Short-term stem mortality of 10 deciduous broadleaved species following prescribed burning in upland forests of the Southern US

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A, B, C, D, E, F, G, H

Abstract. In upland forests of the Southern US, management is increasingly focussed on the restoration and maintenance of resilient structures and species compositions, with prescribed burning being the primary tool used to achieve these goals and objectives. In this study, we utilised an extensive dataset comprising 91 burn units and 210 plots across 13 National Park Service lands to examine the relationships between the probability of stem mortality \((P_{m})\) 2 years after prescribed fire and stem size and direct fire effects for 10 common deciduous broadleaved species. Post-fire stem mortality ranged from 6.9% for *Quercus alba* to 58.9% for *Sassafras albidum*. The probability of stem mortality was positively associated with maximum bole char height (CHAR) and inversely related to diameter at breast height (DBH) for all 10 deciduous broadleaved species. Model goodness-of-fit varied, with the poorest fit generally associated with fire-tolerant species and best fit generally associated with fire sensitive species. The information presented contributes to our understanding of post-fire stem mortality and may contribute to the development of fire-related stem mortality models following prescribed burning for eastern tree species. Models should be validated with independent datasets across upland forests types to test for spatial relationships before widespread application.


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Introduction

In upland forests of the Southern United States (US), management efforts are increasingly focussed on the restoration and maintenance of resilient structures and species compositions, with prescribed burning being the primary tool used to conduct these restoration efforts. In 2014, prescribed fires were conducted on \(\sim2.4 \times 10^6\) ha of forestland throughout the 13-state region comprising the Southern US (Melvin 2015). Specific objectives associated with prescribed burning often include hazardous fuel reduction, restoration of open understorey conditions (Sparks et al. 1998), establishment and development of ecologically desirable *Quercus* (e.g. Soucy et al. 2005; Arthur et al. 2012) and *Pinus* reproduction (Jenkins et al. 2011), site-preparation (Waldrop 1997), and the reduction in the abundance of mesophytic and fire-sensitive species (e.g. *Acer rubrum*, *A. saccharum*, *Nyssa sylvatica*) (Brose et al. 2014). Quantitative data related to the factors associated with species-specific post-fire stem mortality in the forests of this region are particularly
important as restoration goals achieved by prescribed burning must balance a multitude of ecosystem goods and services (Ryan et al. 2013), including resultant changes to forest structure (Arthur et al. 2015) and post-fire fuel dynamics (Battaglia et al. 2008; Stephens et al. 2009), effects on timber production and quality (Wiedenbeck and Schuler 2014), recreation (Vaux et al. 1984), and aesthetics (Anderson et al. 1982). As restoration and prescribed burning efforts increase across the Southern US, quantitative information that describes and forecasts species-specific stem mortality will be required to understand the effects of alternative burn prescriptions and fire regimes on forest structure and composition over time and across the landscape (Reinhart and Dickinson 2010).

Post-fire stem mortality is the result of injury to, or consumption of, essential plant tissues, including crown foliage and branches, cambium and the root system (Grayson et al. 2017). Heating of these vital plant tissues disrupts critical physiological processes such as water transport, nutrient uptake and photosynthesis. The amount of damage an individual tree can withstand before mortality occurs varies within and across species. Within a species, trees of larger size and, correspondingly, greater bark thickness (Hengst and Dawson 1994) are able to withstand greater heating and crown and cambium damage (Harmon 1984). Across species, the ability to withstand the direct effects of fire is variable. Species-specific thresholds of crown damage are generally the primary variable controlling mortality of coniferous species (McHugh and Kolb 2003) whereas bole char height often influences stem mortality of deciduous broadleaved species (Regelbrugge and Smith 1994; Cocking et al. 2012).

