginia (Pinus virginiana Mill.), and pitch pines (Pinus rigida Mill.). Adults oviposit under the bark and larvae tunnel through the cambium, girdling the tree (Drooz, 1985). There can be several generations per year and infestations spread quickly.

Following an outbreak, forest structure shifts from mature and over-mature pines to regenerating seedlings and competing hardwoods, and the associated invertebrate community is...
expected to shift concurrently. Numerous herbivores are attracted to vigorously growing pine seedlings and have the potential to impact regeneration success. The pales weevil (Hyllobius pales Herbst) and eastern pine weevil (Pissodes nemorensis Germar) (Coleoptera: Curculionidae) are attracted to damaged and dead pines and stumps, where they mate and lay eggs. Adults feed on bark, which girdles branches and stems and can cause mortality of regenerating seedlings (Drooz, 1985). The Nantucket pine tip moth (Rhyacionia frustrana Comstock, Lepidoptera: Tortricidae) causes disfigurement and reduced growth from larval tunneling in developing tips and shoots (Berisford and Kulman, 1967). Larvae of conifer sawflies (Hymenoptera: Diprionidae) and pine webworm (Tetralopha robustella Zeller, Lepidoptera: Pyralidae) cause defoliation that reduces growth and can cause mortality (Drooz, 1985).

Catastrophic losses occurred in the Cumberland Plateau region of the southeastern US due to a southern pine beetle outbreak from 1999 to 2002. Kentucky lies in the center of the Cumberland Plateau, and although this heavily forested state is dominated by hardwoods, there is an ecologically important pine component that covers about 5% of the total forested area (KDF, 2004). Because the pine component is so small, southern pine beetle outbreaks are somewhat rare, occurring approximately every 25 years (Townsend and Rieske-Kinney, 2000). Though infrequent, these outbreaks are especially devastating because they result in the loss of an important and limited habitat. Virtually the entire pine habitat was drastically altered during the most recent outbreak, which forced the evacuation of colonies of the federally endangered red-cockaded woodpecker (USDA, 2002). The infrequent occurrence of beetle outbreaks, the very diverse forest type with a prominent hardwood component, variable topography, and varying approaches to forest management exacerbate the issues associated with pine forest regeneration in this region. A shift in forest composition towards hardwoods may follow the loss of pine (Blair and Brunett, 1976), and unless measures are taken to prevent hardwood conversion, pine-associated flora (Harrington et al., 2000) and fauna (USDA, 2002) may decline.

Restoration efforts, including prescribed burning and seedling planting, began quickly following the outbreak. Prescribed burning is being utilized as site preparation because it increases natural pine regeneration and seedling growth (Vose et al., 1993), releases nutrients into the soil (Stark and Steele, 1977), alters the canopy structure and light environment (Zobel, 1969; Coleman and Rieszke, 2006) and reduces vegetative competition (Vose et al., 1995; Waldrop, 1997). The number and vigor of remaining seed-producing trees and the success of naturally regenerating and planted seedlings may ultimately determine regeneration success (Cain, 1993; Shelton and Cain, 2000).

The revegetation dynamics of shortleaf pine forests following SPB mortality, the processes affecting shortleaf pine regeneration, and the effects of prescribed fire following catastrophic losses due to SPB in the Cumberland Plateau region have not been studied. Little is known about the extent to which prescribed fire affects shortleaf pine regeneration, and no studies have assessed the impact of insects on shortleaf pine seedling regeneration (but see Coyne, 1967). Our broad objective was to assess the interacting effects among prescribed fire, herbivory, and shortleaf pine regeneration following widespread mortality caused by SPB. Specifically our objectives were to determine: (1) the effects of prescribed fire on the survival and growth of naturally regenerating and planted pine seedlings, (2) whether prescribed fire alters the incidence and seasonal activity of insect herbivores affecting pine regeneration, and (3) the extent to which prescribed fire influences herbivore pressure. We monitored the shortleaf pine seedling survival and growth, measured the incidence and effects of mammalian and arthropod herbivores, and compared the incidence and seasonal activity of insect herbivores attacking the seedlings in burned and unburned stands.

2. Methods

Research plots were established in three shortleaf pine dominated forest stands in the Daniel Boone National Forest (Pulaski Co., KY USA) as a part of a larger study investigating the ecological impacts of SPB disturbance and prescribed fire. On 19 April 2001 a prescribed fire burned all of Stand 1 and a portion of Stand 2, but Stand 3 remained unburned (Coleman and Riese, 2006). The fires were low intensity cool burns, consistent with the prescribed fire protocol of the Daniel Boone National Forest. Stand 1 (36°58’06"N; 84°24’28"W) was approximately 4.4 ha at 340 m elevation with a north-facing slope of 9.2°. Stand 2 (36°58’01"N; 84°24’35"W) was approximately 20 ha, at 347 m elevation with a southeast-facing slope of 7°. Stand 3 (36°57’40"N; 84°24’47"W) was approximately 30 ha at 317 m elevation with a south-facing slope of 7°. The SPB outbreak of 1999–2002 resulted in the mortality of nearly 100% of the shortleaf pine in these stands. Subsequent stand composition consisted of a hardwood overstory, including the common pine associates Quercus spp. and Acer rubrum, with large, numerous gaps in the canopy and regenerating hardwoods and pines in the understory. Plots were established in May 2005 in burned and unburned areas to assess shortleaf pine regeneration success and to monitor the prevalence and impact of regeneration insects. Three plots were placed in each of the burned portions of Stands 1 and 2 and three plots were placed in each of the remaining unburned portions of Stands 2 and 3, for a total of 12 plots. All plots were spaced at least 30.5 m apart.

