Overstory tree mortality resulting from reintroducing fire to long-unburned longleaf pine forests: the importance of duff moisture

J. Morgan Varner III, J. Kevin Hiers, Roger D. Ottmar, Doria R. Gordon, Francis E. Putz, and Dale D. Wade

Abstract: In forests historically maintained by frequent fire, reintroducing fire after decades of exclusion often causes widespread overstory mortality. To better understand this phenomenon, we subjected 16 fire-excluded (ca. 40 years since fire) 10 ha longleaf pine (*Pinus palustris* Mill.) stands to one of four replicated burning treatments based on volumetric duff moisture content (VDMC): wet (115% VDMC); moist (85% VDMC); dry (55% VDMC); and a no-burn control. During the first 2 years postfire, overstory pines in the dry burns suffered the greatest mortality (mean 20.5%); pine mortality in the wet and moist treatments did not differ from the control treatment. Duff reduction was greatest in the dry burns (mean 46.5%), with minimal reduction in the moist and wet burns (14.5% and 5%, respectively). Nested logistic regression using trees from all treatments revealed that the best predictors of individual pine mortality were duff consumption and crown scorch ($P < 0.001$; $R^2 = 0.34$). Crown scorch was significant only in dry burns, whereas duff consumption was significant across all treatments. Duff consumption was related to moisture content in lower duff (Oa; $R^2 = 0.78$, $P < 0.001$). Restoring fire to long-unburned forests will require development of burn prescriptions that include the effects of duff consumption, an often overlooked fire effect.

Résumé : Dans les forêts qui avaient l'habitude de se maintenir grâce à de fréquents incendies, la réintroduction du feu après plusieurs décennies d'exclusion cause souvent beaucoup de mortalité dans l'étage dominant. Afin de mieux comprendre ce phénomène, nous avons soumis 16 peuplements de pin à longues aiguilles de 10 ha protégés contre les incendies (env. 40 ans sans feu) à un des quatre traitements répétés de brûlage sur la base du contenu volumétrique en humidité de la litière : brûlis mouillé, 115 %; brûlis humide; 85 %, brûlis sec, 55 % et un témoin non brûlé. Durant les deux premières années après le passage du feu, les pins de l'étage dominant dans les brûlis secs ont subi la plus forte mortalité (moyenne = 20,5 %); la mortalité du pin dans les brûlis mouillés et humides n'était pas différente de celle du traitement témoin. La réduction de la litière était la plus importante dans les brûlis secs (moyenne = 46,5 %) avec une réduction minimale dans les brûlis humides (14,5 %) et mouillés (5 %). La régression logistique à plusieurs critères de classification appliquée aux arbres de tous les traitements a révélé que les meilleures prédicteurs de mortalité d'une tige de pin étaient la consommation de litière et le roussissement de la cime ($P < 0,001$; $R^2 = 0,34$). Le roussissement de la cime était significatif seulement dans les brûlis secs tandis que la consommation de litière était significative dans tous les traitements. La consommation de litière était reliée au contenu en humidité dans la partie inférieure de la litière (Oa; $R^2 = 0,78$; $P < 0,001$). Réintroduire le feu dans des forêts qui n'ont pas brûlé depuis longtemps va exiger le développement de prescriptions de brûlage qui incluent les effets de consommation de la litière, un effet du feu souvent oublié.

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Introduction

The frequency, intensity, and severity of fires have been drastically altered in many contemporary landscapes (Agee 1993; Covington et al. 1997; Wade et al. 2000; Keane et al. 2002). Fire exclusion in ecosystems historically maintained by frequent fires leads to increased tree and shrub density, changed species composition, altered nutrient cycles, and

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fuel accumulation (Covington and Moore 1994; Gilliam and Platt 1999; Varner et al. 2000; Wade et al. 2000; Keane et al. 2002). When fires do occur after a prolonged period of suppression, the changed living and dead fuels result in altered fire behavior and effects (Wade et al. 2000; Varner et al. 2005). Although reinitiation of historic fire regimes is an obvious component of most approaches to restoring fire-suppressed forests, woodlands, and savannas worldwide, burning ecosystems where fire has been excluded for extended periods often fails to achieve the desired results (Fulé et al. 2004; Varner et al. 2005).

Among the impediments to restoration of fire-excluded coniferous forests is the excessive tree mortality resulting from reintroduction of fire (Wade et al. 1997; Varner et al. 2000; Stephens and Finney 2002; McHugh and Kolb 2003; Fulé et al. 2004). In ecosystems maintained by frequent low-intensity fires, the likelihood of fire-induced mortality generally decreases with increasing tree diameter (e.g., Ryan and Reinhardt 1988; Wade and Johansen 1986; Ryan et al. 1988). In restoration fires, in contrast, tree mortality follows varying patterns, sometimes increasing with increasing tree diameter (Kush et al. 2004) and occasionally with bimodal peaks of mortality in small- and large-diameter trees (Swezy and Agee 1991; Varner et al. 2000; McHugh and Kolb 2003). The mechanism responsible for increased mortality caused by restoration fires is unclear, with different investigators emphasizing damage to canopy (Ryan and Reinhardt 1988; Menges and Deyrup 2001), stem vascular tissue (Ryan and Frandsen 1991; McHugh and Kolb 2003), and root tissues (Swezy and Agee 1991, McHugh and Kolb 2003), as well as indirect effects of these damages on tree stress and defense against pathogens (Ostrosina et al. 1997; Feeney et al. 1998; Ostrosina et al. 1999; Menges and Deyrup 2001; McHugh et al. 2003; Sullivan et al. 2003; Perrakis and Agee 2006). Determining causes of fire damage should help managers predict fire-caused mortality and inform burn prescriptions to avoid or reduce postfire tree mortality.

Restoration of longleaf pine (*Pinus palustris* Mill.) ecosystems in the southeastern United States after long periods of fire suppression is a major conservation and management goal (Landers et al. 1995; Wade et al. 1997; Varner et al. 2000). Reference longleaf pinelands have parklike stand structure, are often monodominant, and have a fire return interval of 1–10 years (Wade et al. 2000). Since European settlement, 97% of longleaf pinelands have been lost (Noss et al. 1995), and only half of all remnant stands are burned regularly (Outcalt 2000). Fire-excluded longleaf pinelands are characterized by high overstory tree density, an increase in hardwood density and richness, reduced understory species richness, and thick forest floor accumulations (Gilliam and Platt 1999; Kush and Meldahl 2000; Varner et al. 2005). Overstory longleaf pine mortality in restoration fires can be as high as 75%–95%, causing radical shifts in ecosystem structure and composition and defeating restoration goals. This conflict between restoration objectives and outcomes has confounded pineland restoration efforts regionwide (Varner et al. 2005).

In 2001, a large-scale restoration experiment was initiated to examine the correlates of mortality in long-unburned longleaf pine forests. Motivated by the reported correlations of conifer mortality with duff consumption by regional managers and reports from western US coniferous forests (Swezy and Agee 1991; Ryan and Frandsen 1991), varying duff volumetric moisture contents were used as treatments. We hypothesized that overstory pine mortality would increase with duff (Oe + Oa) consumption and decrease with day-of-burn duff moisture content. Additionally, we examined the relationship between pine mortality and damage to canopy, stem, and roots at the stand and individual tree levels. The effects of tree, fuel, and burn characteristics were tested as predictors of stand-level overstory pine mortality in restoration fires.

