Restoring Fire to Long-Unburned *Pinus palustris* Ecosystems: Novel Fire Effects and Consequences for Long-Unburned Ecosystems

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Abstract

Biologically rich savannas and woodlands dominated by *Pinus palustris* once dominated the southeastern U.S. landscape. With European settlement, fire suppression, and landscape fragmentation, this ecosystem has been reduced in area by 97%. Half of remnant forests are not burned with sufficient frequency, leading to declines in plant and animal species richness. For these fire-suppressed ecosystems a major regional conservation goal has been ecological restoration, primarily through the reinitiation of historic fire regimes. Unfortunately, fire reintroduction in long-unburned Longleaf pine stands can have novel, undesirable effects. We review case studies of Longleaf pine ecosystem restoration, highlighting novel fire behavior, patterns of tree mortality, and unintended outcomes resulting from reintroduction of fire. Many of these pineland restoration efforts have resulted in excessive overstory pine mortality (often >50%) and produced substantial quantities of noxious smoke. The most compelling mechanisms of high tree mortality after reintroduction of fire are related to smoldering combustion of surface layers of organic matter (duff) around the bases of old pines. Development of effective methods to reduce fuels and competing vegetation while encouraging native vegetation is a restoration challenge common to fire-prone ecosystems worldwide that will require understanding of the responses of altered ecosystems to the resumption of historically natural disturbances.

Key words: ecological restoration, fire suppression, Longleaf pine, prescribed fire, smoldering duff combustion.

Introduction

Southeastern U.S. pine forests and savannas dominated by Longleaf pine (*Pinus palustris*) and a biologically diverse understory covered an estimated 37 million hectares prior to European settlement (Frost 1993). During the past centuries, southeastern forestlands have been logged, farmed, subdivided, and planted with faster-growing southern pines (Croker 1987). Remnant areas not converted have been degraded by several decades of fire suppression (Croker 1987; Frost 1993). These landscape changes caused a 97% decline in the area of Longleaf pine ecosystems, making them among the most imperiled ecosystems in the United States (Noss et al. 1995).

Of the remnant area of Longleaf pine ecosystems, only about half is frequently burned (Outcalt 2000), leading to substantial alterations in ecosystem structure and composition. Pre-settlement fire regimes were typified by short fire-return intervals (FRI = 1–5 years), low-intensity surface fires ignited by lightning and late Holocene Native Americans (Christensen 1981). Fire suppression transforms these once open savanna–woodland ecosystems into closed canopy forests, with reduced floral and faunal species richness, as well as heavy accumulations of surface fuels (Heyward 1939; Engstrom et al. 1984; Mushinsky 1985; Ware et al. 1993; Gilliam & Platt 1999; Kush & Meldahl 2000; Kush et al. 2000; Varner et al. 2000; Provencher et al. 2001*b*). Overstory density, species richness, and basal area increase in response to fire suppression (Ware et al. 1993; Gilliam & Platt 1999; Varner et al. 2000), whereas understory species richness and cover decrease (Gilliam & Platt 1999; Kush et al. 2000; Varner et al. 2000). Whereas organic matter on the forest floor was scarce in pre-settlement ecosystems, in the absence of frequent fires there are substantial accumulations of surficial organic horizons, particularly around the bases of large pines (Heyward & Barnette 1936; Brockway & Lewis 1997; Varner et al. 2000; Kush et al. 2004).

To reverse or reduce the further decline of southeastern Longleaf pine ecosystems, many fire-excluded stands with remnant mature pine overstory have been targets for ecological restoration (Hermann 1993; Landers et al. 1995; Wade et al. 1998; Provencher et al. 2001*b*). In long-unburned pinelands, the objectives of restoration are typically to (1) maintain the remnant pine overstory; (2) reduce hardwood midstory; (3) enhance or reestablish native plants and animals; (4) reduce accumulated fuels; and (5) reduce native and non-native invasive species populations (Wade et al. 1998; Varner et al. 2000; Provencher et al. 2001*b*). Efforts at restoring community structure and

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composition have generally included the complementary actions of altering species composition by removing invasive species, reducing stand density, and reducing fuel loads. In highly altered systems, reintroduction of understory species is increasingly common (Bissett 1996; Cox et al. 2004; Jenkins et al. 2004). The most common approach to restoration of long-unburned southern pine communities has been the reinitiation of historical fire regimes with prescribed fires.

