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Resprouting by seedlings of four North American deciduous broadleaved tree species following experimental burning

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Abstract

In eastern North American *Quercus* forests, the historic fire regime, characterized by periodic, low-intensity surface fire, facilitated the development and maintenance of mid-successional *Quercus* forests across multiple spatial and temporal scales. One physiological mechanism favoring *Quercus* over mesophytic and/or shade-tolerant deciduous broadleaved species is prolific and vigorous resprouting following topkill. Generalizations regarding interspecific differences in fire-induced resprouting are confounded by interactions between biotic and abiotic factors. The goal of this study was to quantify resprout dynamics by 2- and 3-year-old seedlings of four prominent deciduous broadleaved species (*Acer rubrum*, *Liriodendron tulipifera*, *Quercus alba*, and *Q. rubra*) following topkill via experimental burning, where seedling age, competition, fire intensity, and light were controlled. Resprouting was independent of fire intensity and seedling size. The resprout rate of *Q. rubra* (82%) was greater than that of *A. rubrum* (53%), *L. tulipifera* (56%), and *Q. alba* (52%). A second burn conducted a year later did little to inhibit resprouting by topkilled individuals. After both burns, *L. tulipifera* sprouts were significantly taller than the other species. Although absolute height of *Q. rubra* sprouts was greater than *A. rubrum* after the first burn, absolute height of *Q. rubra* sprouts was lower than *A. rubrum* following the second burn. Results suggest that broad, cross-genus generalizations may not accurately reflect interspecific differences in resprout potential, which may have implications related to the ability to regenerate and recruit *Quercus* under a re-introduced periodic fire regime.

Keywords *Quercus* · Vegetative reproduction · Prescribed fire · Restoration

Introduction

Vegetative reproduction via the stimulation of the bud bank (i.e., resprouting) following complete or partial removal of aboveground biomass is an important source of regeneration in fire-prone forests across the globe (Clarke et al. 2013; Pausas and Keeley 2014; Poulos et al. 2018). In both eastern and western North American *Quercus* forests, angiosperms and some gymnosperms are capable of resprouting in response to disturbance, including fire-induced topkill. Across North America, most species capable of resprouting due so from aerial and basal bud banks; a few (*Fagus grandifolia*, *Sassafras albidum*, *Cercis canadensis, Liquidambar styraciflua*, *Robinia pseudoacacia*, *Populus* spp.) are also capable of resprouting from underground buds (Clarke et al. 2013). Although resprouting can lead to long-term in situ persistence (Bond and Midley 2001; Zywiec and Holeska 2012), interspecific differences in the propensity to resprout and corresponding resprout survival and growth determine the relative contribution of resprouting individuals to postdisturbance forest structure and composition (Dietze and Clark 2008; Keyser and Zarnoch 2014; Keyser and Loftis 2015).

In eastern North American *Quercus* forests, periodic fire, driven in part by anthropogenic ignitions (Guyette et al. 2002, 2006), interacted with other disturbance agents (e.g., drought and herbivory) to promote and maintain forest types dominated by mid-successional *Quercus* species

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across multiple spatial and temporal scales (Delcourt et al. 1998; McEwan et al. 2011; Frelich et al. 2017). The fire-*Quercus* hypothesis postulates that *Quercus*' superior ability to resprout following fire-induced topkill was an important factor that favored the survival, growth, and recruitment of *Quercus* over other mesophytic species (*Acer rubrum*, *Acer saccharum*, *Liriodendron tulipifera*, and *F. grandifolia*) under the historic fire regime (Brose et al. 2013).

Contemporary land-use changes coupled with reduced ignitions and fire suppression efforts have greatly reduced fire occurrence across landscapes dominated by *Quercus* species. This, coupled with a long-term increase in moisture availability (Pederson et al. 2013) has, in part, led to the "mesophication" of contemporary eastern *Quercus* forests (Nowacki and Abrams 2008). Today, *Quercus* remains a canopy dominant. However, relative to historic (i.e., pre-European settlement) conditions, forest density is greater and understory light availability is lower (Hanberry et al. 2014). These conditions have, over time, facilitated the establishment and development of mesic, shade-tolerant species in the subcanopy and regeneration strata (Lorimer 1984; Nowacki and Abrams 2008; Fei et al. 2011), which is directly linked to widespread *Quercus* regeneration and recruitment failure across eastern North American *Quercus* forests (Dey 2014). The reintroduction of fire into *Quercus*-dominated systems may slow or reverse the mesophication process by altering the proportion of *Quercus* versus mesophytes in the woody regeneration layer and, over time, create light conditions conducive to the eventual overstory recruitment of *Quercus* species (Hutchinson et al. 2012; Arthur et al. 2012).

The superior resprouting of *Quercus* relative to non-*Quercus* competitors is one of the cornerstones of the fire-*Quercus* hypothesis (Brose et al. 2001). Interspecific differences in the ability to resprout following topkill are driven by differences in seedling morphology, functional traits, and growth strategies (Bond and Midley 2001; Clarke et al. 2013). *Quercus* species possess a conservative growth strategy (i.e., high root:shoot) (Villar-Salvador et al. 2015) that supports rapid resprouting and growth following topkill (Sander 1971). In addition, *Quercus* species exhibit hypogeal germination (Menes and Mohammed 1995) which results in the basal bud bank being located below the soil surface where buds are protected from fire (Clarke et al. 2013). In contrast, mesophytic competitor species, including *A. rubrum* and *L. tulipifera*, preferentially allocate biomass above-rather than belowground (i.e., low root:shoot) (Barnes and Van Lear 1998; Villar-Salvador et al. 2015). Unlike *Quercus*, mesophytic competitors display epigeal germination (Menes and Mohammed 1995), which results in the basal bud bank being located above the soil surface, where it may be susceptible to damage and mortality during fire (Brose et al. 2013). This, coupled with small carbohydrate reserves could negatively affect resprout production and growth (Cruz et al. 2003a) following fire-induced topkill, thus conferring an advantage to *Quercus* species.

In eastern North American forests, interspecific differences in postfire resprout dynamics have implications for sustaining *Quercus* under a re-introduced fire regime (e.g., Alexander et al. 2008). As efforts to incorporate prescribed fire into land resource management plans expand across eastern North America, with the intent to promote *Quercus* regeneration and recruitment, it is increasingly necessary to understand the intricacies related to postfire regenerative strategies of both *Quercus* and non-*Quercus* competitors. Broad generalizations regarding interspecific differences in fire-induced resprouting (e.g., Abrams 1992; Brose et al. 2013) are confounded by interactions between myriad biotic and abiotic factors, including seedling morphology, fire intensity, as well as the light and competitive environment prior to, and after fire (Canadell et al. 1991; Lloret and López-Soria 1993; O'Hara and Berrille 2010; Keyser and Zarnoch 2014).