2.1. Seedling growth

In each plot, naturally regenerating shortleaf pine seedlings (n = 15/plot) that established following the 2001 prescribed fire were located in spring 2004 and designated for observation. In addition to the natural regeneration, shortleaf pine seedlings (2–0) were planted in each plot (n = 15/plot) in the spring of 2005. Naturally regenerating seedlings were spaced at least 0.5 m apart and artificially regenerating seedlings were planted at 1.5 m intervals. All competing vegetation growing in a 0.5 m radius surrounding each seedling was clipped and removed in
the spring and midsummer. Because of the mature hardwoods present in the stands, it was not feasible to remove limbs that overtopped the seedlings. Thus, the vegetation removal freed the seedlings from competition for growing space and soil moisture, but did not prevent competition for sunlight.

Seedling heights were measured from a pre-determined mark at ground level to the highest terminal bud. Basal stem diameter consisted of an average of two perpendicular measurements taken at the pre-determined mark. Height and basal stem diameter measurements were recorded on 4 May 2004, 15 March and 13 December 2005 for the naturally regenerating seedlings and 15 March and 13 December 2005 for the planted seedlings, providing 2 years of growth data for the naturally regenerating seedlings, and 1 year of growth data for the planted seedlings. At the time of seedling planting the average heights were 38.4 and 13.2 cm for naturally and artificially regenerating seedlings, respectively. Both absolute and relative growth rates were calculated.

1. Absolute growth rate (Hunt, 1990): \[ AGR = \frac{\text{final measurement} - \text{initial measurement}}{(\text{time}_2 - \text{time}_1)}. \]

We used AGRs (1), which does not account for initial seedling size, because we have 2 years of growth data for natural seedlings and only 1 year for planted seedlings.

2. Relative growth rate (Ledig, 1974): \[ RGR = \frac{\text{final measurement} - \text{initial measurement}}{(\text{time}_2 - \text{time}_1)}. \]

Relative growth rates (2) account for differences in initial seedling height and better depict seedling growth potential.

2.2. Herbivore seasonal activity

Sampling stations (n = 18) were established in association with experimental seedlings to monitor seasonal activity of regeneration insects. Two pitfall traps (Tilles et al., 1986) targeting walking pine weevils were placed in each sampling station, and consisted of 10 cm × 17.5 cm PVC pipe with each end covered with a plastic lid. Eight evenly spaced holes (4 mm diameter) were drilled around the circumference 10 cm from the bottom, and traps were placed in the ground so that the holes aligned evenly with the soil surface. Traps were baited with 70% ethanol in 12 ml vials (8.5 cm × 1.8 cm) and turpentine (W.M. Barr & Co. Inc., Memphis, TN) in 8 ml vials (6.0 cm × 1.4 cm) (Rieske and Raffa, 1991), which was replenished every 2 weeks. A 2.5 cm² piece of Vapona® pest strip (Dichlorvos, Scotts Canada, Mississauga, Ontario) was placed in the bottom of each trap to kill trapped arthropods.

To target flying pine weevils, one flight trap (Klepzig et al., 1991) was placed in each plot and consisted of an inverted 3.8 l milk jug with three sides removed and a 125 ml plastic bottle containing a 2.5 cm² piece of Vapona® pest strip securely attached to the bottom. Each trap was attached to the top of a 1.0 m wooden stake (3.1 cm × 3.1 cm) and baited with ethanol and turpentine as described above.

In 2004, two wing traps (Trece Inc., Salinas, CA) baited with Nantucket pine tip moth pheromone (Trece Inc., Salinas, CA) were placed in each plot at reachable heights of 1.2 m or greater. In 2005, one additional wing trap baited with conifer sawfly pheromone \(((2S, 3S, 7S)-3,7$-dimethyl-2-pentadecy1 acetate) (Högberg et al., 1990), which is attractive to adult males of several species that occur in Kentucky (Rieske et al., 2001), was included in each plot. Traps were positioned at least 6.0 m from each other.

Traps were monitored at 2-week intervals from late June through mid-October in 2004. In 2005, collections occurred weekly from 30 March through 20 July, and at 2-week intervals from 20 July to 13 October. Weevils (Millers et al., 1963) and Nantucket pine tip moth tips (McCullough et al., 1998) were identified. Although no suitable keys exist for adult male conifer sawflies based on morphological characteristics, previous studies show at least three species co-exist in Kentucky (Rieske et al., 2001).