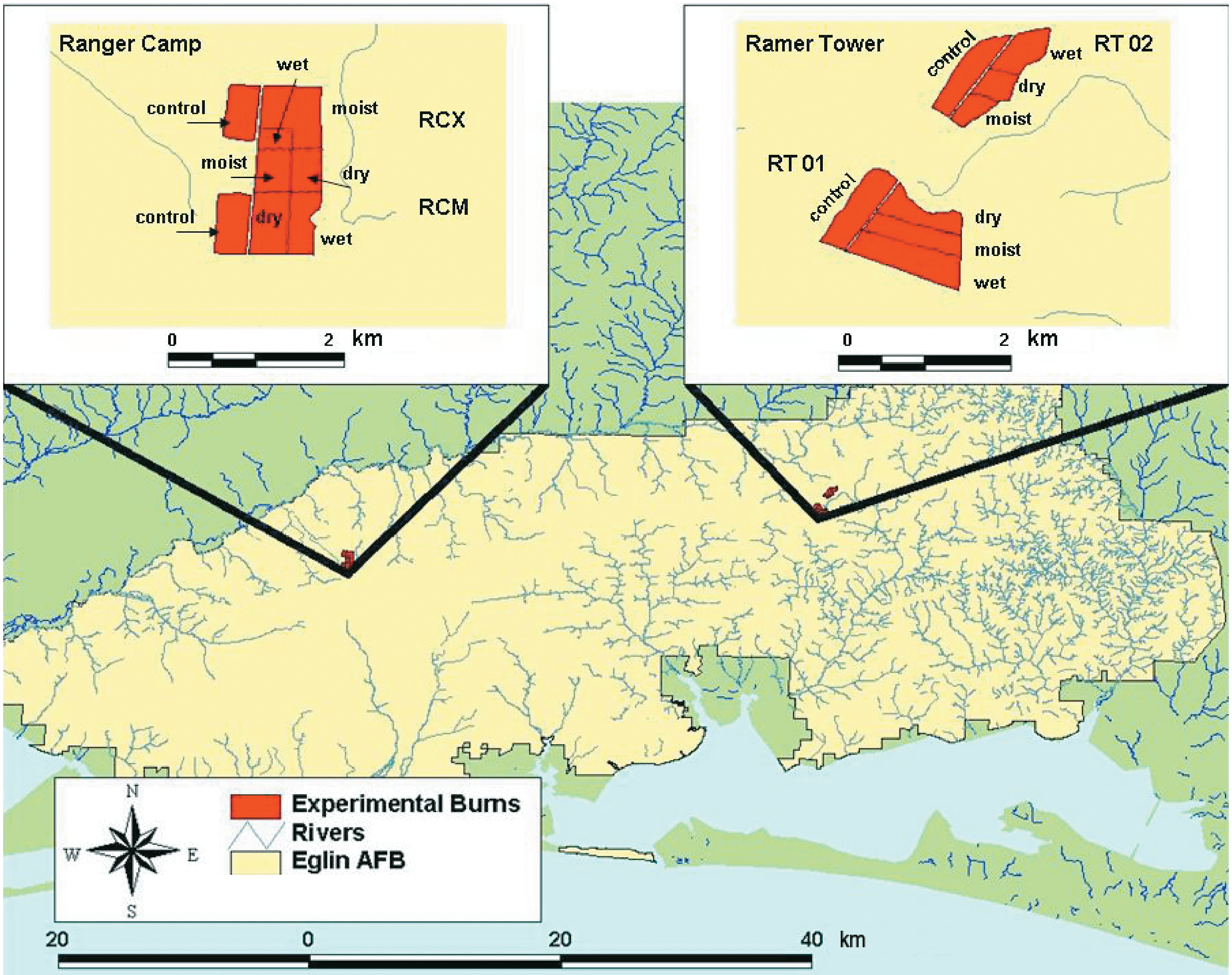
Methods

Study area

Experimental burns were conducted in four longleaf pine forest blocks in which fire had been excluded for 35–45 years at Eglin Air Force Base on the Florida Panhandle, USA (30°38′N, 86°24′W; Fig. 1). All blocks had heavy downed woody and duff fuel loads (ranging from 3.14 to 7.63 $kg{\cdot}m^{-2}$), sparse remnant longleaf pine overstory (45–200 $trees{\cdot}ha^{-1}$ >10 cm DBH), and the altered midstory and canopy tree species composition typical of long-unburned xeric pine forests on the southeastern Coastal Plain, dominated by *Quercus laevis* Walt., *Quercus geminata* Small, *Pinus clausa* (Chapman ex Engelm.) Vasey ex Sarg. var. *immuginata*, and *Ilex vomitoria* Ait. All sites are within the Southern Pine Hills District of the Coastal Plain Physiographic Province with deep, well-drained sandy soils (Brown et al. 1990). Soils of the study sites are Typic Quartzipsamments of the Lakeland series with mean depth to water table exceeding 200 cm (Overing et al. 1995). The climate of the area is subtropical, characterized by warm, humid summers and mild winters, with mean temperatures of 19.7 °C and mean annual precipitation of 1580 mm, most of which falls from June to September (Overing et al. 1995). Elevations of the study sites are 52–85 m above sea level, and all sites have gentle topography with minimal variation in slope and aspect.

Stands at each of four sites were randomly assigned to one of three burning treatments and a no-burn control. The four sites were located at Ramer Tower (two sites; RT01 and RT02 burned in 2001 and 2002, respectively) and at Ranger Camp (two sites; RCX and RCM both burned in 2002; Fig. 1). Using data from on-site weather stations (methods described in Ferguson et al. 2002), each site was burned on target day-of-burn volumetric duff moisture content (DMC; percentage of dry mass): dry (55% DMC); moist (85% DMC); wet (115% DMC) predicted by weather station data. Moisture contents of the forest floor horizons (Oi, Oe, and Oa) and woody fuels (1, 10, 100, and 1000 h time lag classes) were estimated based on day-of-burn collections in each burn unit (n = 5 per fuel class; Table 1.) Fire weather (ambient air temperature, relative humidity, and wind speed) and behavior (flame length and rate of spread) were recorded every 15 min by trained observers in each of the 12 experimental fires (Table 1). Prescribed burns were conducted during February to April 2001 and 2002. Dry burns were conducted during March and April, whereas moist and wet burns were earlier, occurring in February and March; this problem was due to operational necessity and regional

Fig. 1. Study site locations in northern Florida of experimental prescribed fires to examine correlates of mortality resulting from reintroduction of fire into fire-excluded (ca. 35–45 years since fire) longleaf pine (*Pinus palustris*) forests.



weather during 2001 and 2002. All fires were ignited using narrow strip head fires or spot-grid ignition, both methods typical of southeastern US prescribed burning (Wade and Lunsford 1989). We attempted to minimize variation in flame length and rate of spread among burns by narrowing or broadening the width between successive strips; all strips were 10–30 m apart and flame heights rarely exceeded 2 m.