Models that quantify the factors affecting stem mortality following wildfire have been developed for several species in the western US (Hood et al. 2010; Grayson et al. 2017), and, subsequently, incorporated into fire effects models (e.g. the First-Order Fire Effects Model (FOFEM); Reinhart 2003). In general, these studies have found incipient and delayed fire-related mortality is accurately predicted using combinations of morphological characteristics (e.g. diameter at breast height (DBH) and bark thickness; Keyser et al. 2006) and measures of direct fire effects, such as crown volume scorched (Hood et al. 2010) and bole or bark char severity (Brice et al. 2008). Research suggests that damage to the root system, measured indirectly with dust consumption and moisture content (Varner et al. 2007) or ground char severity ratings (McHugh and Kolb 2003), may also contribute to post-fire stem mortality (Stephens and Finney 2002).

Prescribed fires are conducted under conservative environmental conditions and result in lower fire intensity and severity than observed during uncontrolled wildfires (Morrison and Renwic 2010). This is especially true in the forest types of the Southern US, where prescribed fires are generally of low intensity (Varner et al. 2007; Arthur et al. 2015). Models that quantitatively describe the relationship between direct fire effects and individual tree attributes on post-fire stem mortality following prescribed burning are lacking for most of species prevalent in upland forests in the Southern US. For eastern deciduous broadleaved species, the limited information available suggests combinations of stem size and maximum height of bole char are most strongly correlated with stem mortality (i.e. topkill) following wildfire for Quercus coccinea, Q. montana, Q. rubra, Q. velutina, Acer rubrum, Nyssa sylvatica, Carya glabra and Amelanchier arborea (Regelbrugge and Smith 1994). Although these are some of the only quantitative models describing the effects of tree attributes and direct fire effects of post-fire stem mortality for deciduous broadleaved species, the equations were developed from a limited sample size originating from a single wildfire in the mountainous region of Virginia. In this study, we explore the influence of individual tree attributes and direct fire effects on species-specific stem mortality 2 years following prescribed fire for 10 deciduous broadleaved tree species common throughout upland forests of the Southern US using easily obtained tree morphological and fire effects data. Using fire effects monitoring data collected from prescribed burn units across the Southern US, we tested the hypothesis that, regardless of the deciduous broadleaved species examined, the probability of post-fire stem mortality would decrease as stem size increases and increase as the severity of direct fire effects increases.

**Methods**

**Study sites and data collection**

A total of 210 0.1-ha (20 × 50-m) plots were established in 91 prescribed burn units throughout 13 United States Department of Interior, National Park Service (NPS) lands (Fig. 1; Table S1, available as Supplementary material to this paper) using a standardised NPS vegetation monitoring protocol (US Department of the Interior National Park Service 2003). Prescribed fires, which ranged in size from 0.4 to 2072 ha across the 91 units, were completed mostly in the late dormant to early growing season (80% between January and April; 14% between May and August; 6% between September and December) between 1997 and 2012. Since Park establishment, minimal active (i.e. harvesting) management has occurred on NPS lands. In some prescribed burn units there was evidence of fire (charcoal visible in the soil or charred decades old stumps), but no recent fire (within the last 20 years) was documented. The prescribed fires were ignited as is typical in the Southern US uplands – primarily strip-head fires, except on steep slopes where fires were ignited on ridgelines and allowed to back down slopes. In large helicopter-ignited units, spot-grid ignition patterns were used (Wade and Lunsford 1989).

Prior to burning, individual trees were tagged, and species, status (live or dead), and stem diameter at 1.4 m above groundline (DBH; cm) were recorded. Overstorey trees (stems >15 cm DBH) were inventoried in the entire 0.1-ha plot, and understory trees (stems ≥2.5 cm and ≤15 cm DBH) were inventoried in one-quarter of the larger plot. Direct fire effects for each tagged tree were measured within ~1 month post-burn. Not all Parks measured post-burn metrics on understory trees, which limited the number of smaller trees in this study. The only direct fire effect consistently measured on the deciduous broadleaved species was maximum bole char height (CHAR). Maximum bole char height (m) was measured from the ground level to the highest point on the bole where char was evident regardless of slope (e.g. uphill, side hill or down hill) position. Although CHAR can be influenced by a variety of factors, it is positively correlated with fire intensity (Williams et al. 1998; Rebain...
Status of individual trees (live or dead) was recorded two years following each prescribed fire. Because total tree height and height to the base of the live crown were not measured and recorded, we were unable to create variables that describe CHAR relative to total tree height or the percentage of crown that was potentially damaged or killed. Trees recorded as dead included those that were top-killed (i.e. main bole killed but potentially sprouting) as a result of the fire. Species composition, as inferred by forest type, varied considerably among plots and burn units (Table S1).