2.3. Herbivore pressure

To characterize herbivore pressure on regenerating seedlings, in 2005 arthropod and mammalian herbivory was manipulated with a combination of insecticide applications and fencing (Adams and Rieske, 2001). Both naturally regenerating (n = 145) and planted (n = 181) seedlings received the four seedling treatments in the burned and unburned stands.

To exclude mammalian herbivores, seedlings were fenced with wire tomato cages (1.0 m × 30.5 cm diameter) enclosed with 2.5 cm × 3.5 cm chicken wire embedded in the ground and surrounded at the base by 15 cm metal flashing on 18 March. Seedlings were protected from arthropod herbivores by applying the synthetic pyrethroid bifenthrin (Talstar® GH FMC, Philadelphia) with a handheld spray bottle (1.56 ml Talstar® GH/L water) until run-off at 14-day intervals beginning 14 April and ending 13 October.

Insecticide applications to fenced seedlings (+I/+F) protected against both arthropod and mammalian herbivory (n = 5 /plot). Fenced seedlings without insecticide (−I/+F) protected against mammalian herbivory only (n = 5 /plot). Similarly, the insecticide application minus the fence (+I−/F) protected seedlings only against arthropod herbivory (n = 3 /plot). Finally, unprotected seedlings (−I−/F) served as negative controls (n = 2 /plot) (Adams and Rieske, 2001). Because of limited numbers of naturally regenerating seedlings in the burned portion of the second stand, the replication for seedling treatments +I+/F was n = 2, and for −I−/F, n = 3.

At 14-day intervals, each seedling was visually evaluated for debarking caused by pine weevils, and injury was rated based on a six-point scale of severity modified from Sydow and Örlander (1994). A rating of 0 = no feeding, 1 indicated <10% debarking, 2 = 11−25% debarking, 3 = 25−50% debarking resulting in girdled branches, 4 = 51−75% debarking with girdled branches, and 5 indicated the main stem had been 100% girdled. Damage ratings > 3 often indicated weevil mortality. Frequency and severity of Nantucket pine tip moth attack (% of infested tips) (Berisford et al., 1984), conifer sawfly defoliation (% needle removal) (Beal, 1942), and pine webworm infestation (number of frass nests) (Hertel and Benjamin, 1977) were also recorded.
2.4. Statistical analysis

All data were tested for the assumptions of the ANOVA and transformed when necessary. Data that failed to meet the assumptions following transformation were analyzed using the Mann–Whitney nonparametric test and the Z test statistic. Sample sizes and P-values are reported.

Multivariate analysis of variance (MANOVA, SAS Institute, 1999) was used to assess seedling performance using site treatment (burned versus unburned) and regeneration type (natural versus planted) as main effects. Seedling height and basal stem diameter growth were measures of seedling performance. Due to differences in available growth measurements and seedling variability, both absolute and relative growth rates were calculated and analyzed. The Wilks’ Lambda test statistic was used to assess overall significance of the multivariate model, which was followed by univariate analyses of individual response variables using a fixed effects model and Satterthwaite’s approximation for degrees of freedom. Least squares means were calculated to analyze pairwise comparisons. Due to the unbalanced nature of the experimental design, in which each stand received a different fire treatment, the interaction of stand and fire created an incomplete two-way table. Consequently, the multivariate analysis could not be used to determine the effects of stand characteristics, such as slope, aspect and elevation, on seedling performance. To compensate for this, stand main effects and stand interaction with regeneration type were omitted from the analysis and absorbed into the stand by fire and regeneration type by stand by fire variability/error terms. Stand effects on seedling performance were instead analyzed using the MIXED procedure (SAS Institute, 1999), with stand as the fixed effect and plot as the random effect.

Prescribed fire effects on insect seasonal activity was assessed using repeated measures mixed model analysis of variance (PROC MIXED, SAS Institute, 1999) with fire treatment as the fixed effect and plot as a random effect. Trap type within trapping stations were treated as sampling units within each plot. Date and treatment interactions were determined with Tukey’s multiple comparisons.

The GLM procedure was used to evaluate the presence or absence of herbivore pressure on regenerating seedlings. To assess the impact of herbivore pressure on seedling growth, we used the MIXED procedure with naturally regenerating seedlings as the experimental units. Tukey’s multiple comparisons were used to assess the interaction of fire and seedling treatments on absolute and relative growth rates. Frequency tables (PROC FREQ, SAS Institute, 1999) were developed to illustrate the distribution of herbivore damage ratings. Fisher’s exact test detected associations between damage ratings and site treatment.

Canonical correlation analysis (CANCORR, SAS Institute, 1999) was used to assess the relationship between the best linear combination of response variables describing seedling performance (survival, and height and diameter absolute growth rates) with the best linear combination of response variables describing herbivore pressure (frequency and severity of pine weevil, Nantucket pine tip moth and pine webworm attack).