Field data collection

Characteristics of surface fuels and vegetation were measured in each ca. 10 ha stand prior to and following prescribed burns. Forest floor depth was measured by horizon (litter (Oi horizon) and duff (Oe and Oa horizons)) at the base of each of 50 randomly selected pines >15 cm diameter at breast height (DBH; 1.37 m); the largest DBH of all pines was 63 cm) per plot. In one block (RT01), 20 trees per treatment were measured. Forest floor depth was measured at each tree using eight 20 cm pins buried flush with the litter surface prior to burning, evenly spaced and offset from the stem approximately 10 cm. Total woody fuel loading was estimated for each plot (n = 15 per plot) using Brown's (1974) planar intercept method with modifications. Ten hour fuels were censused in 3.05 m transects, 100 and 1000 h fuels (divided into sound and rotten categories) were tallied in 10.06 m transects, and 1 h and forest floor fuels were collected in 1 m^2 plots, dried, and weighed. Fuel loading corrections for slope were made by transect; we used default values for wood specific gravity and particle angle. Total height, live crown height, DBH, and distance and direction to plot centers of all 680 overstory pines (>15 cm DBH) were recorded.

Initial fire effects measurements were made on all 510 trees in the burned treatments within 3–4 weeks following the experimental fires. Scorch height and maximum height of needle consumption were measured using a clinometer. Percent of canopy volume scorched was estimated for 450 trees in the burned plots (no canopy damage was censused in the RT01 block) by the same two trained observers based on the methods in Peterson (1985). Postfire reductions in forest floor depth at individual trees were measured as the mean difference (%) between the pre- and post-fire exposure

Table 1. Fire weather and fuel moisture values for each 10 ha experimental prescribed burn in long-unburned longleaf pine forests at Eglin Air Force Base in northern Florida.

					Fuel moisture content (% dry mass)*					
Treatment and site	Burn date	Relative humidity (%)	Air temperature (°C)	Wind speed ($m \cdot s^{-1}$)	Oi	Oe	Oa	10 h	100 h	1000 h†
Wet										
RT01	18 Feb. 2001	26	17	0.45	18	69	102	26	54	83
RT02	05 Mar. 2002	24	12	0.89	27	70	125	43	61	—
RCX	14 Mar. 2002	64	20	1.34	22	76	133	42	45	77
RCM	04 Mar. 2002	21	8	0.89	35	91	137	52	66	86
Mean		34	14a	0.89	26a	76a	124a	41a	57a	82
Moist										
RT01	27 Mar. 2001	24	16	0.45	14	41	117	20	44	119
RT02	22 Feb. 2002	43	17	1.34	17	43	79	25	45	—
RCX	08 Mar. 2002	35	24	1.79	16	45	112	22	28	70
RCM	22 Feb. 2002	37	18	0.45	14	27	102	18	39	64
Mean		35	19ab	1.01	15b	39b	103a	21b	39b	84
Dry										
RT01	26 Apr. 2001	43	32	0.45	16	18	40	18	15	92
RT02	24 Mar. 2002	39	23	0.89	12	27	87	13	22	—
RCX	07 Apr. 2002	60	19	1.34	11	46	64	9	13	33
RCM	24 Apr. 2002	53	28	0.89	7	11	59	14	18	47
Mean		49	26a	0.89	12b	26b	62b	14b	17c	57
P		0.28	0.03	0.93	<0.01	<0.001	<0.01	<0.001	<0.001	0.40

Note: Prescribed fire treatments were based on day-of-burn measured volumetric duff moisture content. Different letters following treatment means denote significant differences among column means determined with ANOVA followed by post hoc Tukey's honest significant difference test with $\alpha = 0.05$. Sites are as follows: RT01, Ramer Tower 2001 burns; RT02, Ramer Tower 2002 burns; RCX, Ranger Camp xeric 2002 burns; RCM, Ranger Camp mesic 2002 burns.

*Fuel moisture content for each fuel category was calculated based on day-of-burn collections of five samples per fuel category.

†1000 h fuel moisture contents are based on the means of both sound and rotten downed fuels (R. Ottmar, unpublished data).

of duff pins. Stem char heights were estimated to the nearest 0.1 m with a height pole at four cardinal directions, and any basal damage was noted. Evidence of pathogens was noted for all tagged trees. Following initial postburn surveys, tree mortality and any signs of decline or disease were surveyed 6, 12, 18, and 24 months postburn. Trees killed by lightning (common in longleaf pine forests; $n = 6$ in this study) were excluded from censuses and further analyses.

Data analysis

The study was designed as a randomized block design with four treatments and four replicates per treatment. The four treatments were based on day-of-burn volumetric duff moisture content (wet, moist, dry, and a no-burn control), collected on the morning of each burn (Table 1).

At the burn block level, analysis of variance was used to detect effects of treatment duff moisture (wet, moist, dry, and control) on pine mortality. If differences were detected, a post hoc Tukey–Kramer honest significant difference (HSD) test was used to detect differences between treatments. The same design was used to test for effects of duff moisture treatments (wet, moist, and dry) on forest floor reduction (cm and percent), stem char height, and canopy damage (percent scorch, scorch height, and percent canopy consumption). When necessary, non-normal data were transformed to better meet the assumptions of parametric analyses (all transformations are listed in tables and figures). To account for the within-treatment variation, we tested plot fire environment and fuel moisture variables as predictors of pine mortality in stepwise regressions with the following variables: relative humidity (%); air temperature; moisture contents of litter (Oi), fermentation (Oe), and humus horizons (Oa); and moisture contents of 10, 100, and 1000 h fuels. The role of crown scorch (plot means of scorch height and percent of canopy volume scorched), height of stem char, and duff consumption in pine mortality were also evaluated using plot means in a stepwise regression.

Given the substantial within-plot variation in fire effects and postfire tree mortality and the need to predict or better understand individual tree postfire mortality, we used a nested logistic regression approach to determine drivers of postfire mortality (Stephens and Finney 2002; Perrakis and Agee 2006). Probability of individual pine mortality was modeled as a function of preburn fuel characteristics (DBH, prefire duff depth, crown height, and total tree height), duff moisture treatment (wet, moist, and dry), and fire effects (percent duff consumed, duff depth reduction, char height, percent crown scorch, and scorch height). When variables were highly correlated (e.g., crown scorch height and percent crown scorch), the less correlated variable was removed from subsequent model iterations. Akaike's information criteria (AIC) were utilized to rank competing regression models (Gotelli and Ellison 2004).

Results

Duff consumption, stem char, and canopy damage varied among the 12 experimental fires (Table 2). Across all 12 burns, mean duff consumption at the bases of the pines

Table 2. Effects of 10 ha prescribed burns in long-unburned longleaf pine forests at Eglin Air Force Base in northern Florida.