Statistical analyses
We conducted Wilcoxon Rank Sum Tests ($\alpha = 0.05$) to determine whether the distribution describing individual tree attributes (DBH) and direct fire effects (CHAR) differed between trees recorded as live and dead 2 years following prescribed burning. Mortality data are categorical with a binary outcome (live or dead). Consequently, we used generalised linear mixed effects modelling to predict the probability of stem mortality two years post-fire:

$$P(m) = \frac{1}{1 + e^{-\left(\beta_0 + \beta_1 X_1 + \beta_2 X_2 + \ldots + \beta_n X_n\right)}}$$

where $P(m)$ is the probability of mortality 2 years following prescribed burning, $\beta_0$ through $\beta_n$ are regression coefficients, and $X_i$ though $X_n$ are explanatory variables. Tree-level explanatory variables tested were DBH and CHAR. Results from correlation analysis revealed DBH and CHAR were not strongly correlated ($r < 0.50$) and could, therefore, be utilised together during model fitting. Models were fitted using maximum likelihood methods and the LaPlace method in PROC GLIMMIX (SAS Institute 2015). Burn unit and plot nested within burn unit were included as random effects to account for the hierarchy in the dataset (i.e. plots nested within burn units and trees nested within plots). For Nyssa sylvatica, the inclusion of random
intercepts associated with both burn unit and plot resulted in convergence issues. Therefore, for this species, we included only burn unit as a random effect. Minimum sample size required to develop stem mortality models was set to 40 dead trees (20 times the number of explanatory variables; Hosmer et al. 2013).

Model goodness-of-fit was assessed using receiver operating characteristic (ROC) curve analysis. The ROC curve is a plot of the true positive rate (i.e. trees observed dead and predicted dead) v. the false positive rate (i.e. trees observed live but predicted dead) across a range (0 to 1) of cutoff points (Hosmer et al. 2013). Models with ROC values ≥0.7 are considered to have an acceptable discrimination between live and dead trees, ROC values ≥0.8 indicate excellent discrimination, and ROC values ≥0.9 indicate outstanding discrimination (Hosmer et al. 2013).

We utilised the bootstrapping procedure outlined by Harrell et al. (1996) to produce an adjusted ROC value that represented the optimism adjusted measure of predictability. The first step in the internal validation process was to generate apparent ROC values from the model fitted to the original dataset (ROCapp). Species-specific datasets were then resampled with replacement to produce 250 replicate datasets that were each the size of the original species-specific dataset. The model fitted to the original dataset was fitted to each of the 250 replicate datasets and ROC values calculated (ROCboot). The models fitted to the resampled data were then applied to the original dataset and ROC values were calculated (ROCorig). The difference between ROCboot and ROCorig were averaged to provide the estimate of optimism (O), with the optimism adjusted measure of predictability (i.e. honest estimate of internal validity; Harrell et al. 1996) of the original model (ROChon) calculated as ROCapp – O. For eight species, there were convergence issues during model fitting of one or more bootstrapped samples. Therefore, for six species (Cornus florida, Oxydendrum arboreum, Quercus alba, Q. coccinea, Q. marilandica, Q. velutina), ROChon values are based on no less than 244 bootstrapped samples, whereas the ROChon values for Sassafras albidum and Nyssa sylvatica were based on 163 and 184 bootstrapped samples respectively. Although the most robust form of validation utilises external independent data, the bootstrap method described above is the preferred method of internally validating predictive logistic regression models (Steyerberg et al. 2001). The ROChon values reported reflect the population average or marginal effects.