The goal of this study was to examine and quantify seedling-resprout dynamics in relation to topkill conducted via experimental burning of four deciduous broadleaved species common to *Quercus*-dominated forests in eastern North America under controlled burning and postburn growing conditions—*A. rubrum*, *L. tulipifera*, *Q. alba*, and *Q. rubra*. *A. rubrum* and *L. tulipifera* were selected, because they are strong competitors and often interfere with *Quercus* during the regeneration process. *Q. alba* and *Q. rubra* were selected, because these two species are widely distributed across eastern North America, with *Q. alba* representative of the white *Quercus* group (*Leucobalanus*) and *Q. rubra* representative of the red *Quercus* group (*Erythrobalanus*). Specific questions addressed were: (1) does topkill via experimental burning differentially affect the ability to resprout within and among species? (2) Are there intra- and interspecific differences in postburn resprout growth and dynamics? (3) What abiotic and biotic factors influence postburn resprout growth and dynamics?

Methods

Study site and experimental design

This study was conducted on the Bent Creek Experimental Forest Administrative Site in Asheville, NC, USA (35.5°N, 82.6°W, elevation 2100 m). The study area lies within the southern region of the Blue Ridge physiographic province of the Appalachian Mountains range. Annual precipitation is evenly distributed throughout the year and averages 1200 mm annually. Winters are cool, with daily January temperatures averaging 2.3 °C, and summers are warm, with daily July temperatures averaging 22.3 °C.

In March 2015, 36 bareroot (1–0 stock) *Quercus alba* L., *Quercus rubra* L., *Acer rubrum* L., and *Liriodendron tulipifera* L. seedlings were planted using a KBC bar in outdoor raised beds at a spacing of 0.75 m. Planting slits were large enough so the roots were not bent (i.e., J-shaped). Care was taken to ensure that the root collar of all planted seedlings was located slightly below groundline when the planting slit was closed. The location of root collar at the time of planting is of particular importance, as root collar location (below, at, or above groundline) can influence whether a seedling-resprouts postfire (Brose and Van Lear 2004). The nursery stock had not been root sheared nor had the roots of the seedlings been trimmed. Root length, prior to planting, averaged (standard deviation) 0.19 (0.03), 0.28 (0.05), 0.26 (0.04), and 0.29 (0.03) cm for *A. rubrum*, *L tulipifera*, *Q. alba*, and *Q. rubra*, respectively. Planting beds, which were 1.6 m × 18.8 m, were located in open sky conditions, and received unobstructed sunlight (i.e., no shading from forest canopy adjacent to the beds) daily between 0900 and 1700 h. Planting stock was obtained from nearby state forest nurseries in Virginia (*A. rubrum*) and Tennessee (*Q. alba*, *Q. rubra*, and *L. tulipifera*). Planting beds were comprised of similar soil medium (combination of existing soil material and a layer of newly added topsoil) and were exposed to similar environmental conditions (e.g., sunlight, temperature, and precipitation). Prior to planting, beds were tilled using a commercial rototiller to a depth of ~ 0.75 m to facilitate planting and to ensure that there was an even distribution of soil medium within rooting depth. For the first 2 months, seedlings were watered weekly using a soaker hose, after which artificial watering was eliminated. Planting beds were manually weeded bi-monthly throughout the length of the study.

In addition to the 36 planted seedlings, 20 *Q. alba*, *Q. rubra*, *A. rubrum*, and *L. tulipifera* were destructively sampled in March 2015 (at the time of planting) to obtain information on patterns of above- and belowground biomass allocation. The seedlings selected for destructive sampling were randomly selected from the nursery stock. Root collar diameter (mm, average of two perpendicular measurements) was measured directly above the point of basal swelling. Seedlings were severed at root collar and categorized into either aboveground (foliage, stems, and branches) or belowground (roots) biomass. Belowground biomass was washed to remove residual soil material. Above- and belowground portions were oven dried at 60 °C for 1 week and weighed (0.01 g).

Experimental burns were conducted in June 2016 and again in June 2017. Although June is outside the period of time most prescribed burns are conducted in the region, this time period (i.e., primary part of the growing season) has been shown to significantly affect resprout dynamics for the species examined to a greater extent than burning during the dormant season (Brose and Van Lear 1998). Prior to burning in both 2016 and 2017, groundline diameter (mm, average of two perpendicular measurements) and height (m) of the seedlings were measured on all live individuals. Experimental burns were implemented using a propane vapor torch on individual seedlings, making the individual seedlings the experimental unit. Prior to burning, the soil surrounding each seedling was cleared of leaf litter and woody fuels to avoid the potentially confounding effects fuel load may have on resprouting. Each seedling was surrounded by a three-sided stainless-steel shield to reduce the likelihood that burning treatments would affect surrounding seedlings (see ESM Fig. S1). Seedlings were burned using the propane torch for a total of 4 min. Two minutes into the start of the burn, the metal shield was turned 180° and the opposite side of the seedling was burned to ensure complete girdling of the stem. Heat from the propane torch was concentrated on the lower 5 cm of a seedling's stem.

Temperature during each burn was recorded using a HOBO® Type-K Thermocouple datalogger and a Type-K Thermocouple probe manipulated to encircle the lower 10 cm of the seedling's main stem (Onset Computer Corporation, Cape Cod, MA, USA). Dataloggers were programmed to record temperature every second during the 4-min experimental burn. The Type-K Thermocouple used measures heat only at the tip of the probe. Because the tip of the thermocouple probe was approximately 10 cm from groundline and the flame/heat form the propane torch was focused on the lower 5 cm of a seedling's stem, the temperatures recorded and reported likely underestimate the temperature experienced at the base of the stem. Nonetheless, this temperature measurement provides a measure of fire intensity that was consistently measured across all experimental burns.

Resprout density (i.e., total number of the new shoots originating from the base of each topkilled stem) and height of the dominant (i.e., tallest) resprout were recorded every 2 weeks following each of the two burns through the end of the growing season (by the second week in October), for a total of eight, 2-week measurement intervals in both 2016 and 2017. Between June and October 2016 and June and October 2017, daily temperature averaged 20.8 and 18.9 °C, respectively. Precipitation between the same months in 2016 and 2017 totaled 339 and 556 mm, respectively.