	Forest floor		Duff			Canopy scorch		
Treatment and site	Loss (cm)	Loss (%)	Loss (cm)	Loss (%)	Stem char height (m)	Height (m)	%	Pine mortality (%)*
Wet								
RT01	1.3 (1.0)	24 (8)	0.2 (0.3)	2 (4)	1.0 (0.6)	—	—	0
RT02	3.7 (2.3)	33 (15)	0.5 (1.3)	5 (15)	1.4 (0.8)	4.5 (5.6)	5.8 (11.3)	0
RCX	3.2 (2.3)	33 (13)	0.3 (1.3)	4 (13)	0.9 (1.7)	4.1 (4.2)	4.3 (5.2)	0
RCM	7.9 (4.9)	49 (14)	1.2 (2.9)	9 (17)	2.1 (1.4)	10.3 (6.1)	23.6 (26.7)	2
Mean	4.0	35a	0.6a	5a	1.4	6.3	11.2	0.5a
Moist								
RT01	3.4 (3.2)	28 (17)	0.9 (1.8)	9 (17)	1.2 (1.0)	—	—	0
RT02	3.3 (2.8)	31 (19)	1.0 (2.2)	11 (20)	1.0 (0.8)	3.5 (4.3)	8.8 (15.4)	4
RCX	7.8 (5.0)	52 (16)	2.3 (2.7)	22 (20)	3.1 (1.5)	10.2 (4.7)	35.9 (32.7)	6
RCM	7.4 (4.7)	56 (16)	1.4 (3.0)	16 (23)	5.1 (2.8)	16.7 (3.4)	71.7 (29.7)	2
Mean	5.5	42a	1.4ab	14.5a	2.6	10.1	38.8	3.0a
Dry								
RT01	10.3 (4.7)	73 (26)	6.2 (4.0)	63 (34)	1.2 (1.0)	—	—	22
RT02	6.9 (3.2)	63 (14)	1.6 (2.0)	25 (23)	2.8 (1.6)	8.4 (6.3)	34.3 (36.6)	10
RCX	6.7 (3.6)	72 (11)	2.8 (2.6)	49 (18)	3.1 (1.4)	11.9 (3.1)	58.4 (31.4)	8
RCM	9.6 (5.0)	73 (17)	4.6 (3.9)	49 (27)	4.1 (2.2)	15.3 (3.7)	70.4 (33.7)	42
Mean	8.4	70b	3.8b	46.5b	2.8	11.9	54.4	20.5b
P	0.08	<0.01	0.01	<0.001	0.30	0.33	0.15	<0.001

Note: Values are plot means with SDs given in parentheses. Prescribed fire treatments were based on day-of-burn duff moisture content. Treatment means within a column with different letters are significantly different determined using ANOVA followed by post hoc Tukey's HSD (α = 0.05).

*Percent tree mortality is the cumulative mortality of all pines >15 cm DBH. Within each block, there were 50 trees measured per treatment, except in RT01 where 20 trees were monitored. Mortality values for 2001 burns include surveys 36 months postburn; mortality values for all 2002 burns include surveys 24 months postburn.

ranged from 2% to 63% (0.2–6.2 cm). Duff consumption in the dry burns was six times greater than in wet burns and three times greater than in moist burns (Table 2). Mean height of stem char was 2.24 m across all burns; individual plot means ranged from 0.9 to 5.1 m with no apparent treatment effect (Table 2). Mean percentage of pine crown scorch and scorch height ranged from 4.3% to 71.7% and from 3.5 to 16.7 m, respectively, across all burned plots and was independent of treatment (Table 2). For reference, pine heights across all blocks averaged 16.4 m, with a mean height to live crown of 8.2 m, neither of which differed by treatment. Because of the low intensity of all the prescribed burns, only three trees (<0.7% of all burned trees) suffered any needle loss during the fires (crown "consumption" in contrast to crown "scorch," where needles are heated, not combusted); needle consumption did not exceed 10% of the total crown volume of any of these three pines and, therefore, was not included in analyses.

Overstory longleaf pine mortality for all plots during the first 2 years after the fires ranged from 0% to 42%, with only three plots exceeding 10% tree mortality (Table 2). Variation in mortality was greatest among the four dry burns, where overstory pine mortality ranged from 8% to 42%. Soon after the fires, all pines in the burned blocks produced new foliage, and none showed obvious signs of decline; mortality generally lagged 12–18 months behind fires. All of the pines that died showed signs of bark beetle attack (primarily black turpentine beetle, *Dendroctonus terebrans* (Olivier, 1795) and *Platypus flavicornis* (Fabricius, 1776)). The former species was also present in some surviving pines. Overstory pine mortality during the first 2 years after fires differed among treatments; dry burns averaged 20.5% mortality, moist burns averaged 3.0%, and both wet and control burns suffered <1% mortality over the 2 years postburn (Fig. 2; F = 10.56, df = 12, P < 0.001).

At the whole-plot level, fuel environment and fire effects variables contributed to pine mortality (Table 3). Among fuel variables, lower duff (Oa) moisture content was negatively related to probability of tree mortality. Among fire effects variables, tree mortality was directly proportional to bole char and duff reduction. When all fuel environment and fire effects variables were included in a variety of single and multiple regression models (Table 3), the model with the highest R^2 (0.57) and lowest AIC (5.1) included only duff consumption (P <0.01).

$$\text{log longleaf pine mortality (\%)} = -2.93 + 0.15\ (\text{\% duff consumption})$$

Although a higher AIC (15.9 versus 5.1 for the prior model) was found, the model that incorporated stem char height with duff consumption explained more (82%) of the variance (Table 3).

The results of the logistic regression of individual tree mortality supported the importance of fire effects parameters demonstrated in the plot-based analyses. Combining trees from all of the treatments in a nested logistic regression model revealed that the likelihood of a tree dying was related to a combination of canopy scorch and duff consumption (Table 4; R^2 = 0.34, P < 0.001). This analysis revealed that, whereas duff consumption was an important factor across all treatments, canopy scorch was significant only in

Fig. 2. Effects of burning treatment on cumulative overstory longleaf pine mortality 2 years postfire at Eglin Air Force Base, Florida. Treatments were based on day-of-burn duff moisture contents (wet, 115% duff moisture content (DMC); moist, 85% DMC; dry, 55% DMC) and an unburned control. All treatments were replicated four times over the 2 years of the study. Bars represent the ranges of plot mortalilty. Bars with different letters are significantly different ($p < 0.05$).

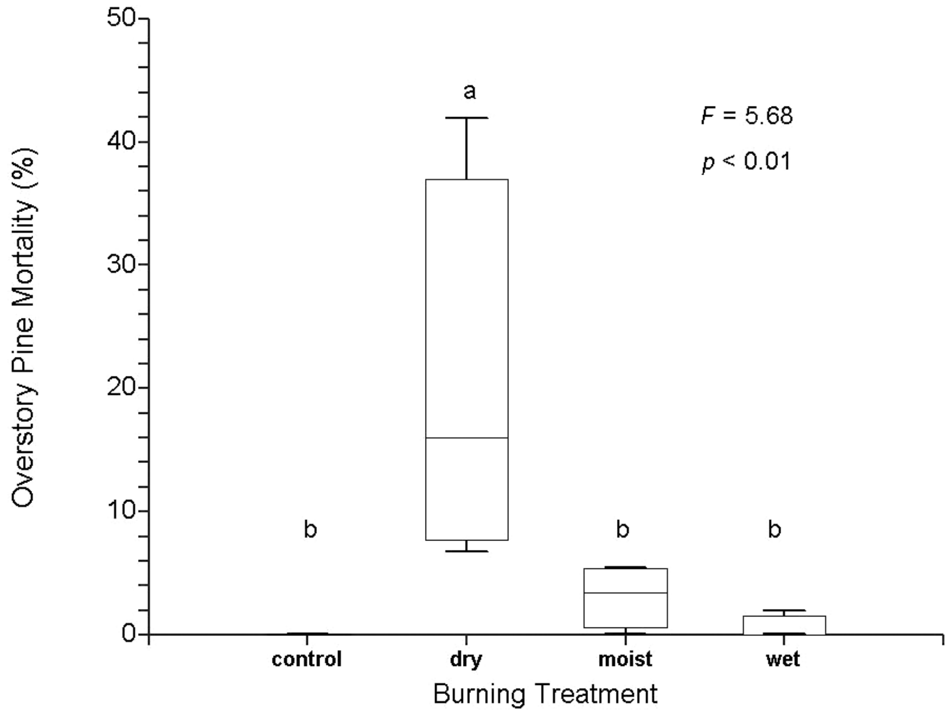


Table 3. Stepwise multiple regression results for predictors of block-level longleaf pine mortality caused by prescribed restoration burns in long-unburned pinelands at Eglin Air Force Base in northern Florida.