Our objectives in this review are to (1) describe the effects of fire exclusion on southern pine ecosystems; (2) review the outcomes of fire reintroduction and restoration; (3) review the hypothesized causes of restoration fire mortality of overstory pines in both the Southeast and analogous ecosystems worldwide; and (4) present a fuels-based perspective for setting restoration priorities that minimizes catastrophic overstory mortality.

Effects of Fire Exclusion on Longleaf Pine Ecosystems

Overstory Responses to Fire Suppression

With fire exclusion, southeastern pinelands have experienced structural and compositional shifts from open savanna–woodlands to closed canopy forests. Frequently burned savanna structure is typified by a spatially variable but mostly open canopy with stand densities of 130–250 trees/ha greater than 10 cm in diameter at breast height (dbh), and basal areas of 12–20 m^2/ha (Wahlenberg 1946; Platt et al. 1988; Boyer 1990; Palik & Pederson 1996; Varner et al. 2003*a*; Fig. 1a). Throughout its range, Longleaf pine is monodominant or occurs with scattered fire-resistant oaks (primarily *Quercus geminata*, *Q. incana*, *Q. laevis*, *Q. margaretta*, and *Q. marilandica*) and hickories (*Carya tomentosa* and *C. pallida*; Peet & Allard 1993; Varner et al. 2003). With the cessation of fire-induced mortality, the cover and density of shrubs and trees increase in the midstory and canopy (Gilliam et al. 1993; Brockway & Lewis 1997; Gilliam & Platt 1999; Kush et al. 2000; Varner et al. 2000; Provencher et al. 2001*a*, 2001*b*; Fig. 1b). The species that benefit from fire suppression include many fire-susceptible species (e.g., *Q. hemisphaerica*, *Q. nigra*, *Acer rubrum*, *Liquidambar styraciflua*, *Magnolia grandiflora*, and *Nyssa sylvatica*) that alter stand structure by increasing tree densities, leaf areas, and basal area. Stand composition is degraded as canopy species richness increases.

Understory Responses to Fire Suppression

Without fire in Longleaf pine ecosystems, understory communities undergo radical shifts in cover and richness. Frequently burned pineland understory communities are among the most species-rich outside of the tropics (Peet &

Figure 1. (a) A frequently burned Longleaf pine ecosystem reference condition at Eglin Air Force Base, Florida. Pristine pinelands are rare in current landscapes of the southeastern United States (Photo by D. Herring). (b) A typical long-unburned (37 years since fire) Longleaf pine forest at the Ordway-Swisher Preserve, Florida. Many pinelands throughout the southeastern United States have undergone decades of fire suppression, leading to increases in the midstory, organic forest floor soil horizons, and decreases in plant and animal species richness (Photo by J. M. Varner).

Allard 1993; Provencher et al. 2003; Varner et al. 2003*b*; Kirkman et al. 2004). Typical burned understories contain 20–30 species/m^2, with dominance by bunchgrasses (*Aristida stricta*, *Schizachyrium scoparium*, and *Andropogon* spp.), asters, legumes, and other forbs including several rare and endemic plant species (Hardin & White 1989; Peet & Allard 1993). Without fire, increased overstory and midstory canopy cover, as well as leaf litter deposition, reduce sunlight reaching the forest floor, leading to the loss of light-demanding understory grasses, forbs, and pine seedlings (Provencher et al. 2001*a*, 2001*b*; Waters et al. 2004). After several decades of fire suppression, herbaceous species richness is often less than 2 species/m^2, pine seedlings are lacking, and the understory becomes dominated by woody species (Varner et al. 2000; Kush et al. 2004).

