



Post-fire resprouting of shortleaf pine is facilitated by a morphological trait but fire eliminates shortleaf × loblolly pine hybrid seedlings



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ABSTRACT

Concurrent with fire exclusion, shortleaf pine × loblolly pine hybrids have increased throughout the southeastern USA and may threaten the genetic integrity of shortleaf pine. Historically, fire favored shortleaf pine over other southern pine species, especially loblolly pine, with which it shares a broad sympatric natural range. Shortleaf pine seedlings have a morphological adaptation (basal crook) that lowers dormant buds to the soil surface where they are presumably protected from fire to facilitate resprouting after topkill. To evaluate this presumption, we tested (1) the functional role of the basal crook in protecting dormant buds by measuring resprouting after exposing the lower stem of shortleaf pine to fire and protecting from fire the lower stem (and dormant buds) of loblolly pine (which lacks a basal crook) and (2) the occurrence and importance of the basal crook morphological adaptation in F1 shortleaf × loblolly pine seedlings by comparing morphology and post-fire resprouting of the hybrids to both parents. Fire exposure of shortleaf pine seedling dormant buds caused seedling mortality, while protecting loblolly pine dormant buds facilitated resprouting. Hybrid pines have basal crooks intermediate to the strong crook of shortleaf pine and loblolly pine's non-crooked stem. Fire top-killed loblolly pine and shortleaf × loblolly pine seedlings, and they did not resprout, while 57% of shortleaf pine resprouted after topkill during two dormant season and one growing season burns. This highly significant difference shows that the basal crook is important for shortleaf pine resprouting after topkill by fire. Fire is an important tool to reduce shortleaf × loblolly pine hybrids, and to provide a competitive advantage to shortleaf pine relative to loblolly pine, for ecosystem restoration and maintaining the genetic integrity of shortleaf pine.

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1. Introduction

Shortleaf pine (*Pinus echinata* Mill.) has the widest distribution of any pine in the southeastern USA. While the species is broadly distributed, shortleaf pine abundance has decreased over the last century. McWilliams et al. (1986) estimated that shortleaf pine forest type suffered an approximately 50% reduction from the 1950s to the late 1970s, and Oswalt (2011) quantified a loss of an additional half of remaining shortleaf pine forests between the 1980s and 2010. Factors for this decline include the interruption of historic fire patterns, land use change, and replacement of shortleaf pine with planted stands of more productive timber species, especially loblolly pine (*P. taeda* L.) (Tauer et al., 2012). In addition to these threats, shortleaf pine is at risk to hybridization with and

introgression towards loblolly pine. Introgression between the loblolly pine and shortleaf pine has increased from 3.3% to 45.7% since the 1950s in shortleaf pine stands when current seedling populations were compared to adult trees originating from the same areas (Stewart et al., 2012). Hybridization may imperil the genetic integrity of shortleaf pine and reduce the resilience of pine seedlings to fire and drought (Tauer et al., 2012).

Fire is historically associated with shortleaf pine forests. In an early account, Mattoon (1915) documents the link between fire and shortleaf pine, "Its range over the drier uplands is coincident with a region of frequent forest fires, yet it is saved by notably abundant reproduction practically everywhere." With prolonged fire exclusion, shortleaf pine is replaced by later successional angiosperm tree species (Guldin, 1986). The most prominent trait of shortleaf pine to survive burning is the ability of seedlings and saplings to vigorously resprout after topkill from fire (e.g., Mattoon, 1915).

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A plant species' ability to resprout following topkill from fire is an important attribute for success and persistence in a landscape that experiences periodic fire (Pausas et al., 2016; Pausas and Keeley, 2014). There are a number of traits that facilitate resprouting after fire, including maintaining dormant buds at or below the soil surface where the low thermal conductivity of the soil protects and insulates these buds (Clarke et al., 2013). Other traits that afford protection of buds by soil is cryptogean germination and seeds that germinate at the soil surface but subsequently bury their hypocotyl region through hypocotyl or root contraction (Fisher, 2008). In the southeastern USA, longleaf pine (*Pinus palustris* Mill.) seedlings have a 'grass stage' where the terminal bud remains at the soil surface for several years where it is protected by dense foliage (Bower, 1990).

Shortleaf pine seedlings form a morphological attribute, colloquially identified as a 'basal crook', in which the seedling bends at a point low in the hypocotyl region to lay along the ground. Shortly thereafter, the stem bends upward at a point just above the hypocotyl causing the stem to grow vertically from this point. This process leaves a horizontal basal crook section 2.5–7.5 cm long (Mattoon, 1915; Stone and Stone, 1954) that contains dormant buds that are formed in the axils of the primary needles. Open-grown seedlings develop the basal crook in the first year, but shade-grown seedlings may develop it as late as 3–9 years (Little and Somes, 1956).

