For. Sci. 63(4):377–387
https://doi.org/10.5849/FS-2016-029R2
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silviculture

Early Stump Sprout Development after Two Levels of Harvest in a Midwestern Bottomland Hardwood Forest

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Sprouting is an important source of regeneration for hardwood trees but has not been studied extensively in bottomland hardwood forests. We quantified the sprouting responses of 11 bottomland hardwood species or species groups after two levels of overstory harvest, including clearcutting with reserves (CCR) (residual basal area ~2.0 m^2/ha) and basal area retention (BAR) (residual basal area ~8.0 m^2/ha), in northern Missouri. The probability of sprout presence after one growing season decreased with increasing parent tree dbh for boxelder, river birch, hickories, hackberry, and American elm, as well as for eastern cottonwood and pin oak after three growing seasons. Harvest treatment affected the probability of sprout presence after three growing seasons for silver maple and American elm, with higher probabilities in CCR than BAR. After three growing seasons, height of the dominant sprout per stump was greater in CCR than in BAR across species. The sprouting probabilities and subsequent survival and growth of sprouts suggest that promoting coppice regeneration would favor silver maple, American elm, and American sycamore at the expense of oak species, river birch, and eastern cottonwood.

Keywords: bottomland oak, clearcut with reserves, partial harvest, regeneration, sprouting probability

Sprouting is a common response to tissue damage for woody plants and is a source of regeneration that contributes to the composition and development of forest ecosystems (Bond and Midgley 2001, Del Tredici 2001). Sprouting generally requires the storage of carbohydrates in the root system, often with a trade-off in the rate of initial seedling growth or amount of seed production (Iwasa and Kubo 1997, Bond and Midgley 2001). However, the ability to sprout provides a mechanism for persistence through disturbance, particularly disturbance regimes of relatively high frequency and low severity (Chapin et al. 1990, Bellingham and Sparrow 2000, Bond and Midgley 2001). Sprouts can have a competitive advantage over other sources of regeneration such as seeds or smaller advance reproduction released from suppression in recently disturbed areas (White 1991, Dietze and Clark 2008, Vickers et al. 2011), because rapid early growth of sprouts is supported by an established root system with stored carbohydrates (Del Tredici 2001). Thus, sprout-origin regeneration contributes to sustaining predisturbance species composition (Dietze and Clark 2008). Several studies have shown that sprouts can constitute the majority of the dominant trees within the regenerating cohort after harvesting (Boring et al. 1981, Beck and Hooper 1986, Arthur et al. 1997), although the capacity to sprout varies by species and site conditions.

Sprout production varies among species and in relation to parent tree size, tree age, and site productivity (Dey et al. 1996a, Bellingham and Sparrow 2000, Weigel and Peng 2002). In general, sprout production and persistence decrease as parent tree size increases for upland oaks (*Quercus* spp.) (Dey et al. 1996a, Weigel and Peng 2002) and some associated southern Appalachian species (Keyser and Loftis 2015). Sprouting of upland oaks has been reported to decrease with increasing parent tree age and to be lower on sites of lower potential productivity (Lynch and Bassett 1987, Dey and Jensen 2002, Weigel and Peng 2002). Silvicultural practices, such as the retention of overstory trees after harvesting, have been found to have few effects on sprout production but potentially affect sprout survival and growth rates (Dey and Jensen 2002, Dey et al. 2008, Keyser and Zarnoch 2014). By incorporating estimates of sprouting occurrence with subsequent sprout growth rates, models have been developed to estimate the contribution of sprouting to stand

Manuscript received August 2, 2016; accepted February 7, 2017; published online March 2, 2017.

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Acknowledgments: *Funding for this project was provided by the Missouri Department of Conservation through Cooperative Agreement No. 371, with support from the National Institute of Food and Agriculture, USDA McIntire-Stennis Project 233870. We appreciate the efforts of numerous individuals who assisted with the establishment and implementation of this project, including Anthony Elliot, Brian Root, Eric Kurzejeski, David Gwaze, and John Kabrick.*

development after regeneration harvest (Dey et al. 1996a, 1996b, Gould et al. 2007). Thus, understanding sprouting dynamics has been important for development of silvicultural practices for specific regeneration objectives (Sander et al. 1976, Dey et al. 1996a, Gould et al. 2007).

The importance of sprouting as a source of forest regeneration has been widely studied in upland oak ecosystems of the central and eastern United States (Sander et al. 1976, Cook et al. 1998, Larsen and Johnson 1998), but there have been relatively few studies on the sprouting dynamics of bottomland hardwood ecosystems of the central United States. In general, upland oak species are believed to rely more heavily on sprouting as a source for regeneration than bottomland oak species (Johnson et al. 2009), although sprouting can be a common and important source of regeneration for bottomland oak species as well (Clatterbuck and Meadows 1993, Johnson and Deen 1993, Meadows and Stanturf 1997). In a bottomland hardwood forest in the Mississippi River floodplain of Missouri, Kabrick and Anderson (2000) found that pin oak (*Quercus palustris* Münchh.), willow oak (*Quercus phellos* L.), and cherrybark oak (*Quercus pagoda* Raf.) had sprouting probabilities similar to that of upland white oak (*Quercus alba* L.), but the relatively low vigor of the bottomland oak sprouts suggested that other regeneration sources would be important for ensuring oak regeneration success.