	Parameters					
Dependent variable	β_0	β_1	β_2	R^2	P	AIC*
Fuel environment variables						
log pine mortality (%)	6.26	–0.07 (Oa % moisture)		0.45	0.04	19.8
Fire effects variables						
log pine mortality (%)	–1.01	0.23 (stem char height)	0.03 (% duff reduction)	0.82	<0.001	15.9
Combined model (fuel environment + fire effects)						
log pine mortality (%)	–2.93	0.15 (% duff reduction)		0.57	<0.01	5.1

*Akaike's information criteria (AIC) values rank competing regression models; models with lower AIC values approximate modeled responses better than models with higher AIC values.

the dry burn treatment. No fuel environment parameters were incorporated into this model, because fuel environment variables were measured at the plot level, not at individual plot trees, which may explain the low R^2 value.

Overstory mortality results reveal that pines died across all size classes (Fig. 3), particularly in dry burns. Across all burning treatments, large pines in the 35–45, 45–55, and 55–70 cm DBH range (n = 126, 25, and 5 trees, respectively) suffered respective postfire mortality rates of 36%, 50%, and 80% after 2 years. Large pine mortality appeared related to the presence of deeper accumulations of forest floor fuels surrounding the bases of large trees.

Discussion

In this study, maximum forest floor fuel reduction was linked strongly to the greatest overstory pine mortality (Fig. 4). Restoration of long-unburned southeastern pine forests is complicated by the often opposing goals of reducing duff fuels while retaining mature overstory pines. Most models of fire-caused mortality assume that, as tree size, bark thickness, and canopy height increase, so does resistance to fire damage (e.g., Martin 1963; Ryan et al. 1988). Pine mortality increased with size of tree in dry burns (Fig. 3), a phenomenon observed in other coniferous forests (Stephens and Finney 2002; McHugh and Kolb 2003) and in previous longleaf pineland restoration burns in areas with deep forest floor accumulations (Kush et al. 2004). In addition to postfire reductions in conifer survival, others have found postfire reductions in growth (Busse et al. 2000; Elliott et al. 2002) linked to fire-caused reductions in forest floor and duff, making these results of general relevance.

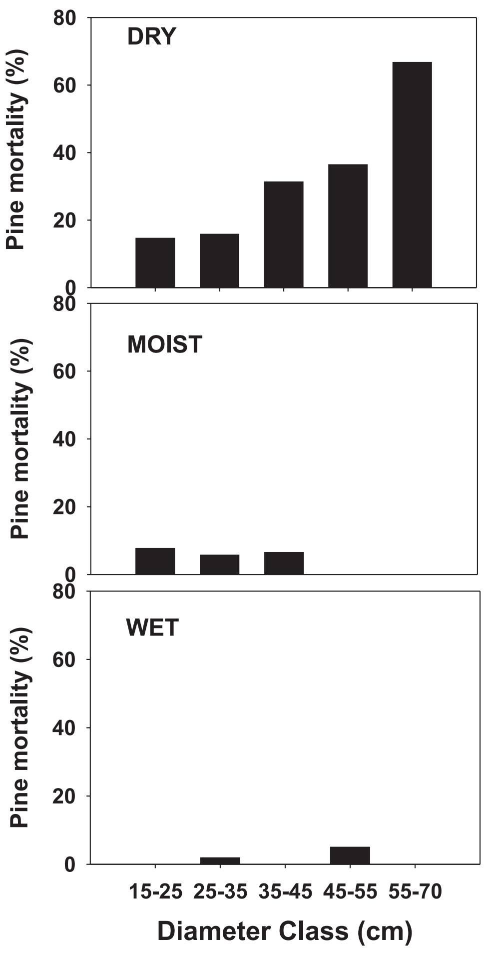
Fire-induced overstory pine mortality lagged 12–18 months after the burns, consistent with reports in other

Table 4. Modeled nested logistic regression of postfire individual tree longleaf pine mortality at Eglin Air Force Base in northern Florida, USA.

Treatment	Fire effect	Parameter estimate	χ^2	*P*
Intercept		3.16	21.29	<0.001
Dry	Crown scorch (%)	–0.03	11.65	<0.001
Moist	Crown scorch (%)	–0.01	0.32	0.57
Wet	Crown scorch (%)	–0.03	1.39	0.24
Dry	Duff consumption (%)	–0.04	15.44	<0.001
Moist	Duff consumption (%)	–0.03	7.29	<0.01
Wet	Duff consumption (%)	–0.07	5.03	<0.01
Whole model			96.35	<0.001

Note: Fire effects were nested within treatments and tree status (alive or dead) was the dependent variable. The overall model R^2 was 0.34.

Fig. 3. Diameter distributions of overstory trees (DBH > 15 cm) killed following experimental prescribed fires in long-unburned longleaf pine forests in northern Florida, USA. No overstory pines died in the no-burn control treatment.



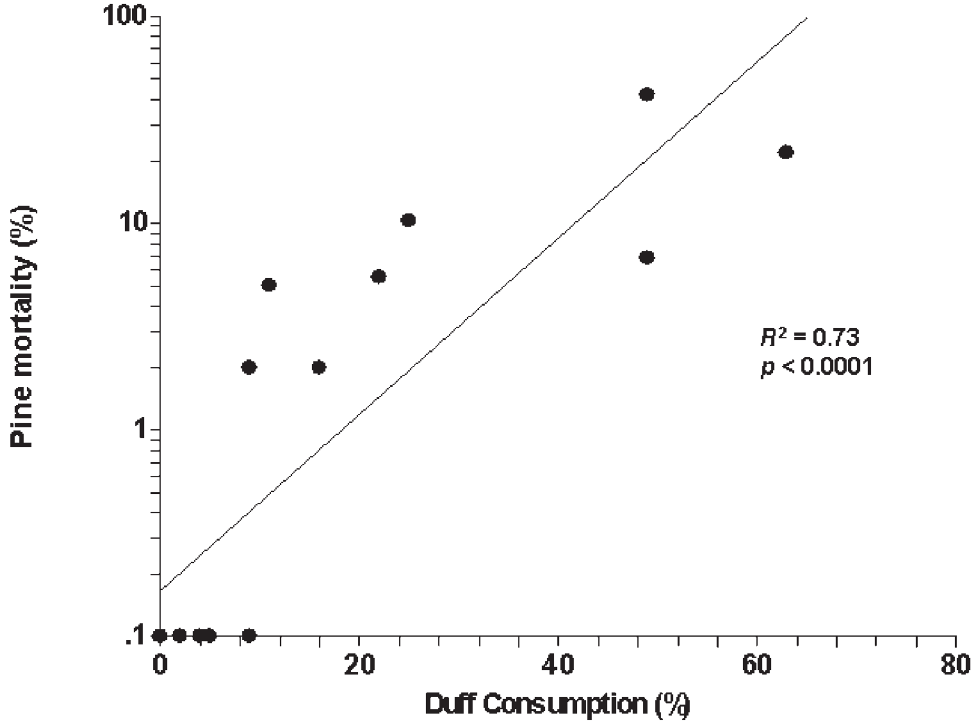
conifers (e.g., Wyant et al. 1986; Stephens and Finney 2002; Agee 2003) and observations by regional forest managers. This lag may have been due to the fact that the large, old trees had several predisposing mortality factors (i.e., reduced physiological condition, high fine root volumes in drought-prone duff, greater duff fuel accumulation, and high stand density resulting from fire exclusion) in addition to the direct fire injuries to roots, cambia, and canopy meristems. Kelsey and Joseph (2003) suggest that the fire-caused root damage may lead to water stress and subsequent declines in tree defenses. Delayed mortality may have also been caused by reduced allocations to defense leading to attack by beetles or susceptibility to fungal pathogens, both common after fires (Ostrosina et al. 1997; Ostrosina et al. 1999; Menges and Deyrup 2001; Kelsey and Joseph 2003; Perrakis and Agee 2006) and detected in our study area. The predominance of bark beetles in surviving and dying pines postfire in this study points to second-order effects of fire damage, particularly linked to smoldering duff as the proximate cause of widespread overstory pine mortality. Future work is needed on the physiological mechanisms of decline and mortality in response to fire damage.