Results

For the deciduous broadleaved species examined, mortality 2 years following prescribed fire ranged from 6.9% for Quercus alba to 58.9% for Sassafras albidum (Fig. 2). The diameter distribution of sampled trees and the proportion of live v. dead trees within a given diameter class varied considerably among the species (Fig. 3). For species other than Sassafras albidum, the DBH of dead trees was significantly smaller than live trees (Table 1). Maximum bole char height was generally low, with median CHAR levels ranging from 0.1 to 0.4 m (Table 1). These low median CHAR values reinforce the fact these were low intensity prescribed burns. The variation in CHAR within and among species was considerable (Fig. 4). However, with the exception of Acer rubrum, CHAR was significantly greater in dead v. live trees (Table 1). For all 10 species examined, the probability of stem mortality 2 years following prescribed burning was significantly influenced by DBH and CHAR (Table 2). The relative influence of DBH and CHAR varied considerably among the species. However, the probability of mortality for these species increased as DBH decreased and CHAR increased (Fig. 5). Many of the fire-sensitive, or pyrophobic species (sensu Thomas-Van Gundy and Nowacki 2013), including Acer rubrum, Nyssa sylvatica and Oxydendrum arboreum, experienced a precipitous decline in the predicted probability of mortality between 0 and 20 cm DBH, with very low predicted probability of mortality beyond 20 cm DBH (Fig. 5). In comparison, fire-tolerant, or pyrophilic species (sensu Thomas-Van Gundy and Nowacki 2013) (e.g. Quercus alba, Q. montana and Q. coccinea) exhibited a more gradual decline in the predicted probability of mortality across the range of stem diameters observed in the data. The ROChon values for all species ranged from a minimum of 0.7394 for Quercus alba to a maximum of 0.9551 for Sassafras albidum, with all models having acceptable (ROChon ≥ 0.7) to outstanding (ROChon ≥ 0.9) discrimination (Table 2). Basic statistics associated with the bootstrapped parameter estimates are provided in the Supplementary material (Fig. S1).

Discussion

The goal of this study was to examine the relationships between easily obtained tree attribute and fire effects data, and post-fire stem mortality 2 years following prescribed fire for deciduous broadleaved species common to upland forests of the Southern US. Stem mortality 2 years following fire varied, with Quercus alba experiencing the lowest rates (6.9%) and Sassafras albidum experienced the highest rates (58.9%) of fire-related stem mortality. Our hypothesis that stem size (i.e. DBH) and severity of fire effects (i.e. CHAR) would significantly predict the probability of stem mortality 2 years following prescribed fire was supported for all 10 deciduous broadleaved species.
Table 1. Attributes of live and dead trees used to develop post-fire stem mortality models

Values represent the median ± s.d. (minimum, maximum). Asterisks (*) indicate a significant difference between trees recorded as live and dead 2 years following prescribed fire according to Wilcoxon Rank Sum Test. DBH, diameter at breast height (cm); CHAR, maximum bole char height (m); Burn units, percentage of all burn units (n = 91) containing a given species; Plots, percentage of all plots (n = 210) containing a given species.