Bottomland hardwood forests provide many economic (e.g., timber and recreation/hunting) and ecological (e.g., wildlife habitats and water quality) services (King et al. 2005), yet are highly dynamic spatially and temporally (Conner and Sharitz 2005). Within the midwestern United States, bottomland hardwood forests are commonly a part of the elm-ash-cottonwood forest type group (Eyre 1980), which occupies approximately 460,000 ha in the state of Missouri (Miles 2016). Midwestern bottomland hardwood forests are important for wildlife species associated with forest habitats within a fragmented agricultural landscape (Best et al. 1995, Rosenblatt et al. 1999). As a result, public agencies commonly manage this forest type for wildlife habitat, with interest in creating or maintaining snags and sustaining hard mast species such as pin oak or swamp white oak (*Quercus bicolor* Willd.) as a minor canopy component of this forest type (Gwaze and Elliott 2011, Olson et al. 2015). These ecosystems are often highly productive and capable of producing valuable sawtimber (Myers and Buchman 1984). Given the presence of shade-tolerant species, high levels of site productivity, and frequent flood events, regenerating oaks is a common challenge for forest managers within bottomland hardwood forests (Oliver et al. 2005). Previous studies have demonstrated the importance of large advance reproduction and stump sprouting for successful oak regeneration, with harvest treatments that initiate sprouting and release advance reproduction recommended for promoting oak regeneration (Clatterbuck and Meadows 1993, Meadows and Stanturf 1997).

Several species associated with the elm-ash-cottonwood forest type group have been reported to sprout vigorously, including silver maple (*Acer saccharinum* L.) (Gabriel 1990), American elm (*Ulmus americana* L.) (Bey 1990), and American sycamore (*Platanus occidentalis* L.) (Belanger 1979). In contrast to upland oak ecosystems, however, little is understood about sprouting dynamics within bottomland hardwood forests. This study was designed to describe sprouting of common tree species within bottomland hardwood forests of Missouri after regeneration harvest with two different silvicultural treatments. Improved understanding of the role of sprouting in bottomland forests would allow managers to refine silvicultural treatments to reach regeneration and management goals. The three specific objectives of this study were the following: to model sprouting probabilities in relation to parent tree dbh (1.37 m height) and harvest treatment for common bottomland hardwood species; to determine effects of species, harvest treatment, and time on number of sprouts per stump, height of the dominant sprout, and stump survival through the first 3 years after harvest; and to determine relationships between sprouting characteristics (number of sprouts per stump and height of the dominant sprout) and parent tree dbh by species.

Methods

Study Sites

This study was established in a bottomland hardwood forest located at Deer Ridge Conservation Area, a public land area managed by the Missouri Department of Conservation in Lewis County of northeastern Missouri (approximately 40°10′30″ N; 91°48′0″ W). The study area included >200 ha of bottomland hardwood forest located adjacent to a channelized segment of the North Fabius River. This forest was selected for the study because it had not been harvested in >50 years, it contained contiguous bottomland forest blocks >20 ha, and state ownership facilitated long-term access and control of management activities. Soils of the study area were dominated by Blackoar silt loam, Fatima silt loam, and Kickapoo fine sandy loam, which each form in alluvium but vary in drainage class. The study area has generally flat topography (0–2% slopes) and is prone to annual flooding events. The 30-year mean annual temperature for the area was 10.9° C, and mean annual precipitation was 1,032 mm (National Oceanic and Atmospheric Administration climate data online[1]). The most common tree species within the study area included those common to bottomland hardwood forests of this region: silver maple, American elm, American sycamore, green ash (*Fraxinus pennsylvanica* Marshall), eastern cottonwood (*Populus deltoides* W. Bartram ex Marshall), boxelder (*Acer negundo* L.), pin oak, bur oak (*Quercus macrocarpa* Michx.), and swamp white oak. Before the start of the study, silver maple and American elm contributed 46% of the stand basal area, whereas oak species combined contributed 13% of the basal area.

Management and Policy Implications

Sprouting is an important source of tree regeneration after harvest. Despite rather extensive research on sprouting dynamics within upland hardwood ecosystems, there has been relatively little research on sprouting in bottomland ecosystems. Understanding sprouting dynamics, including the probability that cut trees will produce sprouts, the persistence of those sprouts through time, and the growth rates of the sprouts that are produced can allow forest managers to anticipate regeneration outcomes after harvest. This study quantifies sprouting dynamics of 11 species or species groups common to midwestern bottomland ecosystems. Although forest managers commonly expect sprouting to contribute to regeneration success of oak species on upland sites, results from this work indicate that sprouting would favor American sycamore, silver maple, and American elm over oak species in these bottomland ecosystems. These results may be further developed to inform regeneration models for bottomland tree species.

Table 1. Number of trees and basal area per hectare of overstory trees (dbh ≥11.4 cm) before (1997) and immediately after (2000) harvest for CCR and BAR treatments.

	CCR		BAR	
Year	Mean	SD	Mean	SD
Trees per hectare				
1997	465.0	163.0	412.0	116.0
2000	20.0	12.0	118.0	32.0
Basal area (m^2/ha)				
1997	28.0	6.5	25.1	4.7
2000	2.0	0.8	7.8	0.8

Experimental Design

The study was part of a research project called the Riparian Ecosystem Assessment and Management (REAM) Project, established to evaluate silvicultural practices for regeneration of bottomland forests of northern Missouri (Olson et al. 2015). The REAM experiment was designed to evaluate the effects of two levels of overstory removal on flora and fauna, with interest in regenerating bottomland oak species. The study was established as a completely randomized design with three levels of overstory harvest as study treatments: an uncut control, clearcutting with reserves (CCR), and basal area retention (BAR). The CCR and BAR treatments were each randomly assigned to eight stands that ranged from 2.5 to 3.5 ha. The CCR treatment harvested nearly all trees >2.5 cm dbh, except for some cavity trees and hard mast trees, particularly oak species, to a target residual basal area of approximately 2–3 m^2/ha basal area to benefit wildlife and retain an oak seed source. The BAR treatment was similar to a shelterwood harvest, with removal of trees ≥11.4 cm dbh to a target residual basal area of 4.7–9.4 m^2/ha. Dominant oak trees were commonly marked for retention in BAR, although a variety of species were retained to maintain species diversity.

Harvest treatments were applied between fall 1999 and spring 2000. All felling was done by chainsaw, and yarding was done with a grapple skidder. In both treatments, stands were treated with a postharvest slashing that cut small residual trees (2.5–20.3 cm dbh) that were not marked for retention. The CCR and BAR treatments created relatively open stands with 4 and 29% of preharvest trees per ha and 7 and 31% of preharvest basal area, respectively (Table 1). The residual basal area for the CCR and BAR treatments fell within their respective targeted ranges immediately after harvesting. Silver maple, the most abundant species before treatment, was the most abundant species retained in both treatments, followed by oaks in CCR and oaks and American sycamore in BAR (Olson et al. 2015).