Data analysis

Linear regression (PROC GLM) was used to develop allometric relationships that quantified the species-specific relationship between root collar diameter and both above- and belowground biomass ($\alpha = 0.05$) of destructively sampled seedlings at the time of planting. R^2 values were used to assess model goodness of fit. Above and belowground biomass data were square-root transformed to improve linearity and heteroscedasticity of residuals.

Differences among species in groundline diameter and height immediately prior to each burn and the average temperature of each 4-min experimental burn were assessed using a one-way analysis of variance. When overall F tests were significant, post hoc tests to analyze differences in least squares means were conducted using the Benjamini and Hockberg (1995) false discovery rate (FDR; $\alpha = 0.05$).

For each burn, a general linear model was used to quantify how resprout density, height of the dominant resprout, and height loss (preburn height—postburn height) at each 2-week measurement interval postburn varied among species and over time. In these models, time (weeks postburn), species, and time*species were fixed effects, with time being the repeated factor. Significant interactions were examined using the SLICE option in PROC MIXED (SAS v. 9.4). Following significant F tests, or partitioned F tests in the case of interactions, post hoc tests to assess differences in least squares means were conducted using the FDR ($\alpha = 0.05$). Pearson correlation coefficients ($\alpha = 0.05$) were used to assess the strength and direction of the relationships between measures of seedling/resprout size prior to burning (groundline diameter and height) and resprout density, dominant resprout height, and height loss at the end of the growing season following the first and second experimental burns.

Five a priori hypotheses (i.e., models) that described the potential effects of species, average temperature during the 4-min experimental burn, height of the dominant stem immediately prior to burn, and groundline diameter immediately prior to burn on resprout production of topkilled individuals (Table S1 of ESM) were developed. Because resprouting is binary (resprouts present/resprouts not present), a generalized linear model (PROC GLIMMIX) was used to model the probability of a resprouting:

$$P(s) = 1/\left(1 + \exp\left(\beta_0 + \beta_1 X_1 + \beta_2 X_2 + \cdots + \beta_n X_n\right)\right) + \varepsilon,$$

where P(s) was the probability of a resprout being present on a topkilled stem at the end of the growing season, β_1 through β_n were regression coefficients, X_1 though X_n, were explanatory variables, and ε was the residual error term. Because only individuals that were alive in June 2017 received a second burn treatment, probability of resprouting models were developed separately for the first and second burns. When appropriate, comparison of odds ratios between species combinations was conducted, with a confidence interval containing one indicating no significant differences between species.

For model hypothesis testing, Akaike's information criterion (AIC) was utilized to determine which models most parsimoniously fit the data. Among candidate models, the best had the lowest AIC, with competing models considered similar in quality when ΔAIC between any two models was < 2.0 (Burnham and Anderson 2002). Akaike weights were calculated to provide further information regarding the strength of evidence for each model.

Results

Biomass allocation patterns

At the time of planting, belowground biomass was accurately predicted by species and root collar diameter ($R^2 = 0.91$), which was positively related to belowground biomass (Fig. 1). Contrasts among species revealed that for a given root collar diameter, belowground biomass was significantly greater in *Q. alba* and *Q. rubra* than either *A. rubrum* or *L. tulipifera*. No difference in belowground biomass (at a given

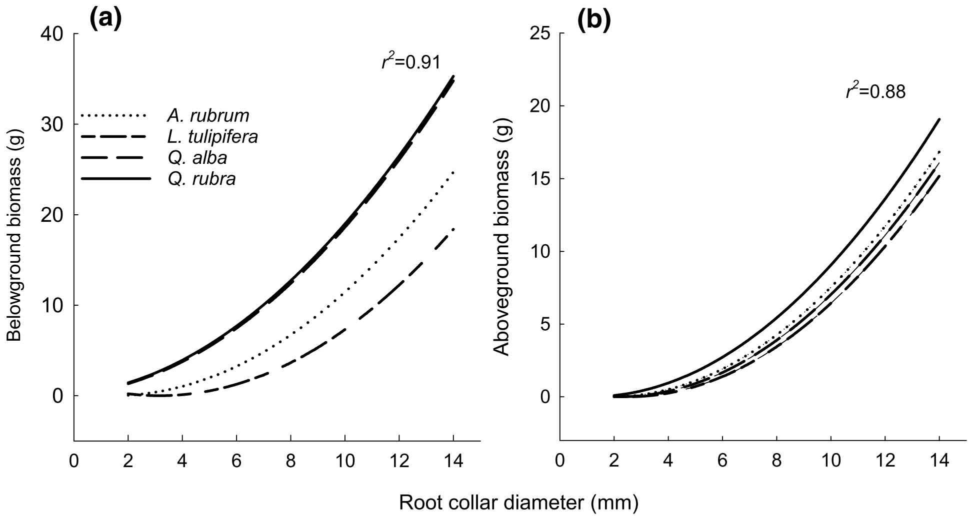

Fig. 1 Relationship between groundline diameter (mm) and **a** predicted belowground biomass (back transformed) and **b** predicted aboveground (back transformed) biomass of destructively sampled seedlings at the time of planting for four species. Goodness of fit, as quantified by r^2 values, are 0.91 and 0.88 for **a** belowground and **b** aboveground biomass, respectively

root collar diameter) was observed between *Q. alba* and *Q. rubra*. Root collar diameter and species were significant predictors of aboveground biomass of seedlings at the time of planting ($R^2 = 0.88$). As root collar diameter increased, aboveground biomass increased for all species. The only significant difference in aboveground biomass between species occurred for *L. tulipifera* and *Q. rubra*, with *Q. rubra* possessing greater aboveground biomass at the time of planting than *L. tulipifera* across the range of root collar diameters.