<table>
<thead>
<tr>
<th>Species</th>
<th>Number of trees</th>
<th>DBH (cm)</th>
<th>CHAR (m)</th>
<th>Burn units</th>
<th>Plots</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acer rubrum</td>
<td>610</td>
<td>16.4 ± 9.0* (2.5, 70.0)</td>
<td>0.1 ± 0.5 (0.0, 3.5)</td>
<td>58</td>
<td>43</td>
</tr>
<tr>
<td>Cornus florida</td>
<td>134</td>
<td>5.3 ± 3.5* (2.5, 23.9)</td>
<td>0.2 ± 0.3* (0.0, 2.0)</td>
<td>25</td>
<td>15</td>
</tr>
<tr>
<td>Nyssa sylvatica</td>
<td>330</td>
<td>10.0 ± 10.9* (2.5, 66.8)</td>
<td>0.2 ± 0.8* (0.0, 5.3)</td>
<td>51</td>
<td>38</td>
</tr>
<tr>
<td>Oxydendrum arboreum</td>
<td>344</td>
<td>15.3 ± 7.8* (2.5, 40.0)</td>
<td>0.2 ± 1.0* (0.0, 7.0)</td>
<td>36</td>
<td>31</td>
</tr>
<tr>
<td>Quercus alba</td>
<td>626</td>
<td>25.6 ± 13.5* (2.5, 84.4)</td>
<td>0.2 ± 0.8* (0.0, 6.5)</td>
<td>66</td>
<td>45</td>
</tr>
<tr>
<td>Quercus coccinea</td>
<td>601</td>
<td>29.7 ± 18.5* (2.5, 82.2)</td>
<td>0.5 ± 0.8* (0.0, 10.0)</td>
<td>66</td>
<td>53</td>
</tr>
<tr>
<td>Quercus marilandica</td>
<td>188</td>
<td>18.3 ± 7.5* (2.9, 45.2)</td>
<td>0.3 ± 0.9* (0.0, 4.8)</td>
<td>26</td>
<td>16</td>
</tr>
<tr>
<td>Quercus montana</td>
<td>830</td>
<td>25.8 ± 14.0* (2.7, 97.0)</td>
<td>0.3 ± 1.0* (0.0, 7.0)</td>
<td>45</td>
<td>37</td>
</tr>
<tr>
<td>Quercus velutina</td>
<td>459</td>
<td>26.8 ± 14.2* (2.7, 76.3)</td>
<td>0.4 ± 0.9* (0.0, 12.0)</td>
<td>64</td>
<td>44</td>
</tr>
<tr>
<td>Sassafras albidum</td>
<td>73</td>
<td>4.3 ± 4.3 (2.5, 25.4)</td>
<td>0.4 ± 0.6* (0.0, 2.9)</td>
<td>13</td>
<td>9</td>
</tr>
</tbody>
</table>

Fig. 3. Diameter distribution (10-cm diameter classes) of live and dead trees used for post-fire stem mortality model development. Note: the scale of the x- and y-axes varies by species.

Fig. 4. Maximum bole char height (CHAR) distribution of live and dead trees used for post-fire stem mortality model development. The distribution represents 0.2-m CHAR classes, with the exception of the largest CHAR class, which includes CHAR values > 1.0 m. Note: the scale of the y-axis varies by species.
Table 2. Parameter estimates (s.e.) associated with species-specific models predicting 2-year stem mortality following a single prescribed burn