Data Collection

Within the interior of each stand, two fixed-area circular plots (0.2 ha) were established for sampling forest structure and composition. Before harvest, each tree ≥11.4 cm dbh within each plot was measured for dbh and species was recorded, and each was tagged for stump sprout measurements after harvest. In the CCR treatment, a random sample of stems <11.4 cm dbh (small stumps) were additionally tagged to quantify sprouting of smaller stems after the slashing treatment. Fifteen small stems each of silver maple and American elm were identified in and around each 0.2-ha plot. In addition, up to 100 small stems of other common species were tagged across all CCR units. Several attributes were recorded for each stem that was tagged, including the species and the preharvest dbh. At the end of the first (2000), second (2001), and third (2002) growing seasons after harvest, the number of live sprouts per stump and the height of the dominant sprout were measured.

Data Analyses

To estimate sprouting probabilities (first objective), we used logistic regression through generalized linear models with a logit link function and a binomial distribution. The logistic model had the form

$$P_s = \frac{\exp(\beta_0 + \beta_1 X_1 + \beta_2 X_2)}{1 + \exp(\beta_0 + \beta_1 X_1 + \beta_2 X_2)} \quad (1)$$

where P_s is the probability of sprouting, X_1 is parent tree dbh, X_2 is regeneration harvest (in which BAR is coded 1 and CCR is coded 0), and β_i are regression coefficients. Because individual trees were located within stands receiving harvest treatments, we nested individual trees within stands using a random statement in the PROC GLIMMIX function in SAS (version 9.3; SAS Institute, Inc., Cary, NC). We first tested for effects of preharvest dbh (continuous variable) and harvest treatment (CCR versus BAR) on sprouting probabilities using only stumps ≥11.4 cm dbh. Logistic models were estimated separately for the following species or species groups: boxelder, silver maple, river birch (*Betula nigra* L.), hickories (*Carya* spp.), hackberry (*Celtis occidentalis* L.), green ash, American sycamore, eastern cottonwood, white oaks (*Quercus bicolor* and *Quercus macrocarpa*), pin oak, and American elm (Table 2). In the absence of significant harvest treatment effects, we modeled sprouting probability based on preharvest dbh using data from only CCR because stumps <11.4 cm dbh were not sampled in BAR. With significant harvest treatment effects, we report results for individuals with pretreatment dbh ≥11.4 cm. Separate analyses were performed for the

Table 2. Sample size and descriptive statistics of parent trees.

	Sample size (n)			dbh (entire sample population)			
Species	BAR dbh ≥11.4 cm	CCR dbh ≥11.4 cm	CCR dbh <11.4 cm	Minimum	Maximum	Mean	SD
Acer negundo (boxelder)	28	7	71	3.8	23.1	9.8	5.1
Acer saccharinum (silver maple)	131	372	198	0.3	116.8	17.7	14.7
Betula nigra (river birch)	4	34	44	3.8	54.1	15.7	12.1
Carya spp. (hickories)	19	12	85	3.6	56.4	9.4	6.8
Celtis occidentalis (hackberry)	8	34	91	3.8	28.7	10.2	5.1
Fraxinus pennsylvanica (green ash)	28	32	90	3.8	60.5	14.4	13.3
Platanus occidentalis (American sycamore)	54	51	51	4.1	76.2	23.4	19.2
Populus deltoides (eastern cottonwood)	43	65	4	8.9	89.9	37.5	21.3
Quercus bicolor/*Quercus macrocarpa* (white oaks)	14	24	0	11.7	62.5	32.1	18.6
Quercus palustris (pin oak)	10	54	0	13.2	77.5	33.9	16.8
Ulmus americana (American elm)	181	263	240	0.3	37.1	12	5.5

Common names for each species or species group are provided parenthetically after the Latin name.

Table 3. Model parameters for estimating probability of a cut stump having at least one live sprout at the end of the first growing season.

Species	Effect	Estimate	SE	*t* value	*P* value
Boxelder	Intercept	3.135	0.801	3.92	<0.001
	dbh	−0.267	0.093	−2.89	<0.001
Silver maple	Intercept	1.939	0.228	8.490	<0.001
	dbh	−0.072	0.010	−7.030	<0.001
	BAR	−0.554	0.228	−2.420	0.016
River birch	Intercept	0.503	0.550	0.91	0.364
	dbh	−0.108	0.045	−2.39	0.019
Hickories	Intercept	3.290	0.645	5.10	<0.001
	dbh	−0.228	0.068	−3.37	0.001
Hackberry	Intercept	3.401	0.710	4.79	<0.001
	dbh	−0.124	0.055	−2.26	0.026
Green ash	Intercept	2.747	0.671	4.09	<0.001
	dbh	0.020	0.053	0.39	0.700
American sycamore	Intercept	−0.728	1.189	−0.61	0.542
	dbh	0.333	0.144	2.30	0.023
Eastern cottonwood	Intercept	0.373	0.560	0.67	0.507
	dbh	−0.008	0.012	−0.68	0.496
White oaks	Intercept	5.903	6.317	0.93	0.360
	dbh	−0.454	0.468	−0.97	0.342
Pin oak	Intercept	0.334	0.828	0.40	0.688
	dbh	−0.056	0.030	−1.89	0.065
American elm	Intercept	2.769	0.303	9.14	<0.001
	dbh	−0.092	0.021	−4.31	<0.001

The model for silver maple included harvest treatment and therefore used only parent trees ≥11.4 cm dbh. The model form follows Equation 1, in which Intercept is the β_0 parameter, dbh is the β_1 parameter, and BAR is the β_2 parameter.

probability of at least one sprout being present at the end of the first growing season after harvest (2000) and at the end of the third growing season after harvest (2002).