The basal crook has been widely speculated to facilitate resprouting by lowering the dormant bud cluster closer to the soil surface where a fire is cooler. In addition, the crook permits the accumulation of soil and duff above the dormant bud cluster, further protecting and insulating the dormant buds. Crooking has been associated with sprouting success following prescribed fire (Little and Somes, 1956). Likewise, the temperature reached at the basal crook during fire was inversely correlated to shortleaf pine resprouting, and resprouting does not occur on charred stem segments (Lilly et al., 2012a). While intuitive, the importance of the basal crook to resprouting following fire has never been directly tested, likely because nearly all naturally regenerated shortleaf pines have basal crooks (Mattoon, 1915; Stone and Stone, 1954; Lilly et al., 2012a) which makes disentangling resprouting potential and the presence of the crook difficult. When topclipped, all shortleaf pine seedlings resprouted (Lilly et al., 2012b). However, resprouting success of seedlings topkilled by fire is variable (Little and Somes, 1956; Lilly et al., 2012a).

While there has been discussion as to the evolutionary pressures that caused resprouting ability to arise (Bradshaw et al., 2011a, 2011b; Keeley et al., 2011), differences in postfire resprouting capacity can determine species composition and ecosystem structure and function. In fire inclusive systems, resprouting ability provides shortleaf pine with a competitive advantage to species that do not normally resprout, such as the closely related loblolly pine (Williams, 1998). Stewart et al. (2015) found that biennially prescribed fires eliminated loblolly pine and most shortleaf pine × loblolly pine hybrid seedlings while favoring shortleaf pine seedlings, but fire exclusion over 30 years in nearby stands resulted in a mixed seedling population of shortleaf pine, loblolly pine, and their hybrids.

Shortleaf pine × loblolly pine hybrid seedlings are likely killed by fire because they form a crook that is intermediate between a crook with 90° angles found in shortleaf pine and no crook found in loblolly pine (Lilly et al., 2012b; Will et al., 2013). The intermediate basal crook has approximately 45° angles where the dormant buds along the hypocotyl region of the hybrid pines are positioned higher above the soil surface (Will et al., 2013) where they might be exposed to fire, resulting in their elimination when a regular fire regime is employed (Stewart et al., 2015). Determining the role of the basal crook has taken on importance in light of the threat of

hybridization between shortleaf pine and loblolly pine. Compared to shortleaf pine, loblolly pine has lower sprouting capacity which is typically lost within three years (Little and Somes, 1956; Campbell, 1985; Lilly et al., 2012b) and does not possess a basal crook. Thus, loblolly pine seedlings generally do not resprout following topkill from fire. Shortleaf pine × loblolly pine F1 hybrid seedlings exhibit rapid height growth like loblolly pine, have resprouting capacity intermediate to parent species following top-clipping, and possess an intermediate crook (Will et al., 2013).

Our goal was to determine the effects of fire on resprouting of shortleaf pine, loblolly pine, and their F1 hybrids and relate this to the presence of the basal crook. We planted seeds and then deployed small-scale fires in early spring and summer of the resulting seedlings' second growing season and the spring before their third growing season. Determining the post-fire resprouting success of shortleaf pine, loblolly pine and the F1 hybrid seedlings indicated the role that fire exclusion plays in facilitating persistence of hybrid pine seedling and saplings and the ongoing change in stand composition and population genetics. We also investigated the importance of the basal crook for fire tolerance in shortleaf pine. We manipulated the height of the dormant buds in proximity to the soil for both shortleaf pine and loblolly pine and then measured resprouting after fire. The basal crook's functional role in shortleaf pine fire adaptation may have profound relevance to the ecology and resilience of the forests of the southeastern USA. Understanding that role will be important for forest management and restoration efforts.

2. Materials and methods

2.1. Seedling origins

Shortleaf pine, loblolly pine, and shortleaf × loblolly hybrid pine seeds were produced at the Oklahoma Forestry Services seed orchard in Idabel, Oklahoma, USA (35°53'N, 94°45'W). Both shortleaf pine and loblolly pine seeds were collected from open-pollinated cones from six shortleaf pines and six loblolly pines originating from the western populations of both species' ranges-- southeastern Oklahoma, southwestern Arkansas, and northeastern Texas. Hybrid pine seeds came from six loblolly pine maternal parents that were control-pollinated with pollen from five shortleaf pine paternal parents. Cones were collected and seeds extracted and stored (−20 °C) using standard protocols.

On 24 January 2013, seeds were removed from storage and soaked in water for 12 h at 4 °C. Seeds that sank were selected for stratification in a refrigerator in a moist paper towel contained in a plastic bag at 4 °C for 56 days. On 28 March 2013, seeds were planted at the Kiamichi Forestry Research Station, Idabel, Oklahoma, USA, which is adjacent to the Oklahoma Forestry Services seed orchard. The field was approximately 0.2 ha and had been tilled prior to planting. The soil was a mixture of Adaton loam (Fine-silty, mixed, active, thermic Typic Endoaqualfs) and Kullit fine sandy loam (Fine-loamy, siliceous, semiactive, thermic Aquic Paleudults), with slope between 0 and 3%.

2.2. Comparing hybrid and parent species resprouting

Seeds were planted in 14 rows, each containing 20 evenly-spaced planting positions, in independent random orders of six loblolly pine and six shortleaf pine (one from each half-sib family) as well as eight hybrid pines (one from each full-sib family) resulting in 280 planting positions (20 per row × 14 rows). In each planting position, five to ten seeds were planted by covering with 1–2 cm of mineral soil. Planting positions were marked and labeled by numbered metal tags attached to stakes. Wire enclosures were

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