<table>
<thead>
<tr>
<th>Species</th>
<th>$b_0$ (Intercept)</th>
<th>$b_1$ (DBH)</th>
<th>$b_2$ (CHAR)</th>
<th>ROC$_\text{cua}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acer rubrum</td>
<td>2.3014 (0.6570)**</td>
<td>$-$0.3267 (0.0470)**</td>
<td>1.1137 (0.3897)**</td>
<td>0.8662</td>
</tr>
<tr>
<td>Cornus florida</td>
<td>$-$0.8727 (0.6910)</td>
<td>$-$0.1814 (0.0761)*</td>
<td>4.1947 (1.3165)**</td>
<td>0.7239</td>
</tr>
<tr>
<td>Nyssa sylvestica</td>
<td>2.7899 (0.9510)**</td>
<td>$-$0.5511 (0.0918)**</td>
<td>1.2888 (0.4222)**</td>
<td>0.8866</td>
</tr>
<tr>
<td>Oxydendrum arboreum</td>
<td>1.9418 (1.2229)</td>
<td>$-$0.4602 (0.1157)**</td>
<td>1.6352 (0.3958)**</td>
<td>0.8365</td>
</tr>
<tr>
<td>Quercus alba</td>
<td>$-$1.8137 (0.4600)**</td>
<td>$-$0.0603 (0.0181)**</td>
<td>0.8666 (0.1418)**</td>
<td>0.7877</td>
</tr>
<tr>
<td>Quercus coccinea</td>
<td>$-$1.6262 (0.4924)**</td>
<td>$-$0.0339 (0.0126)**</td>
<td>0.6901 (0.2109)**</td>
<td>0.7395</td>
</tr>
<tr>
<td>Quercus marilandica</td>
<td>0.3714 (0.8583)</td>
<td>$-$0.1005 (0.0426)*</td>
<td>1.5577 (0.4093)**</td>
<td>0.7625</td>
</tr>
<tr>
<td>Quercus montana</td>
<td>$-$1.4416 (0.6246)*</td>
<td>$-$0.1469 (0.0245)**</td>
<td>1.3159 (0.2321)**</td>
<td>0.8825</td>
</tr>
<tr>
<td>Quercus velutina</td>
<td>0.1122 (0.5614)</td>
<td>$-$0.1287 (0.0263)**</td>
<td>1.2612 (0.2848)**</td>
<td>0.8205</td>
</tr>
<tr>
<td>Sassafras albidum</td>
<td>1.6779 (0.7328)*</td>
<td>$-$1.0299 (0.2655)**</td>
<td>10.2855 (2.5017)**</td>
<td>0.9551</td>
</tr>
</tbody>
</table>

Examined. Stem size has been proven to be a significant predictor of post-fire mortality for both eastern (Regelbrugge and Smith 1994) and western (Hood et al. 2010) species. In the present study, predicted stem mortality decreased as DBH increased for all 10 of the species examined. Although significant, the strength of the relationship between the probability of stem mortality and DBH varied considerably and likely reflected differences in sample size across the diameter distribution and species-specific relationships between DBH and bark thickness. When post-fire mortality models using either stem size or bark thickness are compared, those using bark thickness often perform better than those using stem size (Keyser et al. 2006; Catry et al. 2010). Trees with greater bark thickness experience lower maximum cambial temperatures and an increased time to reach peak temperature, providing greater protection from cambial injury (Hengst and Dawson 1994). Although allometric equations that predict bark thickness from DBH exist for a portion of the upland forest tree species examined (e.g. Harmon 1984; Hengst and Dawson 1994), in eastern forests, where the historic fire regime was dominated by frequent low severity fire (Lafon et al. 2017), it is possible that bark thickness at the base of the bole rather than at breast height is more of a factor influencing fire-related mortality for the species examined (Graves et al. 2014; Hammond et al. 2015). In regard to the limitations of the data, for Acer rubrum, Cornus florida, Oxydendrum arboreum, Nyssa sylvestica and Sassafras albidum, there is a limited number of trees in the larger size classes (e.g. only 5% of the 610 Acer rubrum trees were larger than 30 cm DBH). This lack of data in the larger size classes likely influenced the parameter estimates associated with DBH and the resultant slope of the predicted probability of stem mortality curves (Fig. 5).