Midstory Responses to Fire Suppression

A marked change in fire-excluded pinelands is the advent of a woody midstory. Most frequently burned pinelands, particularly on sites with high net primary productivity, lack a well-developed midstory stratum (Peet & Allard 1993; Landers et al. 1995). The few native shrub and tree species present in frequently burned pinelands include oak and hickory sprouts, Gallberry (*Ilex glabra*), *Vaccinium* spp., Saw palmetto (*Serenoa repens*), and isolated patches or "domes" of *Q. geminata* (Guerin 1988; Peet & Allard 1993). Without fire, hardwoods and shrubs ascend into the midstory where they increase cover and stem density dramatically (Provencher et al. 2001*b*).

Forest Floor Characteristics after Fire Suppression

Frequently burned pinelands have very little organic matter on the forest floor, except some litter (Oi horizon), but this condition is altered radically by fire exclusion. Without frequent surface fires, leaf litter, sloughed bark, fallen branches, and other organic necromass accumulate and decompose into fermentation (Oe) and humus (Oa) horizons absent in frequently burned communities (Fig. 2; Heyward 1939; Switzer et al. 1979). Roots and mycorrhizal hyphae exploit these "duff" horizons, especially near the bases of large pines where duff can accumulate to depths of 25 cm or more (Varner et al. 2000; Gordon & Varner 2002; Kush et al. 2004). Litter accumulation and duff formation further block light from reaching the forest floor (Waters et al. 2004) and may play a significant role in driving changes in nutrient cycling (Wilson et al. 2002).

Responses to Fire Reintroduction: Restoration Case Studies

Flomaton Natural Area

The Flomaton Natural Area is a 27-ha remnant old-growth Longleaf pine stand in Escambia County, Alabama (lat 31°01′N, long 87°15′W). Fire had been suppressed in the stand for 45 years until 1993, when a small trash fire ignited a 3-ha stand isolated by a dirt road. The wildfire was allowed to burn out on its own with no observed canopy scorch and limited stem char (all trees <1 m char height). For several days following the fire, smoldering continued in the deep duff that had accumulated around the large remnant pines. Smoke from these fires was problematic for local residents particularly because emissions from smoldering fires are much more hazardous to human health than relatively benign flaming-phase fire emissions (McMahon et al. 1980; McMahon 1983). Additionally, the danger of reignition remained high as long as smoldering continued. During the first 2 years after the fire, heavy mortality was observed in the overstory Longleaf pines (Kush et al. 2004). Mortality was highest among large pines; 91% of the trees greater than 35 cm in dbh died. Survival was higher among small (10–20 cm dbh) Longleaf, Slash (*Pinus elliottii* var. *elliottii*), and Loblolly (*P. taeda*) pines. Most of the small trees of fire-susceptible hardwood species (primarily *Liquidambar styraciflua*, *Prunus serotina*, and *Acer rubrum*) that invaded during the fire-free period also survived the fire (Kush et al. 2004).

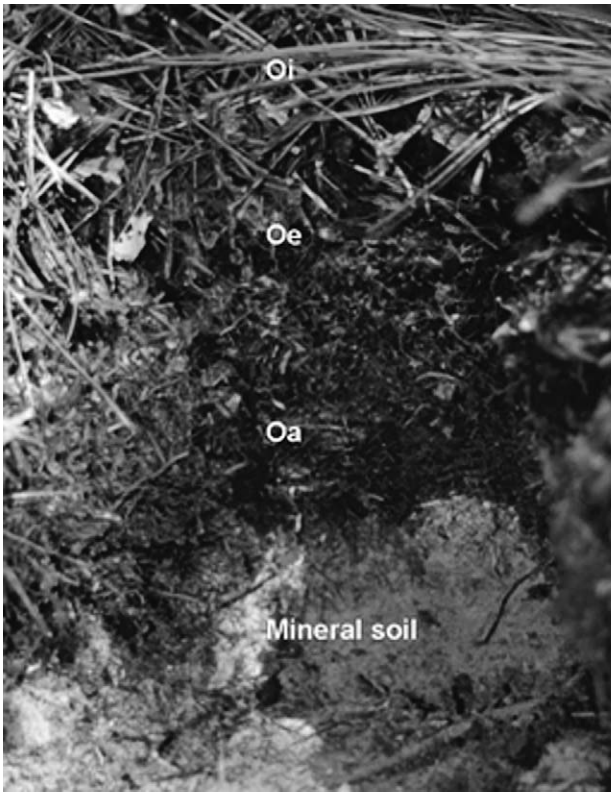

Figure 2. Forest floor development in a long-unburned (approximately 40 years since fire) Longleaf pine forest at Eglin Air Force Base, Florida. In frequently burned pinelands, only a thin Oi horizon forms; Oe and Oa horizons are signs of prolonged fire suppression. In many long-unburned pinelands, organic soil accumulations surrounding large pines can exceed 25 cm in depth.