First experimental burn

Mortality between the time of planting and the first burn in addition to datalogger malfunction during the burn reduced total sample size to 34, 34, 29, and 34 individuals for *A. rubrum*, *L. tulipifera*, *Q. alba*, and *Q. rubra*, respectively. Immediately prior to the first burn, height varied between 0.32 m and 2.78 m (Fig. 2). Mean height at the time of the first burn was lowest for *Q. alba* and greatest for *L. tulipifera*. Across species, groundline diameter immediately prior

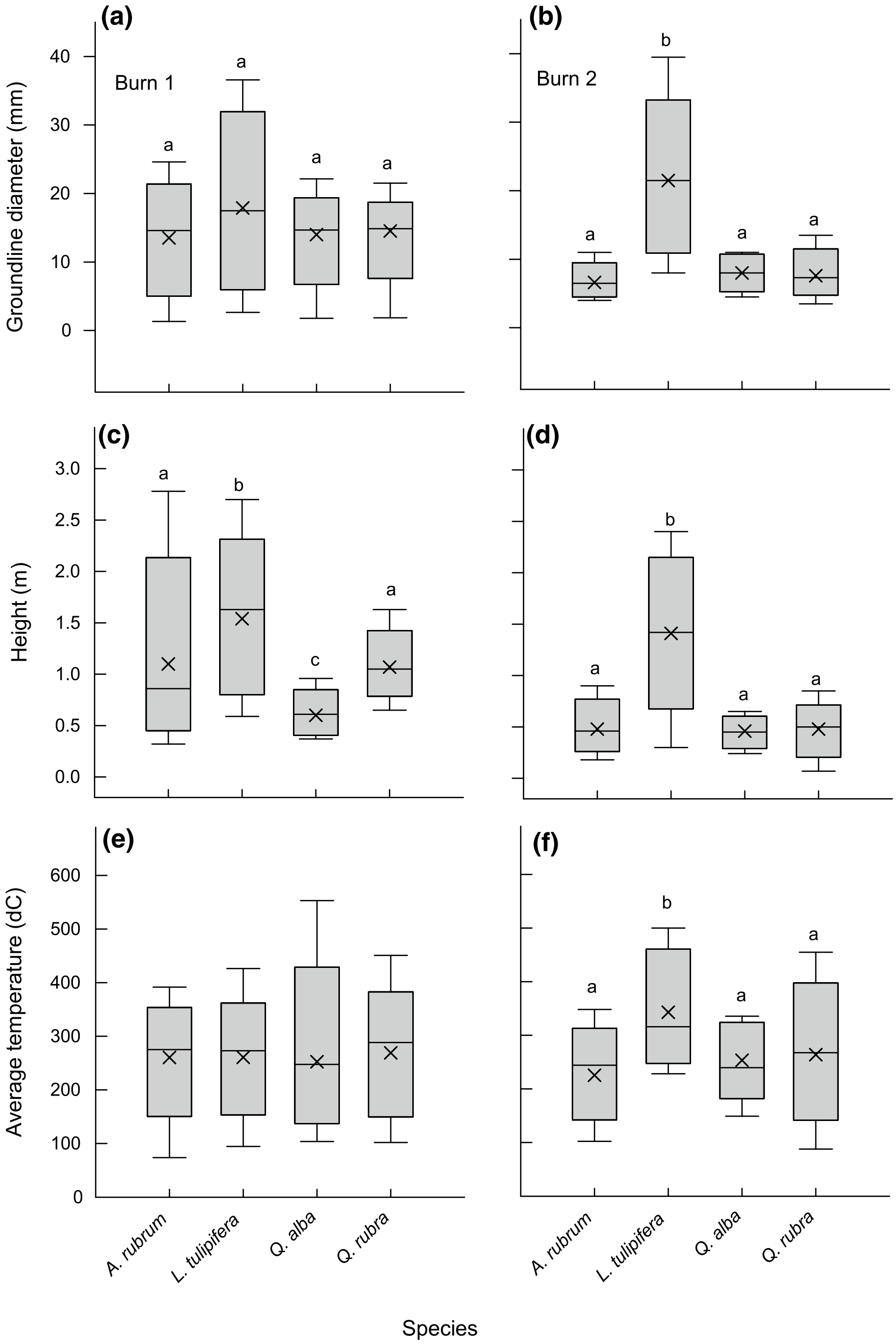

Fig. 2 Box plot displaying range of seedling/resprout characteristics immediately prior to the first and second experimental burns, including **a**, **b** groundline diameter (mm); **c**, **d** height (m), and **e**, **f** average temperature (°C) measured during each 4-min experimental burn. Values represent the minimum, lower quartile, median, upper quartile, and maximum. Letters indicate significant differences in mean values (denoted by '×') among species using a false discovery rate $\alpha = 0.05$

to the first burn averaged 15.0 mm and, after corrections to post hoc multiple comparisons, was found to not differ significantly among the four species. Average temperature recorded during the 4-min experimental burns was 264.6 °C and did significantly differ among the species. Regardless of species, all individuals were topkilled after the first experimental burn. Visual confirmation of topkill (deadening of stems and complete loss of foliage) was observed within 1-week postburn.

The probability of resprouting model that most parsimoniously fit the data was model 2, which contained only the covariate associated with species (Table S1 of ESM). Given the data, this model had a 67% probability of being the best among those considered in this study. The probability of a living resprout existing at the end of the growing season following the first burn was 53, 56, 52, and 82% for *A. rubrum*, *L. tulipifera*, *Q. alba*, and *Q. rubra*, respectively. Probability of resprouting was greater for *Q. rubra* than *A. rubrum*, *L. tulipifera*, and *Q. alba* (Fig. 3).

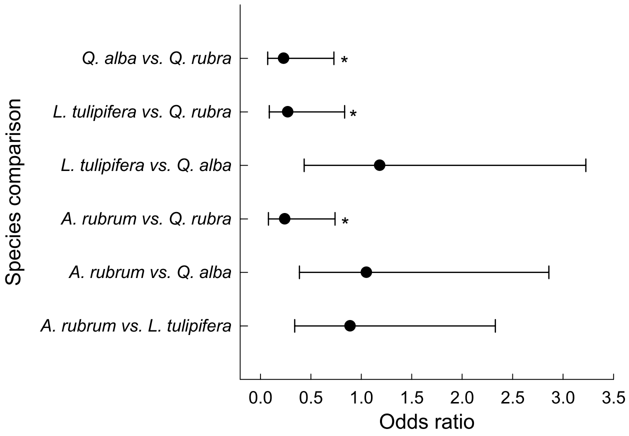

Fig. 3 Odds ratios comparing the odds of a resprout being present between each possible species comparison at the end of the growing season (i.e., eighth, 2-week measurement inventory) following the first experimental burn. Error bars represent 95% confidence interval surrounding the odds ratio. Asterisk indicates a significant difference in odds ratios between species

No significant effects of species or time on resprout density over the course of the growing season were detected. Height of the dominant resprout over the course of the growing season was significantly affected by species ($p < 0.0001$), time ($p < 0.0001$), and the interaction between species and time ($p < 0.0001$). Partitioned *F* tests revealed significant differences in dominant resprout height among species occurred during all 16-week postburn (Fig. 4). By the sixth week postburn, *L. tulipifera* resprouts were consistently taller than *A. rubrum*, *Q. alba*, and *Q. rubra* resprouts. By the end of the growing season (16-week postburn), dominant resprout height of *A. rubrum*, *L. tulipifera*, *Q. alba*, and *Q. rubra* averaged 0.24, 0.87, 0.32, and 0.33 m, respectively, with no significant differences detected between the two *Quercus* species or between *A. rubrum* and *Q. alba*.