The probability of stem mortality for all 10 species examined was positively associated with CHAR. Maximum height of bole char (Regelbrugge and Smith 1994) and maximum bole char height as a percentage of total tree height have been successfully used to predict stem mortality of numerous broadleaved deciduous species including species common to the Mediterranean Basin (Catry et al. 2010), Populus tremuloides (Hély et al. 2003), Quercus kelloggii (Cocking et al. 2012), and various Appalachian hardwood species (Regelbrugge and Smith 1994). Although CHAR can be used to predict post-fire stem mortality, other fire effects, including duff consumption and bark char severity at the base of the bole (Kobziar et al. 2006), have been shown to significantly influence mortality of deciduous broad-leaved tree species. Similarly, morphological characteristics, including bark thickness at the base of the bole (Harmon 1984), measured total tree height (Hély et al. 2003), and live crown ratio or crown base height (Thies et al. 2006) can affect post-fire mortality, and, although time consuming to obtain, should be included in the standard set of measurements obtained during fire-related studies in eastern forests. Although a readily and easily obtained fire effect, CHAR is an oversimplification of fire intensity (Alexander and Cruz 2012) and related injury and does not, by itself, fully explain observed patterns of fire-related stem mortality. Instead fire-related stem mortality is more intricately linked with total heat output, which is a function of residence time or smouldering combustion in the duff layer (Wade 1993; Sackett et al. 1996), which is influenced, in part, by surface fuel loading, arrangement, and moisture content and fire weather parameters (e.g. wind speed, relative humidity, slope) (Burrows 2001; Dupuy et al. 2011). Consequently, in addition to bole char, direct (e.g. cambial kill) (Hood and Bentz 2007) and indirect measurements of cambial damage (e.g. bark char severity ratings, Hood et al. 2008; basal char, Keyser et al. 2006), proxy measurements related to root damage (e.g. ground char, Swezy and Agee 1991; duff consumption, O’Brien et al. 2010), surface fuel consumption, and fire weather conditions (e.g. Keech–Byram Drought Index, KBDI; Jenkins et al. 2011) have been found to be correlated with post-burn survival, and when coupled with char height and crown damage can often improve our understanding and, in some cases, predictability of fire-related stem mortality (Ganio and Progar 2017; Grayson et al. 2017).

The present study provides basic, yet valuable, quantitative evidence related to the effects of prescribed burning on stem mortality of upland deciduous broadleaved tree species and indirectly provides information related the use of prescribed fire to achieve ecological restoration goals and objectives across the Southern US. Information exists regarding the general susceptibility of the various deciduous broadleaved species to stem
Fig. 5. Predicted probability of stem mortality ($P(m)$) 2 years following prescribed fire as a function of diameter at breast height (DBH) (cm) and maximum bole char height (CHAR) (m) for *Acer rubrum*, *Cornus florida*, *Nyssa sylvatica*, *Oxydendrum arboreum*, *Quercus alba*, *Q. coccinea*, *Q. marilandica*, *Q. montana*, *Q. velutina* and *Sassafras albidum*. 

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mortality following prescribed burning (e.g. Hutchinson et al. 2005; Arthur et al. 2015). However, quantitative relationships that describe and link fire effects to stem mortality are, for the most part, lacking for upland tree species in the Southern US. Although direct comparisons among studies are difficult because of differences in the range of tree sizes and fire effects sampled, we did find consistency in the relationship between predicted probability of stem mortality, DBH and CHAR presented in this study and the limited available literature. For example, the steep drop in the probability of stem mortality of two pyrophobic species, Acer rubrum and Nyssa sylvatica, between 5 and 20 cm DBH at low to moderate levels of CHAR observed in our study is comparable to that reported by Regelbrugge and Smith (1994) (Fig. 5). Using the stem-mortality equations created by Regelbrugge and Smith (1994), a Quercus montana tree with DBH of 25.7 cm and CHAR of 0.3 m (median values observed in the present study) has a predicted probability of stem mortality equal to 0.7% compared with 0.8% using the stem mortality models created in the present study. However, as CHAR values increase, differences in the predicted probability of stem mortality become more pronounced, with the data originating after a single uncontrolled wildfire (Regelbrugge and Smith 1994) v: planned prescribed fires conducted across a broad geographic area being a factor that may, in part, explain the differential patterns of predicted stem mortality observed between the two studies.

The information presented in this study can be used, in a general sense, to inform prescribed burning prescriptions aimed at achieving specific goals and objectives. For example, in a Quercus regeneration context, where the goal of prescribed burns is to control the density of pyrophobic species below the upper canopy layer (Brose et al. 2008; Arthur et al. 2012), this study suggests stem mortality of pyrophobic species is most likely (i.e. >50% predicted probability of mortality) to occur in the smallest diameter classes (e.g. <15 cm DBH). Consequently, if the goal is to induce mortality of larger pyrophobic stems, mechanical thinning may be required as fire intensity needed to obtain stem-mortality inducing CHAR levels may exceed that which is generally permitted during normal prescribed burning prescriptions. Interestingly, we found a high susceptibility of Quercus marilandica to fire-related stem mortality at fairly large DBH values (<30 cm, Fig. 4) and only moderate levels of CHAR. This finding suggests that controlling the encroachment of Quercus marilandica (Johnson and Risser 1975) and restoration of open woodland and savanna conditions may be possible anytime during stand development as long as CHAR is sufficient (yet still within acceptable fire behaviour parameters) to cause stem mortality.