In response to the loss of a high proportion of the old-growth pines during the 1993 fire, an aggressive ecological restoration program was initiated on the adjacent 24-ha unburned site. The restoration process began with the mechanized harvesting of all hardwood stems (primarily *Quercus* spp.) greater than 10 cm in dbh with a Morbark three-wheeled feller-buncher (Morbark, Inc., Winn, MI, U.S.A.). Beginning in 1994, prescribed fires were reintroduced at an FRI of 1–3 years (Varner et al. 2000; Kush et al. 2004). All fires were ignited when duff moisture content was high (typically within 2–4 days following large rain events) and were lit to minimize fire residence time and fireline intensity. Canopy scorch was low (<20% of trees) in all fires. Even though the Oe and Oa horizons in the duff were moist when the fires were ignited, smoldering was initiated in deep duff accumulations near tree stems. Occurrences of smoldering continued to be detected for several days postignition, requiring repeated extinguishing with backpack, all-terrain vehicle (ATV), and tractor-mounted water sprayers. As a result of these efforts to control fire intensity and to extinguish duff smoldering when detected, mortality of pines in the 4 years following the fire was reduced to an annual average of 4.2% (Varner et al. 2000), still much higher than typical Longleaf pine mortality (Boyer 1979; Palik & Pederson 1996), but the majority of death occurred in trees less than 20 cm dbh. The fires killed several pines 50–80 cm dbh, but losses of these old pines did not exceed 2 trees ha^{-1} yr^{-1} (Varner et al. 2000; Kush, unpublished data).

Eglin Air Force Base

Eglin Air Force Base is a 188,000-ha military reservation in Okaloosa, Walton, and Santa Rosa counties in the Panhandle of Florida (lat 30°38′N, long 86°24′W). Among the many natural plant communities at Eglin, Longleaf pine communities cover approximately 130,000 ha. Many of Eglin's pinelands have experienced prolonged fire-free periods (McWhite et al. 1999; Hiers et al. 2003), leading to ecosystem conditions similar to those observed at Flomaton.

Reintroduction of fire has been the major method for restoration of Longleaf pine ecosystems in Eglin (McWhite et al. 1999), but the results have been mixed. As a result of fire reintroduction at Eglin, some stands suffered 75–100% overstory pine mortality, whereas in others, pine mortality was 10% or less (McWhite et al. 1999; Gordon & Varner 2002). Aside from the need to understand the mechanisms of variation in this phenomenon, these novel fire effects in such fire-dependent forests are alarming. The huge scales of the restoration efforts at Eglin preclude the individual tree treatments used at Flomaton (Hiers et al. 2003). This situation is relevant to many fire-excluded areas in the Southeast because natural resource managers must operationally manage landscapes, rather than individual trees.

Other Examples

Throughout the pinelands of the Southeast, managers have experienced problems with excessive tree mortality resulting from reintroduction of fire (Table 1; Gordon & Varner 2002). As observed at Flomaton and Eglin, pine mortality following the reintroduction of fire is usually concentrated in the largest-diameter classes with greatest prefire duff accumulations (Varner et al. 2000). The resulting pine mortality, in combination with vigorous resprouting of competing hardwoods, prolonged fire dangers, and smoke emissions plague restoration of stands throughout the southeastern United States. These unintended outcomes are major deterrents to additional restoration burning regionwide.

Cause of Pine Mortality after Fire Reintroduction

Hypothesized mechanisms for mortality of large trees after the reintroduction of fire involve the direct effects of fire such as root damage (Ryan & Frandsen 1991; Swezy

Table 1. Reports of excessive overstory Longleaf pine mortality following reintroduction of fire into pine ecosystems after decades of fire suppression.