Height loss (preburn height − postburn height) was significantly affected by species ($p < 0.0001$) and time ($p = 0.0112$), but no significant interaction between species and time was detected. Across the 16-week postburn, *L. tulipifera* and *A. rubrum* lost an average of 0.91 m in height, while *Q. alba* lost an average of only 0.31 m (Table 2). Across species, the change in height was greatest during the first 8 weeks, after which time height loss stabilized.

Preburn groundline diameter and/or preburn height was significantly and positively correlated with resprout density and/or dominant resprout height for *A. rubrum*, *L. tulipifera*, and *Q. rubra* (Table 3). For all species, there was positive correlation between preburn size (groundline diameter or height) and height loss. Significant relationships between attributes of resprout vigor and average temperature during

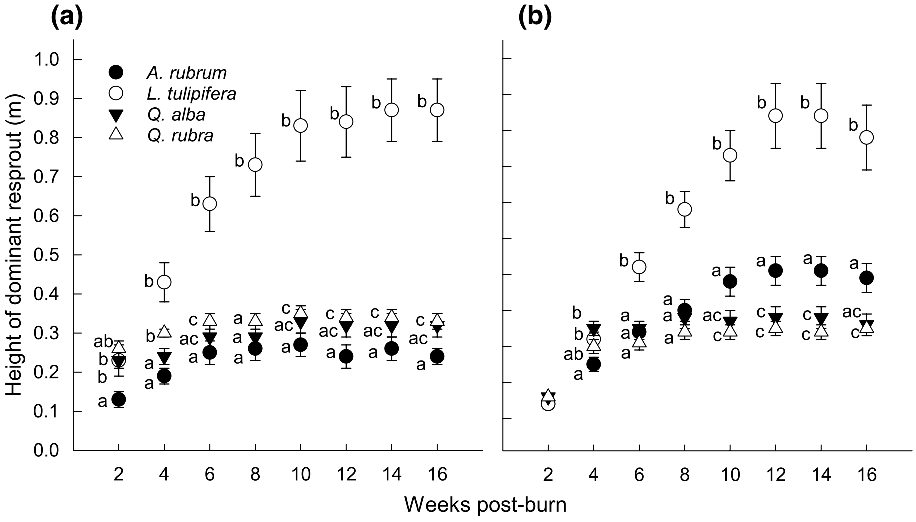

Fig. 4 Dominant resprout height (m) over the course of the growing season following **a** first and **b** second experimental burn for four species. Values and error bars represent the mean and standard error, respectively. Means followed by the same lowercase letter are not significantly different within a given week postfire using a false discovery rate $\alpha = 0.05$

the burn were limited to *Q. alba* and *Q. rubra*, where temperature was negatively associated with dominant resprout height for *Q. alba* and negatively related to height loss for *Q. rubra*.

Second experimental burn

Sample size for the 2017 burn was 19, 20, 15, and 26 for *A. rubrum*, *L. tulipifera*, *Q. alba*, and *Q. rubra*, respectively. Average seedling height and groundline diameter immediately prior to the second experimental burn differed among species, with *L. tulipifera* significantly taller and possessing larger groundline diameters than *A. rubrum*, *Q. alba*, and *Q. rubra* (Fig. 2). Average temperature recorded during the 4-min experimental burns also varied among species, with temperature experienced by *L. tulipifera* significantly greater than *A. rubrum*, *Q. alba*, and *Q. rubra*. Regardless of species, all individuals were topkilled after the second experimental burn. Visual confirmation of topkill was observed within 1-week postburn.

Because not all the response levels of resprouting (present/absent) were observed in each of the predictor variables, testing of hypotheses related to the probability of resprouting following the second experimental burn was not possible (i.e., quasi-separation of the data). Overall, 89, 80, 100, and 92% of topkilled *A. rubrum*, *L. tulipifera*, *Q. alba*, and *Q. rubra* seedlings, respectively, possessed a living resprout at the end of the growing season following the second burn.

Resprout density over the course of the growing season was significantly affected by species ($p = 0.0090$) and time ($p = 0.0001$). At the end of the growing season, resprout density was lowest for *Q. rubra*, with no differences in resprout density observed among *A. rubrum*, *L. tulipifera*, and *Q. alba* (Table 1). Throughout the growing season, resprout density varied between 2.9 resprouts per topkilled seedling 2-week postburn to 3.9 resprouts per topkilled seedling 16-week postburn.

Height of the dominant resprout of topkilled seedlings over the course of the growing season was significantly affected by species ($p < 0.0001$), time ($p < 0.0001$), and the interaction between species and time ($p < 0.0001$). Partitioned *F* tests revealed significant differences in dominant resprout height among species were present between 4- and 16-week postburn (Fig. 4). By 6-week postburn, *L. tulipifera* resprouts were significantly taller than *A. rubrum*, *Q. alba*, and *Q. rubra* resprouts. At week 10, differences in dominant resprout height between *A. rubrum* and *Q. rubra* were observed, with resprouts of *A. rubrum* significantly taller than *Q. rubra*; a trend that persisted through the 16th week postburn.

Height loss (preburn—postburn) was significantly affected by species ($p < 0.0001$) and time ($p < 0.0001$), and a significant interaction between species and time was also detected ($p = 0.0174$). Significant differences in height loss among species were observed throughout the growing season (Table 2). At the end of the growing season, *A. rubrum* and *Q. alba* lost an average 0.15 m in height, while *L. tulipifera* lost 0.69 m in height.