We tested for effects of harvest treatment and differences among species for the number of sprouts per stump, the height of the dominant sprout per stump, and stump survival through time (second objective) using repeated-measures, split-plot analysis of variance. The model included harvest treatment as the whole-plot factor, species as the split-plot factor, and stand as a random effect. An unstructured covariance structure was used for the repeated measures, and degrees of freedom were determined using the Satterthwaite approximation. We tested for significance of pairwise comparisons using Tukey's honestly significant difference test. Because the BAR treatment included only parent trees ≥11.4 cm dbh, we only included parent trees ≥11.4 cm dbh from the CCR treatment. We limited the analyses to including species for which sprouts occurred within at least four stands per treatment (i.e., silver maple, green ash, American sycamore, and American elm).

To determine relationships between sprout characteristics after three growing seasons (number of sprouts per stump and dominant sprout height) and parent tree dbh (third objective), we used mixed-model regression analyses, first using only parent trees ≥11.4 cm dbh and including harvest treatment, dbh, and their interaction as fixed effects in the model. In the absence of significant harvest treatment and parent tree size interactions, we used mixed-model regression with data from only CCR to model relationships between response variables and parent tree dbh. We used a random intercept, specifying the stand as the experimental unit for harvest treatment application. Models were run for each species separately. We used a natural log transformation of number of sprouts for silver maple, green ash, and American elm and a square root transformation of number of sprouts for American sycamore.

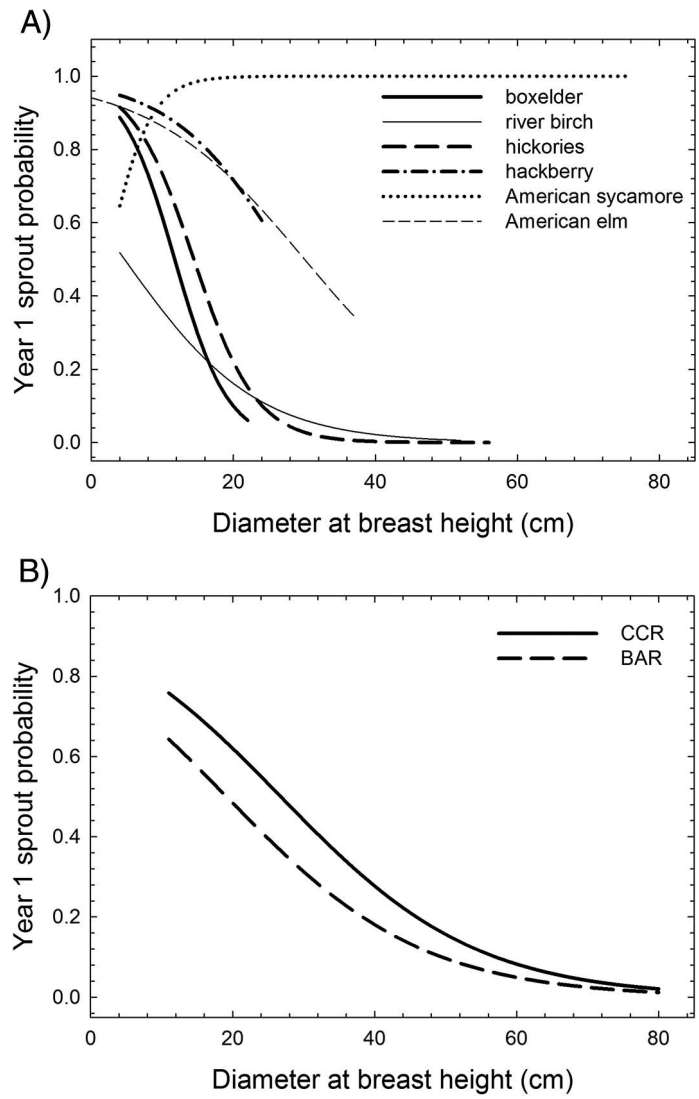

Figure 1. Probability of cut stumps having at least one live sprout at the end of one growing season in relation to parent tree dbh (cm) by species using all data (A) and by treatment for silver maple using parent trees ≥11.4 cm dbh (B).

Scatterplots of height of dominant sprouts and parent tree dbh suggested nonlinear relationships, which we fit using Equation 2 for silver maple, American elm, and American sycamore:

$$y = b_0(1 - e^{(-b_1 x)}) \quad (2)$$

where y is dominant sprout height after three growing seasons, x is parent tree dbh, and b_0 and b_1 are parameters estimated by the model. In all cases, statistical significance was determined using $P < 0.05$.

Results

Sprouting Probabilities

The probability of sprout presence at the end of the first growing season was significantly reduced as parent tree dbh increased for boxelder, river birch, hickories, hackberry, and American elm (Table 3). With the exception of river birch, which displayed low rates of sprouting across all parent tree sizes, these species had high sprouting rates (>60% sprouting probability) when dbh was <10 cm (Figure 1A). In larger trees, sprouting probability decreased

Table 4. Model parameters for estimating probability of a cut stump having at least one live sprout at the end of the third growing season.

Species	Effect	Estimate	SE	*t* value	*P* value
Boxelder	Intercept	2.739	0.745	3.67	<0.001
	dbh	−0.236	0.087	−2.71	0.008
Silver maple	Intercept	1.592	0.248	6.42	<0.001
	dbh	−0.077	0.012	−6.30	<0.001
	BAR	−0.582	0.230	−2.53	0.012
River birch	Intercept	0.193	0.735	0.26	0.794
	dbh	−0.157	0.073	−2.15	0.035
Hickories	Intercept	2.424	0.552	4.39	<0.001
	dbh	−0.182	0.062	−2.92	0.004
Hackberry	Intercept	1.594	1.683	0.95	0.349
	dbh	−0.053	0.101	−0.52	0.604
	BAR	−2.598	1.169	−2.22	0.032
Green ash	Intercept	2.184	0.386	5.66	<0.001
	dbh	−0.034	0.020	−1.65	0.101
American sycamore	Intercept	1.690	0.580	2.91	0.004
	dbh	0.024	0.039	0.62	0.534
Eastern cottonwood	Intercept	3.259	1.851	1.76	0.083
	dbh	−0.230	0.095	−2.42	0.018
White oaks	Intercept	5.903	6.317	0.93	0.360
	dbh	−0.454	0.468	−0.97	0.342
Pin oak	Intercept	4.450	2.571	1.75	0.086
	dbh	−0.294	0.139	−2.12	0.039
American elm	Intercept	1.664	0.488	3.41	0.001
	dbh	−0.072	0.030	−2.40	0.017
	BAR	−0.516	0.200	−2.59	0.010