- Federal agencies
  - USDA Forest Service
    - Ocala National Forest, Florida[a]
    - Talladega National Forest, Alabama[b]
  - U.S. Fish and Wildlife Service
    - Mountain Longleaf National Wildlife Refuge, Alabama[b]
  - Department of Defense
    - Eglin Air Force Base, Florida[c]
    - Fort Gordon, Georgia[b]
    - Fort Jackson, South Carolina[b]
- State agencies & institutions
  - Austin Cary Forest, Florida[b]
  - Autauga Demonstration Forest, Alabama[b,d]
  - Florida Division of Forestry[b,e]
  - Florida Fish and Wildlife Conservation Commission[c]
  - Florida Park Service[f]
  - Georgia Department of Natural Resources[c]
  - North Carolina Division of Parks & Recreation[c]
  - University of Florida[g]
- NGO land management agencies
  - The Nature Conservancy
    - Alabama Chapter[c]
    - Florida Chapter[g]
    - Georgia Chapter[c]
    - Louisiana Chapter[h]
- Forest industry
  - International Paper, Cantonment, Florida[c]

[a] H. G. Shenk 2001, U.S. Forest Service, personal communication.
[b] J. M. Varner, 2003, University of Florida, personal observations.
[c] Varner and Kush 2004.
[d] McGuire, unpublished data.
[e] J. Meeker 2001, Florida Department of Agriculture and Consumer Serivces, personal communication.
[f] E. Johnson 2003, Florida Park Service, personal communication
[g] W. Thomson 2003, The Nature Conservancy, personal communication.
[h] N. McInnis 2000, The Nature Conservancy, personal communication.

& Agee 1991), vascular tissue damage (Martin 1963; Ryan 2000), leaf scorch (Ryan 2000; Menges & Deyrup 2001), or canopy damage (Menges & Deyrup 2001; Fig. 3). Increased insect and pathogen attack of fire-stressed trees has also been suggested as an indirect cause of postfire mortality in these communities (Ostrosina et al. 1997, 1999; Menges & Deyrup 2001).

Where fires have been reintroduced, tree death is reportedly correlated with damage to canopy foliage and branch meristems (Herman 1954; van Wagner 1973; Wade & Johansen 1986; Menges & Deyrup 2001; McHugh et al. 2003). Foliage scorch is considered less stressful than foliage consumption, which is generally associated with damaged branch cambia (Wade & Johansen 1986). Foliage consumption has been correlated with fire-caused mortality of Slash pine in the Southeast (Johansen & Wade 1987; Menges & Deyrup 2001). Nevertheless, pine mortality following reintroduction of fire has been observed without canopy damage following restoration fires (Varner et al. 2000; Kush et al. 2004). Regardless, canopy damage may represent one of many stressors to a tree, exacerbating stem or root damage, and ultimately contributing to excessive pine mortality rates following reintroduction fires.

Postfire tree decline and mortality can also result from fire-caused root damage (Wade & Johansen 1986; Swezy & Agee 1991; Busse et al. 2000). Lateral roots of Longleaf pines are concentrated within the top 30 cm of mineral soil (Heyward 1933; Wahlenberg 1946), and in long-unburned Longleaf pine forests, numerous branch roots grow up into duff horizons (Gordon & Varner 2002). In frequently burned pinelands, soil heating and the resulting root mortality are negligible (e.g., Heyward 1938). With fire suppression and duff accumulation, in contrast, pine roots in duff and in the surface mineral soil can be heated, damaged, or consumed in long-duration smoldering fires where temperatures can exceed lethal values for hours (Flinn & Wein 1977; Wade & Johansen 1986). Smoldering fires spread three orders of magnitude slower than surface fires and are typically concentrated in the lower duff (Oa horizon) beneath a thermal blanket of overlying Oe material (Hungerford et al. 1995). Although localized and small, the smoldering front heats underlying mineral soil to lethal temperatures (>60°C) to maximum depths of 20 cm, often for hours to days post-ignition (Varner, unpublished data). A similar mechanism of duff root heating has been proposed as a cause of tree death and decline in Ponderosa pine stands (*Pinus ponderosa*; e.g., Swezy & Agee 1991; Busse et al. 2000). Given the potential physiological impairment posed by large-scale root heating and consumption, mechanisms involving root damage deserve further study.