Average temperature during the second experimental burn was not significantly correlated with resprout density or dominant resprout height at the end of the growing season (Table 3). However, groundline diameter immediately prior to the second

Table 1 Resprout density (no. resprouts stem^{-1}) of four species following the first and second experimental burn

	Weeks following first experimental burn								
	2	4	6	8	10	12	14	16	Average
Species									
A. rubrum	3.5 (0.5)	4.1 (0.6)	3.9 (0.5)	4.1 (0.5)	3.7 (0.6)	3.7 (0.5)	3.9 (0.5)	3.8 (0.5)	3.8 (0.2)
L. tulipifera	3.6 (0.5)	3.5 (0.5)	3.8 (0.5)	3.8 (0.6)	3.5 (0.5)	3.0 (0.4)	3.4 (0.5)	2.9 (0.4)	3.4 (0.2)
Q. alba	3.4 (0.5)	3.6 (0.5)	3.5 (0.5)	3.4 (0.5)	3.5 (0.5)	3.5 (0.5)	3.4 (0.5)	3.5 (0.5)	3.5 (0.2)
Q. rubra	2.5 (0.2)	2.7 (0.2)	2.7 (0.2)	2.7 (0.2)	2.8 (0.2)	2.6 (0.2)	2.6 (0.2)	2.6 (0.2)	2.7 (0.1)
Average	3.2 (0.2)	3.4 (0.2)	3.4 (0.2)	3.4 (0.2)	3.3 (0.2)	3.1 (0.2)	3.3 (0.2)	3.1 (0.2)	
	Weeks following second experimental burn								
	2	4	6	8	10	12	14	16	Average
Species									
A. rubrum	4.6 (0.6)	4.0 (0.5)	4.3 (0.5)	4.4 (0.5)	4.3 (0.5)	4.3 (0.5)	3.8 (0.4)	4.3 (0.6)	4.2 (0.2)^{A}
L. tulipifera	3.1 (0.4)	4.5 (0.5)	4.4 (0.5)	5.1 (0.7)	5.2 (0.7)	4.6 (0.6)	4.6 (0.6)	5.2 (0.7)	4.6 (0.2)^{A}
Q. alba	2.1 (0.4)	3.2 (0.5)	3.5 (0.4)	3.9 (0.5)	3.7 (0.5)	3.5 (0.4)	3.5 (0.4)	3.6 (0.4)	3.4 (0.2)^{AB}
Q. rubra	2.1 (0.3)	2.8 (0.3)	2.9 (0.3)	2.9 (0.3)	2.9 (0.3)	2.8 (0.3)	2.8 (0.3)	2.8 (0.3)	2.8 (0.1)^{B}
Average	2.9 (0.3)	3.6 (0.2)	3.7 (0.2)	3.9 (0.3)	3.9 (0.3)	3.7 (0.2)	3.5 (0.2)	3.9 (0.3)	

Values represent the mean (one standard error). Uppercase letters indicate significant differences among species at a false discovery rate $\alpha = 0.05$

Table 2 Height loss (preburn height − postburn height) (m) of four species following the first and second experimental burns

	Weeks following first experimental burn								
	2	4	6	8	10	12	14	16	Average
Species									
A. rubrum	1.07 (0.18)	1.01 (0.16)	0.96 (0.15)	0.95 (0.16)	0.95 (0.16)	0.95 (0.16)	0.95 (0.16)	0.98 (0.15)	0.97^{A} (0.06)
L. tulipifera	1.36 (0.12)	1.14 (0.12)	0.89 (0.11)	0.80 (0.10)	0.80 (0.10)	0.70 (0.09)	0.69 (0.09)	0.68 (0.10)	0.85^{A} (0.04)
Q. alba	0.37 (0.04)	0.37 (0.04)	0.33 (0.06)	0.33 (0.06)	0.27 (0.04)	0.28 (0.05)	0.28 (0.04)	0.28 (0.04)	0.31^{B} (0.02)
Q. rubra	0.79 (0.04)	0.76 (0.03)	0.72 (0.03)	0.72 (0.03)	0.71 (0.03)	0.72 (0.03)	0.72 (0.03)	0.73 (0.03)	0.73^{C} (0.01)
Average	0.88 (0.06)	0.83 (0.06)	0.74 (0.05)	0.71 (0.05)	0.68 (0.05)	0.67 (0.05)	0.68 (0.05)	0.69 (0.05)	
	Weeks following second experimental burn								
	2	4	6	8	10	12	14	16	Average
Species									
A. rubrum	0.45^{A} (0.04)	0.36^{C} (0.05)	0.28^{A} (0.04)	0.21^{A} (0.04)	0.12^{A} (0.04)	0.08^{A} (0.04)	0.09^{A} (0.04)	0.11^{A} (0.04)	0.20 (0.02)
L. tulipifera	1.34^{B} (0.16)	1.18^{A} (0.13)	0.98^{B} (0.11)	0.89^{B} (0.10)	0.73^{B} (0.08)	0.63^{B} (0.07)	0.63^{B} (0.06)	0.69^{B} (0.07)	0.88 (0.04)
Q. alba	0.39^{A} (0.03)	0.21^{B} (0.03)	0.23^{A} (0.04)	0.18^{A} (0.04)	0.19^{AC} (0.04)	0.18^{AC} (0.04)	0.18^{AC} (0.04)	0.19^{AC} (0.04)	0.21 (0.01)
Q. rubra	0.44^{A} (0.04)	0.29^{BC} (0.04)	0.28^{A} (0.04)	0.25^{A} (0.04)	0.24^{C} (0.04)	0.23^{C} (0.04)	0.24^{C} (0.04)	0.25^{C} (0.04)	0.27 (0.01)
Average	0.66 (0.07)	0.51 (0.06)	0.44 (0.05)	0.37 (0.04)	0.31 (0.04)	0.27 (0.03)	0.28 (0.03)	0.30 (0.03)	

Values represent the mean (one standard error). Uppercase letters indicate significant differences among species at a false discovery rate $\alpha = 0.05$

Table 3 Pearson correlations coefficients between resprout vigor characteristics [resprout density (no. sprouts stem^{-1})] (DEN), height (m) of dominant resprout (DOMHGT), and height loss (preburn height − postburn height) (HGTL) one growing season after the first and second experimental burn and average temperature (°C) during each experimental burn (TEMP), groundline diameter (mm) immediately prior to burn (PREGLD), and height (m) (PREHGT) immediately prior to burn