3. Results

3.1. Seedling performance

Overall seedling survivorship was 82%. Natural seedling (n = 145) survivorship was higher than that of the planted seedlings (n = 181) (91% versus 74%; Z = 3.93; P < 0.0001). Both naturally and artificially regenerating seedlings experienced lower survival when growing in prescribed fire treated stands (Table 1).

The multivariate analysis of absolute growth rates showed that prescribed fire had no effect on overall seedling performance. Seedling performance was influenced by the type of regeneration (natural versus planted) (F = 341.09; d.f. = 2, 1; P = 0.04) but the interaction between fire and regeneration type had no effect. The univariate analysis revealed a significant interaction between prescribed fire and regeneration type on absolute height growth (Table 2), in which natural seedlings growing in the burned stands experienced the greatest increase in height. The lowest absolute height increase occurred on planted seedlings in burned stands, but this did not differ from planted seedlings in the unburned stands. Seedling absolute diameter growth was not influenced by the interaction between fire and regeneration type (Table 2). However the diameter increase of natural seedlings was greater than that of the planted (F = 294.21; d.f. = 1, 3.63; P = 0.0001). Seedlings in Stand 1 had the greatest absolute diameter growth (F = 4.12; d.f. = 2, 272; P = 0.02), but there was no difference in diameter growth between Stands 2 and 3.

Similarly, the multivariate analysis of relative growth rates revealed that prescribed fire had no effect on seedling performance, nor was there an interaction between prescribed fire and regeneration type. However, seedling performance was influenced by regeneration type (F = 941.40; d.f. = 2, 1; P = 0.02). Relative height growth did not differ between natural and planted seedlings, but relative diameter growth was greater for the natural seedlings (F = 244.65; d.f. = 1, 2.82; P = 0.0008). The seedlings planted in the unburned stands had the lowest relative diameter growth (Table 2), but this difference was marginal (P = 0.06). Relative growth rates did not vary among stands.

Table 1

<table>
<thead>
<tr>
<th>Regeneration</th>
<th>Site treatment</th>
<th>Z/P</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Burned</td>
<td>Unburned</td>
</tr>
<tr>
<td>Natural</td>
<td>85% A b (n = 55)</td>
<td>94% A a (n = 90)</td>
</tr>
<tr>
<td>Planted</td>
<td>65% B b (n = 90)</td>
<td>82% B a (n = 91)</td>
</tr>
</tbody>
</table>

Means within columns followed by the same upper case letter do not differ; means within rows followed by the same lower case letter do not differ.

* Mann–Whitney nonparametric analysis.
3.2. Herbivore seasonal activity

Pales weevil was the most abundant taxon collected in 2004, but abundance did not differ between burned and unburned stands (Table 3). In 2005, marginally more \((P = 0.07)\) pales weevils were trapped in burned than in unburned stands (Table 3). In 2004 weevils were caught in greater numbers in pitfall traps than in flight traps \((F = 17.61; \text{d.f.} = 1, 17; P = 0.0006)\) and there was no difference in pales weevil response based on trap type in 2005. Average weekly trap catches of pales weevils decreased significantly from 2004 \((\bar{X} = 3.07/\text{wk})\) to 2005 \((\bar{X} = 5.4/\text{wk})\) \((Z = 14.53; P < 0.0001; n = 468, 1242)\).

Response to baited pitfall and flight traps was immediate upon deployment in both years. Pitfall trap catch of pales weevils did not differ between burned and unburned stands in 2004 (Fig. 1A). In 2005 (Fig. 1B), pitfall catches were marginally greater in burned stands \((F = 3.32; \text{d.f.} = 1, 136; P = 0.07)\), and significantly greater activity was detected in burned plots during the peaks on 14 April \((F = 12.35; \text{d.f.} = 1, 352; P = 0.0005)\) and 15 June \((F = 21.43; \text{d.f.} = 1, 352; P < 0.0001)\).

There was no difference between fire treatments in the total number of pales weevils caught in flight traps for either year. Flight activity peaked on 13 July 2004 (Fig. 1C) and in April and May in 2005 (Fig. 1D). More weevils were trapped in the burned stands in 2005 on 14 April \((F = 10.91; \text{d.f.} = 1, 272; P = 0.001)\) and 25 May \((F = 3.93; \text{d.f.} = 272; P = 0.05)\) and in the unburned stands on 20 April \((F = 10.91; \text{d.f.} = 1, 272; P = 0.001)\).

Eastern pines weevils did not respond to either trap type in 2004 and responded only to flight traps in 2005. Overall abundance was low \((\bar{X} = 2.1/\text{wk})\) and trap catches did not differ between the burned and unburned stands (Table 3). In 2005, flight activity was immediate upon trap deployment in March and continued through April, with a peak in late March. Eastern pine weevil activity was greater in burned stands on 30 March \((F = 16.56; \text{d.f.} = 1, 272; P < 0.0001)\) and 6 April \((F = 12.17; \text{d.f.} = 1, 272; P = 0.0006)\).