Mortality and fire damage to stem, canopy, and roots

Duff consumption due to smoldering combustion was the only fire effect consistently related to pine mortality across scales and treatments (Tables 3 and 4). Lower duff (Oa) percent fuel moisture explained 78% of variation in duff consumption ($P < 0.0001$), consistent with results from other coniferous forests (Frandsen 1987; Brown et al. 1991; Ottmar et al. 1993). Duff is typically consumed by smoldering combustion, which causes long-duration heating of stems and organic and mineral soil (Swezy and Agee 1991; Hungerford et al. 1995; Haase and Sackett 1998). The long duration (often many hours postignition) of moderately elevated soil temperatures can damage or kill roots (Swezy and Agee 1991) and stem vascular tissues (Ryan and Frandsen 1991).

Stem char has been correlated with decreased growth and increased tree mortality in studies of various conifers (e.g., Dixon et al. 1984; Wade and Johansen 1987), and char height was positively related to longleaf pine mortality in our study (Table 3). The exclusion of small (DBH < 15 cm) fire-susceptible trees in this study may also have reduced the overall effect of char height on tree mortality. It is important to note, however, that measurements of char do not capture the results of long-duration heating during the smoldering phase of combustion. McHugh and Kolb (2003) supplemented char height measurements with char severity (= stem damage) and found strong correlations with postfire mortality. Given the high correlation between char height, canopy damage, and fire behavior, its ease of measurement and persistence, and its potential role in tree mortality, char height can be a valuable postfire measurement even if it is only correlated with causes of tree mortality (Fowler and Sieg 2004).

Fig. 4. Relationship between duff consumption and cumulative postfire mortality of overstory longleaf pines at Eglin Air Force Base, Florida.



Canopy scorch was a significant predictor of longleaf pine mortality in the nested logistic regression and has been associated with postfire mortality in many other conifers (Wyant et al. 1986; Johansen and Wade 1987; Ryan et al. 1988; Menges and Deyrup 2001; Stephens and Finney 2002). The logistic regression models nested by treatment (dry, moist, and wet burns) revealed that the role of scorch was confined to the dry treatment (Table 4), a potential explanation for the contradictory results found in southern pine restoration burns in which scorch was prevalent and a good predictor of mortality (Menges and Deyrup 2001) or absent altogether and, therefore, not related to mortality (Kush et al. 2004). This finding is critical in that it highlights the challenges of interpreting fire effects. Future efforts to understand the role of canopy scorch in tree mortality should attempt to isolate scorch from other types of fire damage.

The results of this study reinforce the need to better understand the mechanisms by which fires kill trees (Ryan 2000; Dickinson and Johnson 2001; Kelsey and Joseph 2003; Fowler and Sieg 2004). Future work on fire-caused mortality should isolate the different types of fire damage (e.g., isolating fire damage to canopy tissues from damage to belowground tissues; Carter et al. 2004) and consider their interactions (e.g., heat from smoldering duff damages vascular tissues in surficial roots and the bases of tree stems rendering trees susceptible to beetle attack). Such studies should combine whole tree physiology models with considerations of fire damage and subsequent increases in tree stress (Dunn and Lorio 1992; Ryan 2000; Kelsey and Joseph 2003; Wallin et al. 2004, Perrakis and Agee 2006).

Challenges to forest restoration using fire

Given the clear role of duff moisture content in causing tree mortality in restoration fires, efforts to understand moisture dynamics of duff should be a high research and management priority. Duff moisture content is controlled by several factors acting at different scales. At large scales, duff moisture is controlled by recent precipitation amount and temporal distribution (Ferguson et al. 2002). Within stands, localized duff moisture can vary with forest floor composition, beneath and between tree crowns, and at small scales in basal duff accumulations (Miyanishi and Johnson 2002; Hille and Stephens 2005). The characterization of basal duff accumulations and the controls on duff ignition and combustion remain pressing issues for the restoration of long-unburned forests.

Burning prescriptions for restoring long-unburned forests will continue to require consideration of traditional synoptic weather variables but should be enhanced to acknowledge the important role of forest floor fuel complexes. Prescriptions should incorporate more robust estimates of time and duration of localized precipitation and drying (Ferguson et al. 2002), and the subsequent effects of these factors on fire behavior, particularly postfrontal smoldering combustion (Frandsen 1987; Miyanishi 2001). Given the diversity in forest floor composition and structure in long-unburned longleaf pine forests, the drying, wetting, and burning behavior of this fuel complex warrants further study.

Prescriptions for fire reintroduction in long-unburned forests should be tailored to local operational scales. For example, it may be operationally feasible to use a combination of wetting and (or) raking away forest floor fuels to minimize potential for long-duration heat damage to high-value trees in small stands. Prefire raking has been used successfully in ponderosa pine (*Pinus ponderosa* Dougl. ex P. & C. Laws.) burning (e.g., Feeney et al. 1998; Wallin et al. 2004) but less often in longleaf pine forests. In addition to the labor intensity of raking, unpublished research on raking Eastern white pine (*Pinus strobus* L.; D.D. Wade, unpublished data) and anecdotes from regional forest managers report what they believe to be raking-induced mortality. Extinguishing smoldering duff fires with tractor, ATV, or backpack-mounted water or foam has been successfully employed in small (<20 ha) restoration fires (Kush et al. 2004). Unfortunately, none of these labor-intensive treatments are appropriate for large-scale restoration burning. Managers of large forestlands throughout the southeastern United States are faced with burning large areas with limited staff and increasing restrictions on smoke generation (Hiers et al. 2003). For large areas, utilizing duff moisture and optimizing burn resources to priority stands must be the rule. In these situations, acceptable thresholds of tree mortality must be balanced with duff and woody fuel consumption and placed in the context of landscape objectives.