	First experimental burn			Second experimental burn		
	TEMP	PREGLD	PREHGT	TEMP	PREGLD	PREHGT
A. rubrum						
DEN	0.106	**0.551**	**0.554**	0.287	0.113	0.01
DOMHGT	0.354	**0.518**	0.326	−0.379	0.467	**0.55**
HGTL	0.259	**0.775**	**0.991**	**0.496**	0.391	0.482
L. tulipifera						
DEN	−0.153	−0.086	0.321	−0.105	0.217	0.441
DOMHGT	0.009	0.133	**0.649**	0.094	**0.742**	**0.859**
HGTL	0.408	0.23	**0.74**	0.193	**0.703**	**0.8**
Q. alba						
DEN	−0.348	0.27	−0.053	0.223	0.279	0.287
DOMHGT	**−0.574**	0.378	0.218	−0.194	0.226	0.249
HGTL	0.424	0.134	**0.757**	0.072	**0.582**	**0.635**
Q. rubra						
DEN	−0.227	0.223	0.276	− 0.132	0.389	0.152
DOMHGT	0.14	0.294	**0.438**	0.341	0.117	0.062
HGTL	**−0.392**	0.07	**0.838**	−0.115	0.398	**0.861**

Significant correlations ($p < 0.05$) are bold

burn was positively correlated with dominant resprout height for *L. tulipifera,* while preburn height was positively correlated with dominant resprout height at the end of the growing season for both *A. rubrum* and *L. tulipifera*. For *A. rubrum*, average temperature during the second experimental burn was significantly and positively associated with height loss at the end of the growing season postburn. For *L. tulipifera*, *Q. alba*, and *Q. rubra*, preburn size (groundline diameter and/or height) prior to burning was significantly and positively correlated with height loss one growing season after the second burn, with the strongest associations detected for *L. tulipifera* and *Q. rubra*.

Discussion

One of the main tenets of the fire and *Quercus* hypothesis relates to the superior resprouting ability of *Quercus* versus mesophytic competitors, particularly under a periodic fire regime (Brose et al. 2001). Although a variety of studies (Brose and Van Lear 1998; Brose 2010), meta-analyses (Brose et al. 2013), and syntheses (Brose et al. 2014; Brose 2014) provide evidence that seedlings of eastern North American *Quercus* species display more frequent and vigorous resprouting than competitor species, results are highly variable. Inconsistency among studies (Brose et al. 2013) regarding interspecific differences in resprout dynamics suggests that there are extraneous factors within and among studies (e.g., seedling age/size, resource availability, fire intensity, etc.) that may influence resprouting and resprout vigor following fire. These inconsistencies limit the further refinement of the role of fire in these ecosystems. This study appears to be the only study specifically designed to assess seedling-resprout dynamics following multiple burns under controlled conditions for select eastern North American forest tree species.

In this study, the probability of resprouting after the first experimental burn varied among species, but was unrelated to fire intensity or size at the time of the burn. One growing season postburn, the resprout rate of *Q. rubra* (82%) was significantly greater than *A. rubrum* (53%), *L. tulipifera* (56%), and *Q. alba* (52%). The significantly greater resprout rate of *Q. rubra* supports the notion that a well-developed root system facilitates resprouting following topkill (Larsen and Johnson 1998; Brose et al. 2013). However, the comparatively low resprout rate of *Q. alba* was surprising given that, for a stem of similar size, it possessed relatively greater belowground root biomass than *A. rubrum* and *L. tulipifera*. Although a statistical comparison among species was not possible due to quasi-separation of data, between 80 and 100% of the stems burned a second time resprouted, suggesting that repeated burning may do little to alter resprouting potential of these four species.

The results specific to the probability of resprouting concur with Alexander et al. (2008) who reported red *Quercus* (*Erythrobalanus* section) seedlings experienced lower rates of mortality than that of both *A. rubrum* and white *Quercus* species (*Leucobalanus* section) following a prescribed burn in mature *Quercus* forests in eastern Kentucky. In contrast, a meta-analysis of resprouting by *Quercus* vs. non-*Quercus* species following fire suggests that resprouting rates of seedlings are significantly greater in the *Quercus* genus than non-*Quercus* competitors (Brose et al. 2013). It should be noted this meta-analysis grouped white and red *Quercus* species, as well as *Carya* species, into a single species group, thereby ignoring potential interspecific differences in resprout potential within the *Quercus* genus (Alexander et al. 2008; Green et al. 2010). An important factor limiting the comparison of seedling-resprout dynamics in response to fire for *Quercus* and non-*Quercus* species among studies is that few studies record the location of the root collar diameter relative to the groundline (i.e., soil surface) prior to fire. Brose and Van Lear (2004) present some of the only data specific to how both the size and location of the root collar influences seedling-resprout dynamics following fire. The authors found that, regardless of species (*Quercus/Carya*, *A. ruburm*, *L. tulipifera*), when the root collar is located about the soil surface (e.g., in the litter or litter/duff), dormant buds are more susceptible to damage during fire, which limits an individual's ability to resprout. In this study, care was taken during planting to ensure that the root collar of individual seedlings was located just below the soil surface. Given that root collar location was strictly controlled in this study, extrapolation of resprout probabilities beyond the location of the root collar in this study is not recommended, as this study did not examine how root collar location influences resprouting probability among species.

Although probability of resprouting was independent of preburn size, this study supports the notion that, for some species, resprout vigor, characterized by dominant resprout height following topkill, is influenced by seedling size prior to topkill (Table 2). However, the positive relationship between size prior to topkill and resprout vigor varied by species and burn. For example, following the first burn, all species other than *Q. alba* displayed a significant, positive correlation between preburn size and dominant resprout height at the end of the growing season. After the second burn, only the two mesophytic species, *A. rubrum* and *L. tulipifera*, exhibited this significant and positive relationship.

Following the removal of aboveground biomass, individuals rely on resources stored in various plant tissues, including belowground structures (e.g., root systems and lignotubers), to initiate and sustain resprouting until photosynthetic capacity to support regrowth is restored (Villar-Salvador et al. 2015; Chapin et al. 1990). Within a species, non-structural carbohydrate and mineral nutrient reserves, both factors linked to resprout ability and vigor (Miyanishi and Kellman 1986; Kruger and Reich 1997a; Zhu et al. 2012; Cruz et al. 2003a), are presumably greater in larger versus smaller individuals (Canham et al. 1999; McPherson and Williams 1998). Consequently, larger individuals often display increased vigor following topkill, and can recover aboveground biomass more rapidly than smaller individuals (Gilbert et al. 2003). The limited and/or inconsistent correlation between size prior to burning and resprout height for the two *Quercus* species could be due to their conservative growth strategy. Following topkill, *Quercus*' large root:shoot ratio is often conserved or even enhanced, with *Q. alba* displaying a more conservative growth strategy than *Q. rubra,* while the root:shoot ratio of competitors remains relatively unchanged following topkill (Barnes and Van Lear 1998; Kruger and Reich 1993; Brose and Rebbeck 2017).