In 2004, Nantucket pine tip moth abundance did not differ between fire treatments (Table 3), but activity (Fig. 2A) was greater in burned stands on 26 July \((F = 4.11; \text{d.f.} = 1, 304; P = 0.04)\) and 10 August \((F = 4.11; \text{d.f.} = 1, 304; P = 0.04)\). Tip moth abundance in 2005 did not differ between burned and unburned plots (Table 3), but activity was greater in the burned plots during the peaks of 22 June \((F = 11.92; \text{d.f.} = 1, 336; P = 0.0006)\) and 29 June \((F = 11.92; \text{d.f.} = 1, 336; P = 0.0006)\) (Fig. 2B). Abundance between 2004 and 2005 \((\bar{X} = 1/\text{wk} \text{ and } \bar{X} = 3.5/\text{wk}, \text{respectively})\) did not differ.

In 2005, conifer sawflies were the dominant taxa \((\bar{X} = 239.8/\text{wk})\) and abundance in wing traps in the burned stands \((n = 195)\) was lower than those in unburned stands \((n = 197)\) (Table 3) during nearly all dates of peak activity.

Table 3
Regeneration insects (lsmeans ± S.E./treatment/interval) captured in baited traps in burned and unburned shortleaf pine stands following catastrophic losses due to southern pine beetle mortality

<table>
<thead>
<tr>
<th>Year</th>
<th>Taxa</th>
<th>Site treatment</th>
<th></th>
<th></th>
</tr>
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<tbody>
<tr>
<td></td>
<td></td>
<td>Burned ((n = 55))</td>
<td>Unburned ((n = 90))</td>
<td></td>
</tr>
<tr>
<td>2004</td>
<td>Pales weevil</td>
<td>1.22 ± 0.33 a</td>
<td>1.32 ± 0.33 a</td>
<td>0.04, 53/0.84</td>
</tr>
<tr>
<td></td>
<td>Eastern pines weevil</td>
<td>0</td>
<td>0</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td>Nantucket pine tip moth</td>
<td>0.09 ± 0.03 a</td>
<td>0.03 ± 0.03 a</td>
<td>2.57, 53/0.12</td>
</tr>
<tr>
<td></td>
<td>Conifer sawflies</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>2005</td>
<td>Pales weevil</td>
<td>0.19 ± 0.16 a</td>
<td>0.08 ± 0.16 a</td>
<td>3.42, 130/0.07</td>
</tr>
<tr>
<td></td>
<td>Eastern pines weevil</td>
<td>0.04 ± 0.02 a</td>
<td>0.02 ± 0.02 a</td>
<td>1.24, 130/0.27</td>
</tr>
<tr>
<td></td>
<td>Nantucket pine tip moth</td>
<td>0.18 ± 0.05 a</td>
<td>0.07 ± 0.05 a</td>
<td>2.01, 130/0.16</td>
</tr>
<tr>
<td></td>
<td>Conifer sawflies</td>
<td>12.2 ± 2.61 b</td>
<td>22.0 ± 2.60 a</td>
<td>Z^2 = 2.54/P = 0.006</td>
</tr>
</tbody>
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Ismeans within rows followed by the same letter do not differ \((P < 0.05)\).

a Conifer sawflies were not monitored in 2004.

b Mann–Whitney nonparametric analysis.
Sawflies were responsive to the baited wing traps throughout most of the sampling period, with activity peaks occurring in July and August.

3.3. Herbivore pressure

Regeneration insects showed a preference for naturally regenerating seedlings over planted seedlings ($Z = 10.45; P < 0.0001; n = 145, 181$). Evidence of herbivore pressure from at least one regeneration insect was detected on 56% of the natural seedlings, while only 4% of the planted seedlings showed signs of herbivore damage. Because herbivore pressure on planted seedlings was negligible, we focused our analysis on naturally regenerating seedlings.

Seedlings protected from arthropod herbivory through insecticide applications (+I) experienced less herbivore pressure than those that were not protected (−I) (Table 4), but this difference was marginal ($P = 0.09$). Seedlings unprotected from both mammalian and arthropod herbivory (−I/−F) suffered the most injury, while unfenced seedlings with insecticide applications (+I/−F) experienced the least herbivore pressure.

Absolute and relative growth rates were unaffected by either fencing (F) or insecticide applications (I) (Table 5). There was a significant interaction between site treatments and seedling treatments in which seedlings unprotected from arthropod herbivory (−I/−F and −I/+F) had greater absolute growth when
growing in the burned areas than in the unburned. Absolute height growth was not impacted by prescribed burning when seedlings were protected from arthropod herbivory (+I/+F and +I/−F) and there were no interactions between site and seedling treatments for absolute diameter growth rate or relative growth rates.

Weevils comprised the greatest component of herbivore pressure, followed by pine webworm and Nantucket pine tip moth (Table 6). There was no evidence of conifer sawfly larval feeding throughout the monitoring period.