Models for silver maple, hackberry, and American elm included harvest treatment and therefore used only parent trees ≥11.4 cm dbh. The model form follows Equation 1, in which Intercept is the β_0 parameter, dbh is the β_1 parameter, and BAR is the β_2 parameter.

sharply for boxelder and hickories but remained >50% for parent trees up to 25 cm dbh for hackberry and American elm. American sycamore was the only species for which sprouting probability increased with increasing parent tree dbh, with sprouting probability near 100% for trees >20 cm. Among the species for which parent tree dbh was not significant, sprout rates across the CCR stands averaged 92.6% for green ash, 38.2% for pin oak, 64.9% for eastern cottonwood, and 30.0% for white oaks. Harvest treatment and parent tree dbh had significant effects on the probability of sprout presence at the end of 1 year only for silver maple (Table 3). Sprouting probability of silver maple decreased with parent tree dbh in both treatments, but the probability of sprout presence was greater in CCR than in BAR (Figure 1B).

After three growing seasons, the probability of sprout presence was significantly reduced as parent tree dbh increased for boxelder, river birch, hickories, eastern cottonwood, and pin oak (Table 4). Each of these species displayed low probabilities of sprout presence after 3 years if parent trees were >20 cm dbh (Figure 2A). For the other species, the percentage of stumps with at least one sprout after year 3 in CCR stands was 85.9% for green ash, 75.7% for American sycamore, and 18.4% for white oaks. The probability of sprout presence was significantly affected by harvest treatment and parent tree dbh for silver maple and American elm, both of which had greater sprout probabilities in CCR than in BAR treatments (Figure 2B). Although parent tree dbh was not significant for hackberry, harvest treatment affected third year sprout probability (Table 4), with 83.1% probability of sprout presence for CCR and 26.8% probability for BAR.

Number of Sprouts per Stump

There was a significant interaction between species and year ($F_{6,\,51} = 3.58$; $P = 0.005$) but no interaction between harvest treatment and species ($F_{3,\,46.9} = 2.20$; $P = 0.100$) or harvest treatment and year ($F_{2,\,51} = 3.04$; $P = 0.056$) on the number of sprouts per stump. Pairwise comparisons indicated no significant differences among species for the number of sprouts per stump after the first (2000) or third (2002) growing season, but American sycamore had significantly more sprouts per stump than silver maple after the second growing season (2001) (Figure 3A). Silver maple sprout numbers significantly decreased from the first to the second growing season (2000–2001), whereas American sycamore and green ash sprout numbers significantly decreased from the second to the third growing season (2001–2002). The number of sprouts per stump significantly decreased in each year for American elm. Among the species not analyzed, the number of sprouts per stump after three growing seasons averaged 2.5 for boxelder, 0.2 for river birch, 2.3 for hickories, 6.1 for hackberry, 3.4 for eastern cottonwood, 3.2 for pin oak, and 3.5 for white oaks. Harvest treatment did not affect the number of sprouts per stump ($F_{1,\,25.8} = 1.46$; $P = 0.2380$) (Figure 3B).

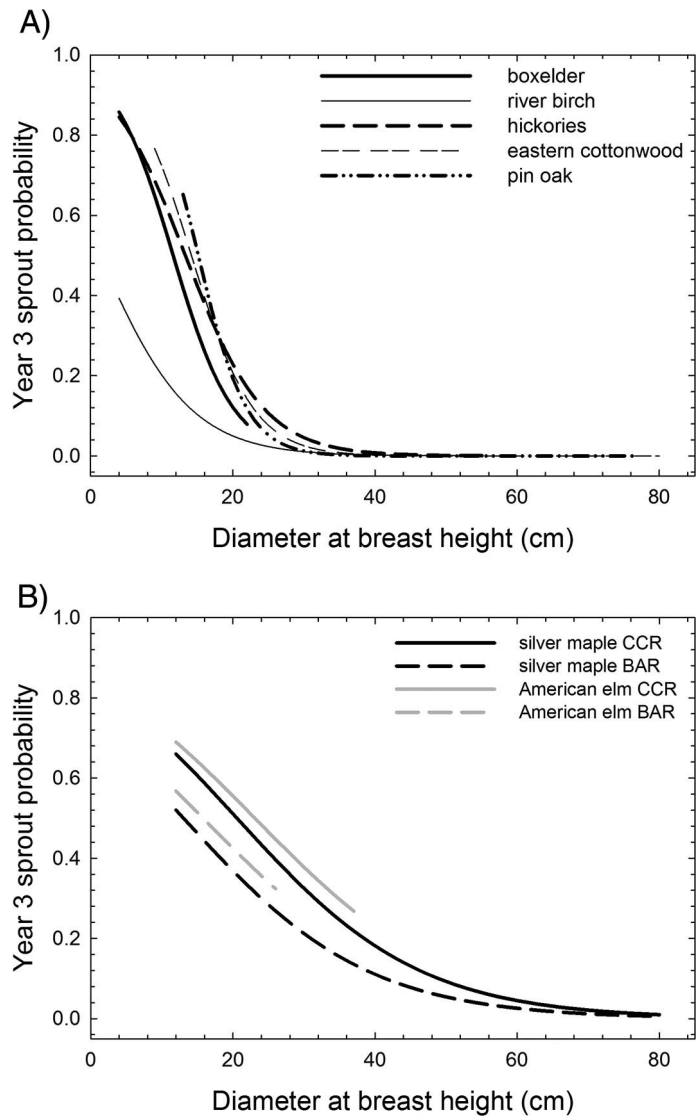

Figure 2. Probability of cut stumps having at least one living sprout at the end of three growing seasons in relation to parent tree dbh (cm) by species using all data (A) and by treatment for silver maple and American elm using parent trees ≥11.4 cm dbh (B).