Studies suggest that *Quercus* species are more resilient to fire in that resprouts recover a greater proportion of their preburn height than mesophytic competitors. For example, Brose and Van Lear (1998) report a larger decrease (relative to preburn) in height 2 years following a summer burn for *A. rubrum* (− 68 cm) and *L. tulipifera* (− 75 cm), compared to a combined white and red *Quercus* group (− 16 cm). Kruger and Reich (1997b) report greater height loss 1-year postburn for mesophytic species versus *Q. rubra*. However, the authors demonstrate that net height following a second burn conducted a year later differed very little between *Q. rubra* and other mesophytic (*Prunus serotina* and *A. saccharum*) species. In this study, all species experienced a loss in height following the first experimental burn, with *Q. rubra* and *Q. alba* displaying the smallest loss in height (Table 2). Height loss at the end of the growing season following the second burn was less than that after the first burn, *L. tulipifera* and *Q. rubra* experienced the greatest height loss, followed by *Q. alba* and *A. rubrum*.

Despite *Quercus*' greater ability to produce resprouts and regain height than mesophytic competitors following fire-induced topkill, few studies report an increase in its stature or competitiveness in the forest understory (e.g., Kruger and Reich 1997b; Brose and Van Lear 1998; Brose 2010), especially when burns occur under closed-canopied conditions (Alexander et al. 2008). In this study, the height of *Q. alba* seedlings remained less than that of both *L. tulipifera* and *A. rubrum* one growing season after the first burn (Fig. 4). One growing season after the second burn, *Q. rubra* was significantly shorter than *L. tulipifera* and *A. rubrum*, with no difference in height between *A. rubrum* and *Q. alba* observed. Prior to the first burn, average groundline diameter of *Q. alba* and *Q. rubra* exceeded the 12.7 mm threshold suggested by Brose (2014) as necessary for *Quercus* resprouts to compete with resprouts of mesophytic competitors. Interspecific differences in absolute height of resprouts observed between this study and other in situ studies are confounded by variability in light availability under partial overstory versus open conditions and by differences in resprout dynamics between species in the red versus white *Quercus* group, which in many instances are combined into a single species group for analysis (e.g., Brose 2010; Brose et al. 2013). For example, in closed-canopied conditions, low light may limit the growth and vigor of mid-tolerant *Quercus* resprouts, and favor resprouting shade-tolerant species (e.g., *A. rubrum*) (Alexander et al. 2008). In contrast, partial overstory conditions created during harvesting may promote *Quercus* resprout development, and suppress resprouts of shade-intolerant species (e.g., *L. tulipifera*) (Brose and Van Lear 1998; Brose 2010).

Conclusions

This study was designed and implemented to test the common assertion that seedlings of the *Quercus* genus are superior resprouters relative to mesophytic competitors following fire-induced topkill. Resprouting following topkill is complex, with in situ heterogeneity of resources (e.g., light and nutrient availability), disturbance intensity, seedling age and size, location of a seedling's root collar relative to groundline, and the abundance of competing vegetation often interacting to directly and indirectly affect inter- and intraspecific variability in resprout potential and vigor (Johansson 1986; Moreno and Oechel 1991; Brose and Van Lear 1998; Kabeya et al. 2003; Cruz et al. 2003b; Brose and Van Lear 2004; Kabeya and Sakai 2005). These confounding factors complicate the broad conclusions and generalizations made regarding seedling-resprout potential and vigor following fire-induced topkill in eastern North American *Quercus* forests, where the reintroduction of fire is often a primary management and restoration goal. In this study, these potentially confounding factors were controlled by conducting treatments in an ex situ homogeneous environment using planting stock of a common age. Because this study was conducted under ex situ conditions, however, care should be taken when extrapolating results to in situ conditions or conditions not mimicked (e.g., older seedlings, non-open sky conditions, location of root collar above groundline, etc.) in this study.

Predictive models of resprout potential exist for damaged and topkilled large (e.g., > 5 cm diameter at 1.4 m above groundline) trees in eastern North American forests (Keyser and Zarnoch 2014; Dietze and Clark 2008). In contrast, little quantitative information exists describing intra- and interspecific differences in resprout potential of seedlings or seedling resprouts, which are primary sources of regeneration in eastern *Quercus* forests (Loftis 1990; Larsen and Johnson 1998). Understanding species-specific resprouting dynamics is critical to understanding of the role of fire in shaping forest structure and composition. Results from this study lend support to the notion that some, but not all *Quercus* species possess greater resprout potential and vigor following fire-induced topkill relative to mesophytic species.

Although numerous studies document the response of the seedling or regeneration layer to fire, comparing effects of fire on resprout dynamics within and among species is confounded by differences in the biotic and abiotic environment within and among study sites. This study demonstrates that under ex situ conditions, there is substantial variability in resprout potential and vigor within and among species classified as fire-tolerant (i.e., *Quercus*) and fire-intolerant (*A. rubum* and *L. tulipifera*). Unfortunately, this study did not examine interspecific differences in postburn biomass allocation patterns (i.e., differences in above- versus belowground growth) following resprouting, or the mechanisms (e.g., changes in photosynthesis, respiration, plant nutrient concentrations, and stored carbohydrate reserves) driving intra- and interspecific differences in resprout dynamics. Quantifying the physiologic mechanisms driving resprouting responses among the suite of species common to eastern *Quercus* forests under a variety of biotic and abiotic conditions will be necessary to fully understand resprout dynamics following aboveground biomass removal, and identify conditions that promote survival and growth of target species following burning. The differences identified in this study demonstrate, even within a genus (i.e., *Quercus*), postburn resprout dynamics are highly variable. Future studies should examine the effects of topkill and subsequent resprouting under varying but controlled environmental conditions not examined in this study (e.g., partial overstory conditions, varying root collar locations, etc.). Given the results of this study, future studies should be analyzed at the species rather than species group level (e.g., *Quercus*, *Quercus*–*Carya*, mesophytic species), as analysis at the species group level (e.g., Brose et al. 2013) does not appear to adequately reflect species-specific postburn resprouting dynamics.

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Author contribution statement TLK conceived, designed, and executed this study and wrote the manuscript. No other person is entitled to authorship.

Compliance with ethical standards

Conflict of interest The author declares that there is no conflict of interest.

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