In restoration fires, managers and forest and fire scientists must recognize the increasingly important role of forest floor fuels and the unintended damage that smoldering fires in duff can cause. Traditional fire effects such as canopy scorch and stem char are readily observed and modeled. Although more subtle, the relationships between duff consumption and overstory mortality deserve increased attention and additional small- and large-scale experimentation. The reason for this oversight may be that this phenomenon was formerly rare but getting more common as fires are being reintroduced after long periods of suppression (e.g., Ryan and Frandsen 1991; Swezy and Agee 1991; Haase and Sackett 1998; Stephens and Finney 2002; McHugh and Kolb 2003; Varner et al. 2005; Perrakis and Agee 2006). While duff smoldering is problematic, land managers are left with the conundrum of having to reduce duff fuels while maintaining a living overstory of large, old trees. Incorporating fuel moisture thresholds in burn prescriptions that include measures of the forest floor fuel complex may help managers avoid widespread overstory tree damage and mortality and successfully reduce fuels when they reintroduce fires after long periods of exclusion.

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References

Agee, J.K. 1993. Fire ecology of Pacific Northwest forests. Island Press, Washington, D.C.

Agee, J.K. 2003. Monitoring post-fire mortality in mixed-conifer forests of Crater Lake, Oregon. Nat. Areas J. **23**: 114–120.

Brown, J.K. 1974. Handbook for inventorying downed woody material. USDA For. Serv. Gen. Tech. Rep. INT-16.

Brown, J.K., Reinhardt, E.D., and Fischer, W.C. 1991. Predicting duff and woody fuel consumption in northern Idaho prescribed fires. For. Sci. **37**: 1550–1566.

Brown, R.L., Stone, E.L., and Carlisle, V.W. 1990. Soils. *In* Ecosystems of Florida. *Edited by* R.L. Myers and J. Ewel. University of Florida Press, Gainesville, Fla.

Busse, M.D., Simon, S.A., and Riegel, G.M. 2000. Tree-growth and understory responses to low-severity prescribed burning in thinned *Pinus ponderosa* forests of central Oregon. For. Sci. **46**: 258–268.

Carter, D.C., Hendricks, J.J., Mitchell, R.J., and Pecot, S.D. 2004. Fine root carbon allocation and fates in longleaf pine forests. For. Sci. **50**: 177–187.

Covington, W.W., and Moore, M.M. 1994. Southwestern ponderosa forest structure: changes since Euro-American settlement. J. For. **92**: 39–47.

Covington, W.W., Fulé, P.Z., Moore, M.M., Hart, S.C., Kolb, T.E., Mast, J.N., Sackett, S.S., and Wagner, M.R. 1997. Restoration of ecosystem health in southwestern ponderosa pine forests. J. For. **95**: 23–29.

Dickinson, M.B., and Johnson, E.A. 2001. Fire effects on trees. *In* Forest fires: behavior and ecological effects. *Edited by* E.A. Johnson and K. Miyanishi. Academic Press, San Diego, Calif. pp. 475–525.

Dixon, W.N., Corneil, J.A., Wilkinson, R.C., and Foltz, J.L. 1984. Using stem char to predict mortality and insect infestation of fire-damaged slash pines. South. J. Appl. For. **8**: 85–88.

Dunn, J.P., and Lorio, P.L. 1992. Effects of bark girdling on carbohydrate supply and resistance of loblolly pine to southern pine beetle (*Dendroctonus frontalis* Zimm.) attack. For. Ecol. Manage. **50**: 317–330. doi:10.1016/0378-1127(92)90345-A.

Elliott, K.J., Vose, J.M., and Clinton, B.D. 2002. Growth of eastern white pine (*Pinus strobus* L.) related to forest floor consumption by prescribed fire in the southern Appalachians. South. J. Appl. For. **26**: 18–25.

Feeney, S.R., Kolb, T.E., Covington, W.W., and Wagner, M.R. 1998. Influence of thinning and burning restoration treatments on presettlement ponderosa pines at the Gus Pearson Natural Area. Can. J. For. Res. **28**: 1295–1306.

Ferguson, S.A., Ruthford, J.E., McKay, S.J., Wright, D., Wright, C., and Ottmar, R. 2002. Measuring moisture dynamics to predict fire severity in longleaf pine forests. Int. J. Wildland Fire, **11**: 267–279. doi:10.1071/WF02010.

Fowler, J.F., and Sieg, C.H. 2004. Postfire mortality of ponderosa pine and Douglas-fir: a review of methods to predict tree death. USDA For. Serv. Gen. Tech. Rep. RMRS-132.

Frandsen, W.H. 1987. The influence of moisture and mineral soil on the combustion limits of smoldering forest duff. Can. J. For. Res. **17**: 1540–1544.

Fulé, P.Z., Cocke, A.E., Heinlein, T.A., and Covington, W.W. 2004. Effects of an intense prescribed forest fire: is it ecological restoration? Restor. Ecol. **12**: 220–230. doi:10.1111/j.1061-2971.2004.00283.x.

Gilliam, F.S., and Platt, W.J. 1999. Effects of long-term fire exclusion on tree species composition and stand structure in an old-growth *Pinus palustris* (longleaf pine) forest. Plant Ecol. **140**: 15–26. doi:10.1023/A:1009776020438.

Gotelli, N.J., and Ellison, A.M. 2004. A primer of ecological statistics. Sinauer, Sunderland, Mass.

Haase, S.M., and Sackett, S.S. 1998. Effects of prescribed fire in giant sequoia – mixed conifer stands in Sequoia and Kings Canyon National Parks. Proc. Tall Timbers Fire Ecol. Conf. **20**: 236–243.

Hiers, J.K., Laine, S.C., Bachant, J.J., Furman, J.H., Greene, W.W., Jr., and Compton, V. 2003. Simple spatial modeling tool for prioritizing prescribed burning activities at the landscape scale. Conserv. Biol. **17**: 1571–1578. doi:10.1111/j.1523-1739.2003.00381.x.

Hille, M.G., and Stephens, S.L. 2005. Mixed conifer forest duff consumption during prescribed fires: tree crown impacts. For. Sci. **51**: 417–424.

Hungerford, R.D., Frandsen, W.H., and Ryan, K.C. 1995. Ignition and burning characteristics of organic soils. Proc. Tall Timbers Fire Ecol. Conf. **19**: 78–91.

Johansen, R.W., and Wade, D.D. 1987. Effects of crown scorch on survival and diameter growth of slash pines. Soc. J. Appl. For. **11**: 180–184.

Keane, R.E., Ryan, K.C., Veblen, T.T., Allen, C.D., Logan, J., and Hawkes, B. 2002. Cascading effects of fire exclusion in Rocky Mountain ecosystems: a literature review. USDA For. Serv. Gen. Tech. Rep. RMRS-91.

Kelsey, R.G., and Joseph, G. 2003. Ethanol in ponderosa pine as an indicator of physiological injury from fire and its relationship to secondary beetles. Can. J. For. Res. **33**: 870–884. doi:10.1139/x03-007.

Kush, J.S., and Meldahl, R.S. 2000. Composition of a virgin longleaf pine stand in south Alabama. Castanea, **65**: 56–63.