Of the eight naturally regenerating seedlings that suffered herbivore-induced mortality, two showed signs of heavy pine weevil feeding, and one was heavily infested with pine webworms. No signs of herbivory were detected on the five remaining seedlings that died, and the cause of death could not be visually determined.

There was a marginal difference (P = 0.08) in the number of weevil-damaged natural seedlings in burned versus unburned stands (Table 6). The majority of the weevil debarking was not severe; 69% of the injured seedlings received a rating of 1, 10% were rated 2, 12% were rated 3, and 5% were rated 4. Only 4% of the seedlings received the rating of 5, indicating the stem had been 100% girdled. There was a marginal association (P = 0.10) between unburned stands and weevil damage severity based on Fisher’s exact test.

Nantucket pine tip moth occurrence was infrequent and did not differ between burned and unburned stands (Table 6). Of the webworm infested seedlings, 84% had 1 frass nest, 11% had 2 frass nests, 5% had 3 frass nests, and 2% had 5 frass nests. The seedlings with 3–5 frass nests were found exclusively in burned stands. A marginal association (P = 0.07, Fisher’s exact test) between burning and webworm damage severity was detected.

The multivariate canonical correlation analysis created a linear combination of seedling performance variables (survivorship, and absolute height and diameter growth rates) to test for correlations with the linear combination of herbivore damage variables (frequency and severity of weevil, Nantucket pine tip moth, and webworm). There was a strong correlation between seedling performance and herbivore damage (F = 4.32; d.f. = 18, 758.5; P < 0.0001). Based on canonical weights we found that absolute diameter growth rate (1.019) was positively correlated with weevil feeding frequency (0.527) and pine webworm severity (0.416). Diameter growth was negatively correlated with pine weevil severity (−0.584). Seedling survivorship (0.954) was

Table 4

<table>
<thead>
<tr>
<th>Seedling treatment</th>
<th>lsmeans (±S.E.)</th>
<th>F_{d.f.}/P</th>
</tr>
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<tbody>
<tr>
<td>−I/−F</td>
<td>0.68 ± 0.08</td>
<td></td>
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<tr>
<td>−I/+F</td>
<td>0.67 ± 0.06</td>
<td></td>
</tr>
<tr>
<td>+I/+F</td>
<td>0.56 ± 0.06</td>
<td></td>
</tr>
<tr>
<td>+I/−F</td>
<td>0.37 ± 0.07</td>
<td>2.21_{3, 31}/0.09</td>
</tr>
</tbody>
</table>

Table 5

<table>
<thead>
<tr>
<th>Absolute growth rate</th>
<th>Site treatment</th>
<th>Seedling treatment</th>
<th>F_{d.f.}/P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Height (cm/year)</td>
<td>Burned</td>
<td>−I/−F</td>
<td>28.15 ± 2.47 a</td>
</tr>
<tr>
<td></td>
<td></td>
<td>−I/+F</td>
<td>31.86 ± 2.39 a</td>
</tr>
<tr>
<td></td>
<td></td>
<td>+I/+F</td>
<td>22.81 ± 2.39 ab</td>
</tr>
<tr>
<td></td>
<td></td>
<td>+I/−F</td>
<td>26.79 ± 2.84 ab</td>
</tr>
<tr>
<td>Diameter (mm/mm/year)</td>
<td>Burned</td>
<td>−I/−F</td>
<td>10.76 ± 2.30 b</td>
</tr>
<tr>
<td></td>
<td></td>
<td>−I/+F</td>
<td>11.92 ± 1.68 b</td>
</tr>
<tr>
<td></td>
<td></td>
<td>+I/+F</td>
<td>14.96 ± 1.64 b</td>
</tr>
<tr>
<td></td>
<td></td>
<td>+I/−F</td>
<td>13.83 ± 1.97 b</td>
</tr>
<tr>
<td>Relative growth rate</td>
<td>Burned</td>
<td>−I/−F</td>
<td>2.64 ± 0.33 a</td>
</tr>
<tr>
<td></td>
<td></td>
<td>−I/+F</td>
<td>3.21 ± 0.31 a</td>
</tr>
<tr>
<td></td>
<td></td>
<td>+I/+F</td>
<td>2.77 ± 0.32 a</td>
</tr>
<tr>
<td></td>
<td></td>
<td>+I/−F</td>
<td>3.46 ± 0.37 a</td>
</tr>
<tr>
<td>Height (cm/cm/year)</td>
<td>Burned</td>
<td>−I/−F</td>
<td>1.06 ± 0.31 b</td>
</tr>
<tr>
<td></td>
<td></td>
<td>−I/+F</td>
<td>0.80 ± 0.22 b</td>
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<td></td>
<td>+I/+F</td>
<td>1.14 ± 0.22 b</td>
</tr>
<tr>
<td></td>
<td></td>
<td>+I/−F</td>
<td>1.44 ± 0.26 b</td>
</tr>
</tbody>
</table>

Table 6

| Naturally regenerating shortleaf pine seedlings (lsmeans ±S.E./treatment) damaged by regeneration insects in burned and unburned stands following catastrophic losses to the southern pine beetle |
|------------------------|------------------------|
| Herbivore               | Site treatment        | F_{d.f.}/P |
| Pales and eastern pine weevils | Burned | 0.31 ± 0.07 a |
|                        | Unburned              | 0.46 ± 0.05 a |
| Nantucket pine tip moth | Burned | 0.11 ± 0.04 a |
|                        | Unburned              | 0.12 ± 0.03 a |
| Pine webworm           | Burned | 0.31 ± 0.05 a |
|                        | Unburned              | 0.16 ± 0.04 b |

lsmeans within rows followed by the same letter do not differ.