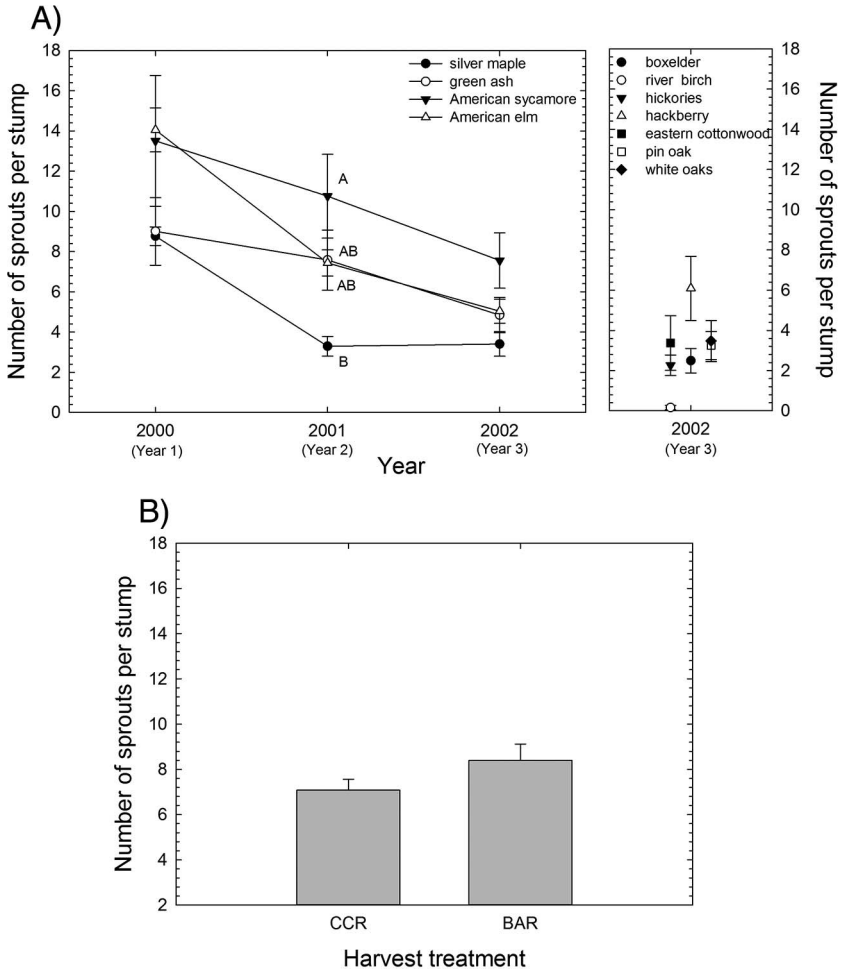

Figure 3. Number of sprouts per stump (mean and SE) by year and species (A) and by harvest treatment (B). Different letters indicate significant differences from pairwise comparisons of species within years in panel A; the right side of panel A shows number of sprouts per stump from 2002 (mean and SE) of species not analyzed statistically because of small sample sizes (points are offset for visibility).

Harvest treatment significantly affected the relationship between parent tree dbh and the number of sprouts per stump at the end of the third growing season for silver maple ($F_{1,\,227} = 7.47$; $P = 0.007$) and green ash ($F_{1,\,41} = 4.74$; $P = 0.035$). For silver maple, the number of sprouts per stump significantly decreased as parent tree dbh increased for BAR ($F_{1,\,34} = 13.24$; $P < 0.001$) but was not related to parent tree dbh for CCR ($F_{1,\,179} = 0.03$; $P = 0.866$) (Figure 4). Green ash displayed the opposite pattern, with the number of sprouts per stump significantly decreasing as parent tree dbh increased for CCR ($F_{1,\,18} = 4.79$; $P = 0.042$) but not related to parent tree dbh for BAR ($F_{1,\,11} = 0.78$; $P = 0.397$) (Figure 4). With data from only CCR, there were significant relationships between the number of sprouts per stump and parent tree dbh for American elm ($F_{1,\,125} = 71.13$; $P < 0.001$) and American sycamore ($F_{1,\,83} = 23.33$; $P < 0.001$). For those species, relationships suggested that the number of sprouts per stump increased with parent tree dbh (Figure 4).

Dominant Sprout Height

There were significant interactions between species and year ($F_{6,\,49.5} = 4.63$; $P = 0.001$) and between harvest treatment and year ($F_{2,\,49.5} = 7.62$; $P = 0.001$) for dominant sprout height. After the first growing season, American sycamore and silver maple had dominant sprouts that were taller than those of American elm (Figure 5A). By the end of the third growing season, American sycamore had the tallest dominant sprouts, followed by silver maple and American elm, with green ash sprouts being significantly shorter than those of each species other than American elm. Dominant sprouts of each species significantly increased in height each year, with the exception of green ash from 2001 to 2002. After three growing seasons, mean dominant heights of the species not analyzed were within the range of heights for the species included in the analysis, with exception of pin oak (2.6 m) and hickories (2.1 m). Harvest treatment had no effect on height of the dominant sprout after the first and second growing seasons but resulted in taller dominant sprouts with the CCR treatment than with the BAR treatment after three growing seasons (Figure 5B). Height of the dominant sprouts significantly increased each year for both harvest treatments. There was no significant interaction between harvest treatment and species ($F_{3,\,40.5} = 0.82$; $P = 0.493$).