Kush, J.S., Meldahl, R.S., and Avery, C. 2004. A restoration success: longleaf pine seedlings established in a fire-suppressed, old-growth stand. Ecol. Rest. **22**: 6–10.

Landers, J.L., van Lear, D.H., and Boyer, W.D. 1995. The longleaf pine forests of the southeast: requiem or renaissance? J. For. **93**: 39–44.

Martin, R.E. 1963. A basic approach to fire injury of tree stems. Proc. Tall. Timbers Fire Ecol. Conf. **2**: 151–162.

McHugh, C.W., and Kolb, T.E. 2003. Ponderosa pine mortality following fire in northern Arizona. Int. J. Wildland Fire, **12**: 1–16.

McHugh, C.W., Kolb, T.E., and Wilson, J.L. 2003. Bark beetle attacks on ponderosa pine following fire in northern Arizona. Environ. Entomol. **32**: 510–522.

Menges, E.S., and Deyrup, M.A. 2001. Postfire survival in south Florida slash pine: Interacting effects of fire intensity, fire season, vegetation, burn size, and bark beetles. Int. J. Wildland Fire, **10**: 53–63. doi:10.1071/WF01009.

Miyanishi, K. 2001. Duff consumption. *In* Forest fires: behavior and ecological effects. *Edited by* E.A. Johnson and K. Miyanishi. Academic Press, San Diego, Calif. pp. 437–475.

Miyanishi, K., and Johnson, E.A. 2002. Process and patterns of duff consumption in the mixedwood boreal forest. Can. J. For. Res. **32**: 1285–1295. doi:10.1139/x02-051.

Noss, R.F., LaRoe, E.T., and Scott, J. M. 1995. Endangered ecosystems of the United States: a preliminary assessment of loss and degradation. USDI Natl. Biol. Serv. Biol. Rep. No. 28.

Ostrosina, W.J., Hess, N.J., Zarnoch, S.J., Perry, T.J., and Jones, J.P. 1997. Blue-stain fungi associated with roots of southern pine trees attacked by the southern pine beetle, *Dendroctonus frontalis*. Plant Dis. **81**: 942–945.

Ostrosina, W.J., Bannwart, D., and Roncadori, R.W. 1999. Root-infecting fungi associated with a decline of longleaf pine in the southeastern United States. Plant Soil, **217**: 145–150.

Ottmar, R.D., Burns, M.F., Hall, J.N., and Hanson, A.D. 1993. CONSUME user's guide. USDA For. Serv. Gen. Tech. Rep. PNW-GTR-304.

Outcalt, K.W. 2000. Occurrence of fire in longleaf pine stands in the southeast United States. Proc. Tall Timbers Fire Ecol. Conf. **21**: 178–182.

Overing, J.D., Weeks, H.H., Wilson, J.P., Sullivan, J., and Ford, R.D. 1995. Soil Survey of Okaloosa County, Florida. USDA Natural Resource Conservation Service, Washington, D.C.

Perrakis, D.D.B., and Agee, J.K. 2006. Seasonal fire effects on mixed-conifer forest structure and ponderosa pine resin properties. Can. J. For. Res. **36**: 238–254. doi:10.1139/x05-212.

Peterson, D.L. 1985. Crown scorch volume and scorch height: estimates of postfire tree condition. Can. J. For. Res. **15**: 596–598.

Ryan, K.C. 2000. Effects of fire injury on water relations of ponderosa pine. Proc. Tall Timbers Fire Ecol. Conf. **21**: 58–66.

Ryan, K.C., and Frandsen, W.H. 1991. Basal injury from smoldering fires in mature *Pinus ponderosa* Laws. Int. J. Wildland Fire, **1**: 107–118. doi:10.1071/WF9910107.

Ryan, K.C., and Reinhardt, E.D. 1988. Predicting postfire mortality of seven western conifers. Can. J. For. Res. **18**: 1291–1297.

Ryan, K.C., Peterson, D.L., and Reinhardt, E.D. 1988. Modeling long-term fire-caused mortality of Douglas-fir. For. Sci. **34**: 190–199.

Stephens, S.L., and Finney, M.A. 2002. Prescribed fire mortality of Sierra Nevada mixed conifer tree species: effects of crown damage and forest floor combustion. For. Ecol. Manage. **162**: 261–271. doi:10.1016/S0378-1127(01)00521-7.

Sullivan, B.T., Fettig, C.J., Ostrosina, W.J., Dlausky, M.J., and Berisford, C.W. 2003. Association between severity of prescribed burns and subsequent activity of conifer-infesting beetles in stands of longleaf pine. For. Ecol. Manage. **185**: 327–340. doi:10.1016/S0378-1127(03)00223-8.

Swezy, D.M., and Agee, J.K. 1991. Prescribed-fire effects on fine-root and tree mortality in old-growth ponderosa pine. Can. J. For. Res. **21**: 626–634.

Varner, J.M., III, Kush, J.S., and Meldahl, R.S. 2000. Ecological restoration of an old-growth longleaf pine stand utilizing prescribed fire. Proc. Tall Timbers Fire Ecol. Conf. **21**: 216–219.

Varner, J.M., III, Gordon, D.R., Putz, F.E., and Hiers, J.K. 2005. Restoring fire to long-unburned *Pinus palustris* ecosystems: novel fire effects and consequences for long-unburned ecosystems. Restor. Ecol. **13**: 536–544. doi:10.1111/j.1526-100X.2005.00067.x.

Wade, D.D., and Johansen, R.W. 1986. Effects of fire on southern pine: observations and recommendations. USDA For. Serv. Gen. Tech. Rep. SE-41.

Wade, D.D., and Johansen, R.W. 1987. Relating wildland fire to defoliation and mortality in pine. *In* Proceedings of the 4th Biennial Southern Silvicultural Conference, 4–6 November 1986, Atlanta, Georgia. *Edited by* D.R. Phillips. USDA For. Serv. Gen. Tech. Rep. SE-42. pp. 107–110.

Wade, D.D., and Lunsford, J.D. 1989. A guide for prescribed fire in southern forests. USDA For. Serv. Tech. Pub. SRS-11.

Wade, D., Custer, G., Thorsen, J., Kaskey, P., Kush, J., Twomey, B., and Voltolina, D. 1997. Reintroduction of fire into fire-dependent ecosystems: some southern examples. Proc. Tall Timbers Fire Ecol. Conf. **20**: 94–98.

Wade, D.D., Brock, B.L., Brose, P.H., Grace, J.B., Hoch, G.A., and Patterson, W., III. 2000. Fire in eastern ecosystems. *In* Wildland fire in ecosystems: Effects of fire on flora. Vol. 2. *Edited by* J.K. Brown and J.K. Smith. USDA For. Serv. Gen. Tech. Rep. RMRS-GTR-42.. pp. 53–96.

Wallin, K.F., Kolb, T.E., Skov, K.R., and Wagner, M.R. 2004. Seven-year results of thinning and burning restoration treatments on old ponderosa pines at the Gus Pearson Natural Area. Restor. Ecol. **12**: 239–247. doi:10.1111/j.1061-2971.2004.00278.x.

Wyant, J.G., Omi, P.N., and Laven, R.D. 1986. Fire-induced tree mortality in a Colorado ponderosa pine/Douglas-fir stand. For. Sci. **32**: 49–59.