Interestingly, model goodness-of-fit, as indicated by ROC_{norm} for fire-tolerant, pyrophilic species was generally lower than that of fire-sensitive, pyrophobic species (Table 2). Although minimum sample size requirements for logistic regression, as determined by the number of dead trees (Hosmer et al. 2013), were met for all species examined, we suspect the lower proportion of dead v. live pyrophobic species (e.g. 6.9% for Quercus alba v. 31.8% for Nyssa sylvatica) affected model performance despite the fact that total sample size on an individual species basis was large (e.g. 830 total trees for Quercus montana). This suggests collection of more data, in particular increasing the sample size of dead or top-killed individuals, may be required to develop robust predictive post-fire stem mortality models for pyrophilic species.

Conclusion

The post-fire stem mortality models presented in this study used easily obtained tree and fire effects data, and should be considered a step towards the development of short- and long-term fire-related mortality models as related to prescribed burning for eastern tree species. The quantitative relationships presented are specific to the geographic areas and the abiotic and biotic conditions from which the data were obtained (Table S1). The data utilised in this study (sample size of dead trees, in particular) were insufficient to test whether factors that influence stem mortality varied across burn units, plots and geographic areas. This represents a substantial limitation of the current study. In the western US, Hood et al. (2010) found significant differences in predicted probability of mortality within a given species and across disparate wildfires. Documented variability among fire events and geographic areas emphasises the need for more intensive data collection efforts in existing and future prescribed burn studies in the Southern US for the purposes of assessing spatial and temporal variability associated with post-fire stem mortality. Therefore, the quantitative relationships presented in this study should not be extrapolated beyond the actual study sites. Although we recommend the relationships presented be externally validated with an independent dataset before being utilised for prescribed burn planning, including risk assessment, prescription development and long-term planning (Reinhardt and Dickinson 2010), the relationships presented here are likely more representative of mortality occurring in southern forests than those that currently exist in nationally supported fire effect models (e.g. Reinhardt 2003).

We emphasise the models we developed do not distinguish between true mortality (death of the main stem without subsequent sprouting) and topkill (i.e. death of main stem with subsequent sprouting). Future efforts should explore relationships between direct fire effects and mortality v. topkill (e.g. Catry et al. 2010), as all species examined are capable of producing root collar or stump sprouts following the death of the main stem. The models we developed examined the effects of tree attributes and fire effects on mortality 2 years post-fire. Evidence from western (Thies et al. 2006) and eastern (Yaussy and Waldrop 2008) forest ecosystems suggests stem mortality can extend through the fourth year post-fire. Lack of more detailed fire effects data and longer tree mortality data limited our ability to explore more complex relationships among delayed tree mortality and the myriad fire effects that result from, among many other factors, variations in fire behaviour (e.g. rate of spread, residence time) and fire intensity, season of burn (Fettig et al. 2010), and fuelbed conditions (German et al. 2004; Van et al. 2007). Climate and associated interactions with fire effects are additional stressors complicating our understanding and the predictability of stem mortality following both wildfire and prescribed fire (van Mantgem et al. 2013). Additional data related to longer-term post-fire mortality, severity of fire effects, and direct measures of fire intensity and behaviour from the range of forest types and resultant
species compositions, edaphoclimatic conditions, and prescribed burning goals and objectives should be collected in efforts to improve upon or expand the knowledge related to post-fire stem mortality following prescribed burning in the Southern US.

Conflicts of interest
The authors declare that they have no conflicts of interest.

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References
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