We found no evidence of harvest treatment effects on the relationships between parent tree dbh and dominant sprout height after the third growing season for any species. With data from only CCR, relationships were significant only for silver maple ($F_{1,\,340} = 124.15$; $P < 0.001$), American sycamore ($F_{1,\,90} = 44.24$; $P < 0.001$), and American elm ($F_{1,\,387} = 88.81$; $P < 0.001$). Generally, dominant sprout height increased with parent tree dbh to between 10 and 20 cm and then leveled out across larger parent tree sizes (Figure 6).

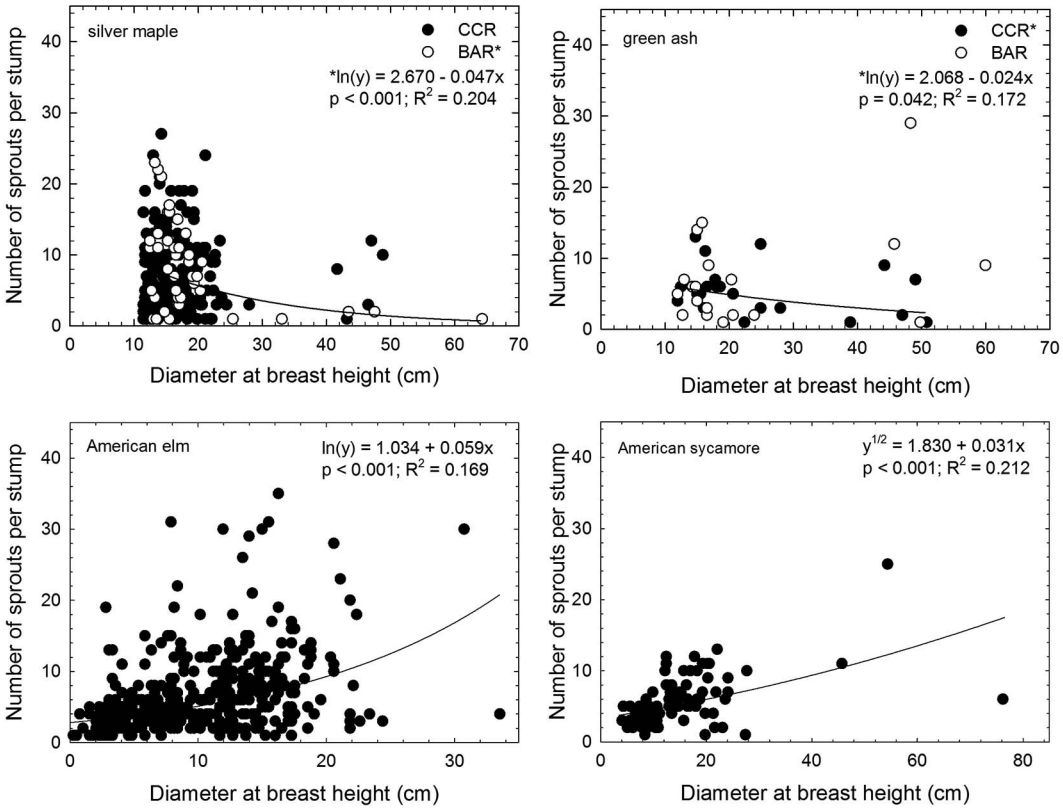

Figure 4. Relationships between parent tree dbh (cm) and the number of sprouts per stump at the end of three growing seasons for silver maple, green ash, American elm, and American sycamore. Harvest treatment interacted with parent tree dbh for only silver maple and green ash; for silver maple, parent tree dbh was significantly related to number of sprouts per stump in only BAR and for green ash only for CCR. Models used transformations of number of sprouts per stump but display back-transformed values.

Sprout Survival

There were no significant interactions among harvest treatment, year, and species ($P \geq 0.127$). We found no significant differences in survival between harvest treatments ($F_{1,51} = 2.25$; $P = 0.140$) or among the species analyzed (silver maple, green ash, American sycamore, and American elm) ($F_{1,51} = 0.05$; $P = 0.984$). Across the species analyzed, stump sprout survival significantly decreased from the second growing season (89.1% survival) to the third growing season (81.7% survival) ($F_{1,51} = 11.01$; $P = 0.002$). Among all species, only river birch (8.3% survival) and eastern cottonwood (9.5% survival) had <65% stump sprout survival after three growing seasons.

Discussion

The bottomland hardwood species included in this study displayed considerable variability in sprouting response after regeneration harvest. In general, sprouting contributes to a life history strategy of persistence that has been associated with root carbohydrate storage, relatively high root to shoot ratios, slow initial rates of shoot growth for true seedlings, large seeds, and relatively low seed production (Kruger et al. 1997, Bellingham and Sparrow 2000, Bond and Midgley 2001), many of which are also characteristics associated with mid to late successional tree species (Grime 1977, Whitmore 1989). River birch and eastern cottonwood are early successional species within bottomland ecosystems (Wolfe and Pittillo 1977, Barnes 1985, Stanturf et al. 2001) and had relatively low sprouting probabilities or low sprout persistence in this study. In contrast, many of the other species included in this study may be associated with later stages of bottomland succession (Stanturf et al. 2001) and had high sprouting probabilities across at least some parent tree sizes. In particular, green ash and American sycamore had high sprouting probabilities, with sprouts that persisted through the first three growing seasons. Previous studies have also found high sprouting rates for green ash (Lesica 2009) and American sycamore, with the latter favored for short-rotation coppice biomass production (Belanger 1979).