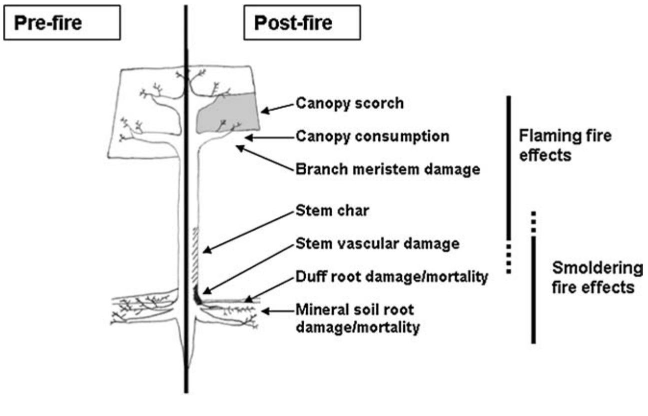

Figure 3. Restoration fires in long-unburned Longleaf pine forests damage canopy, stem, and root tissues often leading to excessive tree mortality. Flaming and smoldering fire can cause direct damage to canopy, stem, and root tissues. Pine mortality has been linked to smoldering combustion of duff near trees, perhaps caused by damage to root and/or stem tissues, or to indirect effects due to increased physiological stress.

Basal cambial damage is another proposed mechanism of tree mortality following fire reintroduction. Basal damage in tree stems can occur during surface fires and during residual smoldering of duff. During surface fires, combustion of litter causes large amounts of heat to be released close to tree stems, leading to stem char (Wade & Johansen 1986; Dickinson & Johnson 2001). Bark, especially the thick accumulations on long-unburned trees, usually insulates the cambium sufficiently against heat damage (Spalt & Reifsnyder 1962; Fahnestock & Hare 1964; Hare 1965; Reifsnyder et al. 1967; Vines 1968; Dickinson & Johnson 2001). In contrast, long-duration heating during smoldering of duff around tree bases can raise temperatures to lethal levels and cause cambial death and tree mortality (Dixon et al. 1984; Ryan & Rheinhardt 1988; Ryan et al. 1988; Dunn & Lorio 1992; Ryan 2000; Dickinson & Johnson 2001). Duff smoldering often continues for hours or days following ignition (Covington & Sackett 1984; Hungerford et al. 1995), long enough to kill the cambium under even thick layers of bark. Cambial damage, even when it does not entirely encircle the stem, is correlated with fire-caused tree mortality in other conifers (e.g., Ryan & Rheinhardt 1988; Ryan et al. 1988; Ryan 2000). Given the long-duration heating observed in reintroduction fires and the potential damage to whole-tree physiology, basal cambial damage appears to be an important mechanism of overstory pine mortality when fires are reintroduced.

Indirect effects of fire reintroduction are reflected in tree physiological stress that, in turn, renders pines susceptible to pests or pathogens. Overall tree stress may be indicated by changes in carbon balance, as indicated by stem or root tissue carbohydrate levels, by reduced resin exudation pressure, or by reduced radial growth (Kozlowski et al. 1991). Past work on southeastern (Davidson & Hayes 1999) and western U.S. conifers (Covington et al. 1997; Ryan 2000; McHugh et al. 2003; Wallin et al. 2003, 2004) has demonstrated that increased physiological stress renders trees more susceptible to pest and pathogen attack. Reintroducing fire to long-unburned Slash pine stands in south Florida led to sharp increases in both