*Mann–Whitney nonparametric analysis.

Infested, and 12% of the seedlings were 25% infested. The infestations never exceeded 25% of available shoots. There was no association between prescribed fire treatments and the severity of Nantucket pine tip moth damage.

Seedlings in burned stands were attacked more frequently by the pine webworm than were seedlings in unburned stands (Table 6). Of the webworm infested seedlings, 84% had 1 frass nest, 11% had 2 frass nests, 5% had 3 frass nests, and 2% had 5 frass nests. The seedlings with 3–5 frass nests were found exclusively in burned stands. A marginal association (P = 0.07, Fisher’s exact test) between burning and webworm damage severity was detected.

A strong correlation existed between the severity of Nantucket pine tip moth damage (F = 4.32; d.f. = 18, 758.5; P < 0.0001). Based on canonical weights we found that absolute diameter growth rate (1.019) was positively correlated with weevil feeding frequency (0.527) and pine webworm severity (0.416). Diameter growth was negatively correlated with pine weevil severity (−0.584). Seedling survivorship (0.954) was

lsmeans within height and diameter rows that are followed by the same letters are not statistically different.
negatively correlated with pine weevil feeding severity (−1.499) and positively correlated with weevil feeding frequency (0.779).

4. Discussion

Our results support previous findings that fire promotes natural pine regeneration (Oosting and Livingston, 1964; Vose et al., 1993). Although seedling mortality was higher in the burned areas, the absolute height growth of natural seedlings in burned stands exceeded 20 cm, suggesting the seedlings were healthier and more vigorously growing than those in the unburned areas (Shelton and Cain, 2000). The naturally regenerating seedlings in our study presumably established themselves immediately following the burn, and gained from the immediate benefits of exposed mineral soil, elevated nutrients, and reduced vegetative and light competition associated with prescribed fire (Lloyd et al., 1990; Waldrop, 1997; Elliott et al., 1999).

Optimally, seedlings are planted within 1 year following a burn to gain immediate benefits of exposed mineral soil and altered competition (Lloyd et al., 1990; Waldrop, 1997; Elliott et al., 1999). The shortleaf pine seedlings in our study were planted 4 years after the prescribed fire, and so did not receive the full benefits of enhanced sunlight and nutrients, and reduced competition provided by the burn. Although we removed vegetation in a 0.5 m radius of both naturally regenerating and planted seedlings, the vegetation removal was not adequate to compensate for nutrient depletion over time, resulting in lower absolute growth of planted seedlings (Cain, 1991; Ludovici and Morris, 1997). The absolute height growth rates of planted seedlings did not differ between fire treatments, and were lower than those of the naturally regenerating seedlings. In addition, shortleaf pine grows slowly during the first years of establishment while the root system develops (McQuilken, 1935), and transplant shock and drought-induced water stress in our planted seedlings may have caused further growth reductions (Ludovici and Morris, 1997). Larger, older seedlings typically experience faster height and diameter growth rates (Cain and Barnett, 1996; Cain and Shelton, 2000), possibly due to more developed root systems. However, the relative height growth rate of the newly planted seedlings was equivalent to that of the natural seedlings, suggesting strong growth potential or competitive ability (Ericsson, 1976; Larocque, 2000).

Regeneration weevil abundance did not differ between burned and unburned stands, but weevils did demonstrate a preference for certain stand characteristics. During peaks of weevil activity in 2005 (14 April and 15 June) the majority of the weevils were trapped in burned stands with an open canopy and abundant naturally regenerating pine seedlings. This is consistent with previous research demonstrating that pine weevil damage is more prevalent in young, open stands (Sydow and Orlander, 1994), and could explain why weevils are attracted to stands that have undergone high intensity burns, where crown scorch and tree mortality often occur, but do not distinguish between low intensity and unburned stands (Fox and Hill, 1973; Hanula et al., 2002).

The drastic drop in pales weevil activity from 2004 to 2005 may be due to multiple factors. The amount of host material suitable for weevil development declines rapidly following SPB overstory mortality, and may have reached a point where weevil populations were no longer sustainable (Rieske and Raffa, 1993a, 1999). Environmental conditions may also have played a role. In 2004, the 9-month (March–October) average air temperature during the spring and summer was 16.67 °C (+0.56 °C deviation from normal) and accumulated rainfall was 111.25 cm (+19.13 cm). Warmer, drought-like conditions prevailed in 2005, with an average 9-month air temperature of 17.78 °C (+1.11 °C deviation from normal), and spring and summer rainfall accumulation of 70.15 cm (−21.62 cm) (UKAWC, 2005; Somerset, KY Weather Station), which may have reduced weevil movement or resulted in weevil mortality (Rieske and Raffa, 1991, 1993a).

Eastern pine weevils are highly attracted to baited flight traps, but response to baited pitfall traps is poor (Rieske and Raffa, 1990, 1993b). In our study there was little response by eastern pine weevils to either trap type. Abundance may have been below detectable levels, or the environmental factors and depleted food supply that influenced pales weevil activity may also have played a role with eastern pine weevils. In 2004, trapping began after the major period of eastern pine weevil activity (Rieske and Raffa, 1993b; Rieske, 2000).

Pine weevil damage occurred more frequently on the vigorously growing seedlings, as illustrated by the positive correlation between feeding frequency and pine absolute diameter growth. When pine weevil feeding is severe, large amounts of bark are removed along the main stem, which reduces basal stem diameter and often results in seedling death (Drooz, 1985).

Flight activity of the Nantucket pine tip moth was greatest in the xeric, open conditions of the burned Stand 1 in both years. Tip moths are highly attracted to unshaded pine seedlings in open stands with minimal surrounding vegetative competition (Berisford and Kulman, 1967; Hertel and Benjamin, 1977). Feeding frequency positively correlated with absolute diameter growth rates, but infestations were infrequent and severity was low in both burned and unburned stands. Tip moths preferentially attack pine saplings (Hertel and Benjamin, 1977; Nowak and Berisford, 2000) and infestations may continue until canopy closure.

Significantly fewer conifer sawflies were trapped in burned stands. The conifer sawfly complex in this region consists of at least three species (Rieske et al., 2001), but the activity pattern we observed suggests that the redheaded pine sawfly (Neodiprion lecontei Fitch) is the prominent species. Redheaded pine sawflies overwinter as prepupae in the topsoil (McCullough et al., 1998). These were probably destroyed by the fire, and coupled with the loss of host material, populations remained suppressed 4 years after the prescribed burn. The sudden drop in sawfly activity in late July was associated with several days of heavy rainfall (UKAWC, 2005), which decreases flight activity (Jonsson and Anderbrant, 1993). Herbivore pressure from conifer sawfly larvae was not observed, despite the abundance of trapped adult males.
However, trap catch can be affected by male migration and skewed sex ratios due to haplodiploidy, and is not an adequate indicator of larval populations (Lyytikäinen-Saarenmaa et al., 1999). Conifer sawflies preferentially attack pine trees that are 1.2–2.4 m tall (Averill et al., 1982), and the height of our regenerating seedlings were well below that.

Pine webworm infestations can be influenced by the intensity of site preparation (Hertel and Benjamin, 1977), and in our study attacks were more frequent in the burned stands (Table 4). The severity of webworm attacks increased with absolute diameter growth rates. However, once seedling height exceeds 60 cm the threat of growth loss or mortality is minimal (Hertel and Benjamin, 1977). By the end of the growing season in 2005 the average heights were 58 cm for natural seedlings and 25 cm for planted seedlings. The artificially regenerating seedlings are still susceptible to pine webworm damage, particularly when growing in the prescribed fire treated areas.

Herbivore pressure from regeneration insects was lowest on seedlings that received insecticide applications, which suggests that the mammalian component of the herbivore complex affecting shortleaf pine regeneration is minimal. Although more than half of the naturally regenerating seedlings experienced herbivore pressure, there was no indication that arthropod herbivory influenced seedling growth.

Four years after the prescribed fire treatment naturally regenerating seedlings were the healthiest and most vigorous. Regeneration herbivores preferentially feed on vigorously growing young pines, which may explain the reduced herbivore pressure on planted seedlings. Although the incidences of Nantucket pine tip moth and conifer sawfly damage was low, seeds of the seedlings age these insects may become a greater threat. However, our evidence suggests that seedling performance is greater on burned sites, and redheaded pine sawfly populations were effectively suppressed following prescribed fire treatments.

Our data suggest that prescribed fire is a useful tool to promote successful regeneration of shortleaf pine following southern pine beetle mortality. Although the activity and abundance of some regeneration insects increased in the burned stands, natural seedling performance was unaffected by herbivore pressure. Following SPB outbreaks the natural seed source for shortleaf pine is depleted, so seedlings should be planted within 1 year following the burn to optimize the benefits of the burn and to supplement natural regeneration. When shortleaf pine seedlings are established simultaneously with hardwood and herbaceous vegetation they can outgrow the competition and achieve dominance in 5–7 years (Lloyd et al., 1990; Cain, 1991). The status of the seedlings following the completion of root development will provide useful insight into the regenerative abilities of shortleaf pine and the interactions between prescribed fire and herbivore pressure following southern pine beetle mortality.

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