Ips and *Platypus* spp. beetles and subsequent overstory mortality (Menges & Deyrup 2001). It follows that if restoration burning in Longleaf pinelands increases tree stress, then growth and defenses would decline and pest and pathogen attacks would increase. However, in many restoration treatments (burning and thinning, thinning alone, and burning alone), resulting physiological condition varies, as does the subsequent susceptibility to decline and disease. Resin exudation pressure, a correlate of a tree's ability to defend itself from bark beetle attack (Raffa & Berryman 1983; Dunn & Lorio 1992), increases following fire reintroduction in Ponderosa pine ecosystems. Tree physiological condition and growth also improve following thinning, raking, and burning in long-unburned Ponderosa pine forests (Feeney et al. 1998; Stone et al. 1999; Wallin et al. 2004). However, reduced radial growth has been correlated with restoration burning in other Ponderosa pine forests (Busse et al. 2000). To what degree restoration treatments in southern pine stands are effective in maintaining, improving, or reducing tree physiological conditions deserves further study, but arguably only within a mechanistic framework that links physiological response to specific tree damages and characteristics of the fuels and fire that caused the damage (i.e., heat damage from smoldering duff fire to stem vascular tissues that causes physiological impairment and reduced defense capability).

Given that evidence supports a mechanistic link between stem and/or root damage as the cause of mortality following fire reintroductions, understanding smoldering combustion appears to be requisite for understanding the mechanism behind tree mortality in long-unburned southern pine forests. Smoldering differs from flaming combustion by being controlled mostly by oxygen availability (as opposed to fuel availability), by lower temperatures (<500°C vs. higher temperatures in flaming combustion), and by longer residence times (Hungerford et al. 1995; Miyanishi 2001). Smoldering elevates temperatures in duff, in the underlying mineral soil horizons, in roots located within these horizons, and in nearby tree stems (Wade & Johansen 1986; Ryan & Frandsen 1991; Swezy & Agee 1991; Hungerford et al. 1995; Schimmel & Granstrom 1996; Haase & Sackett 1998; Dickinson & Johnson 2001; Miyanishi 2001).

Smoldering Duff Fires and Southeastern U.S. Restoration

Determining the correlates and mechanisms of tree mortality following fire reintroduction should be of high priority for southeastern restoration efforts. Given that 50% of all remnant Longleaf pinelands are unburned (Outcalt 2000), successful restoration burning could double the area of functioning Longleaf pinelands. Landscape-scale fire suppression has similarly affected other southern pinelands (dominated by *P. taeda*, *P. elliottii* var. *elliottii*, *P. elliottii* var. *densa*, and *P. echinata*; Noss et al. 1995). A better understanding of restoration burning has the potential to restore the ecological integrity of these important communities. Without a more rigorous understanding of the effects of restoration, continued reintroduction of fire will inevitably lead to more catastrophic overstory mortality and hasten the decline in southeastern pine-dominated ecosystems (Landers et al. 1995; South & Buckner 2003).

Smoldering duff and tree decline and mortality are familiar phenomena in ecosystems maintained by frequent fires outside of the southeastern United States where, in response to fire suppression, deep organic horizons accumulate around large conifers, creating a potential for mortality when fire is reintroduced (Ryan & Frandsen 1991; Swezy & Agee 1991; Haase & Sackett 1998; Stephens & Finney 2002; McHugh & Kolb 2003). It is likely that as native ecosystems continue to be degraded by fire suppression and restoration efforts ensue, we will experience other novel disturbances that will challenge future conservation and restoration.

It is ironic that southeastern U.S. pinelands are imperiled by fire suppression, but the reintroduction of fire often results in the death of a large proportion of the residual pines. Clearly, if fire is to be a useful tool for restoring the remnant stands from which it has been excluded for decades, the fire-induced mortality problem needs to be solved. As described, the consumption of novel fuels in fire-excluded stands plays a major role in contributing to fire-induced pine mortality. Reducing these novel fuelbeds, characterized by well-developed forest floor horizons, should be a primary restoration objective for managers attempting to reintroduce fire into excluded stands. Multiple fires over many years may be necessary for the gradual elimination of these novel fuels prior to meeting ancillary restoration objectives such as midstory reduction or understory restoration. At small scales, extinguishing duff fires can save many of the large old trees for which these ecosystems are valued, but such efforts are expensive and thus unlikely to be viable over large areas. Nevertheless, understanding the patterns and processes of duff fire–induced mortality represents an important step toward restoring and maintaining southeastern pine ecosystems as viable components in our conservation landscape.

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