Bottomland oak species are generally considered less vigorous sprouters than upland oak species (Johnson et al. 2009), and we found relatively low sprouting probabilities for the oak species in this study. In contrast, several previous studies have reported high rates of sprouting for bottomland oak species. For example, Lockhart and Chambers (2007) observed an 80% sprout rate across parent tree sizes in a 30-year-old plantation of cherrybark oak, and Gardiner and Helmig (1997) found nearly complete sprouting within a thinned, 28-year-old plantation of water oak. Given the negative relationships reported between oak sprouting and parent tree age for upland oak species (Lynch and Bassett 1987, Dey and Jensen 2002, Weigel and Peng 2002), it is possible that the lower sprouting rates of oaks observed in our study were due, in part, to greater tree age or to differences in the parent tree size before cutting. In a study from southeastern Missouri, Kabrick and Anderson (2000) found that bottomland oaks, including water oak, cherrybark oak, and pin oak, sprouted at rates comparable to those of upland white oak but less than those of upland chestnut oak (*Quercus prinus* L.), scarlet oak (*Quercus coccinea* Münchh.), and northern red oak (*Quercus rubra* L.). However, of the species observed in their

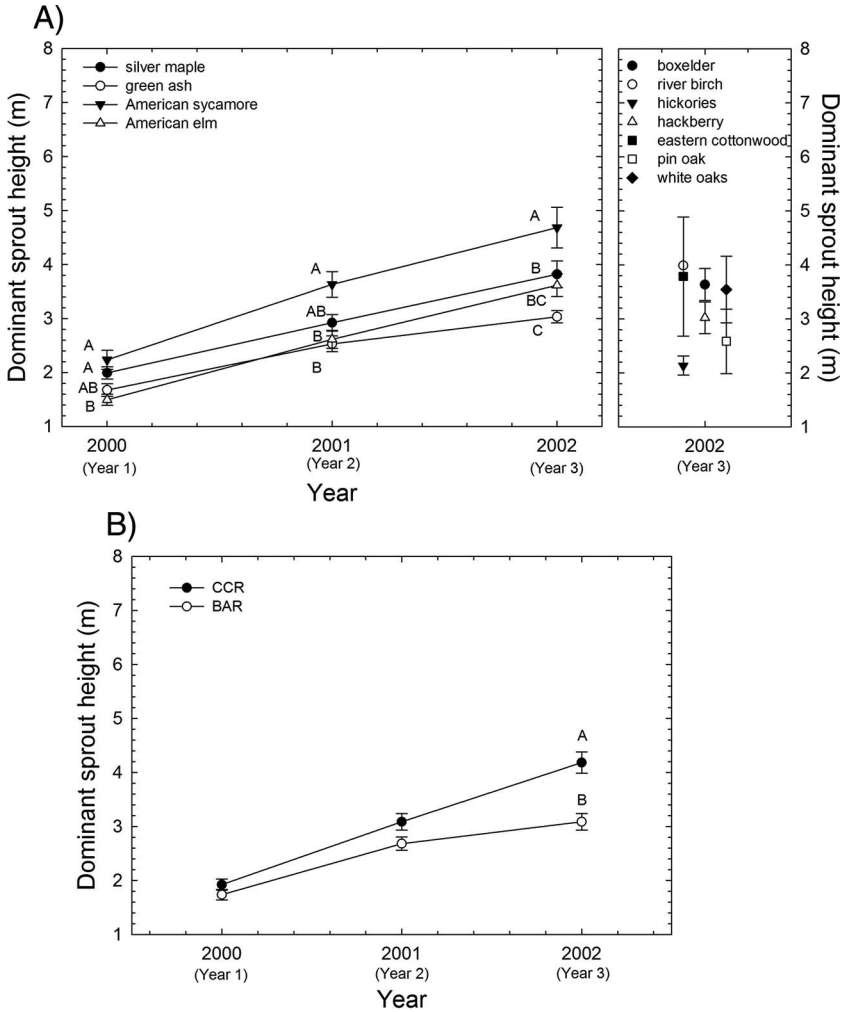

Figure 5. Height of the dominant sprout (mean and SE) by year and species (A) and by year and harvest treatment (B). Different letters indicate significant differences from pairwise comparisons of species within years in panel A and of harvest treatment within years in panel B; the right side of panel A shows dominant sprout height from 2002 (mean and SE) of species not analyzed statistically because of small sample sizes (points are offset for visibility).

study, pin oak had the fewest stumps with sprouts (35%), with sprouting patterns similar to those observed in our study. Little information exists regarding sprouting of swamp white oak or bur oak, although general descriptions of the silvics of these species suggest greater sprouting potential than that observed in our study (Perala 1974, Johnson 1990, Rogers 1990).

Inverse relationships between parent tree dbh and sprouting probabilities have been well-established for upland oak species (Johnson 1977, Dey et al. 1996a, Weigel and Peng 2002) and were observed for several species in our study. However, relationships between first year sprouting probabilities and parent tree dbh were not significant for green ash, eastern cottonwood, or the oaks in our study. These results suggest differences in sprouting dynamics between upland and bottomland oaks, which we found had relatively low rates of sprouting regardless of parent tree size. Recently, Keyser and Loftis (2015) quantified sprouting probabilities for upland hardwood species in the southern Appalachians and found that sprouting probabilities for the majority of nonoak species were not related to parent tree size. Species comparisons from field studies may be confounded by variability in the range of parent tree sizes across species, resulting in a limited representation of sprouting ability. For example, the maximum parent tree dbh for boxelder in our study was 23.1 cm, whereas the minimum parent tree dbh for eastern cottonwood was 21.3 cm. Additional research is warranted to further develop models for sprouting probability of many bottomland hardwood species across a broad range in tree diameters and ages and to determine other factors associated with sprout response.

In general, parent tree size had a weak or no relationship with either the number of sprouts per stump or the height of the dominant sprout after 3 years. For American elm and American sycamore, parent tree size was weakly positively related to the number of sprouts per stump, as has been reported for several hardwood species within uplands of the southern Appalachians (Keyser and Loftis 2015). In contrast, silver maple and green ash both had negative relationships between parent tree dbh and the number of sprouts per stump for one of the harvest treatments, with very few sprouts present on stumps >30 cm dbh after 3 years. Patterns for silver maple, American sycamore, and American elm suggested taller dominant sprouts with increasing parent tree size to approximately 15 cm dbh, although relationships were generally weak. In contrast, Dey et al. (1996a) reported that the height of upland oak sprouts increased with increasing parent tree dbh but then decreased for parent trees >20 cm dbh, and Keyser and Loftis (2015) reported

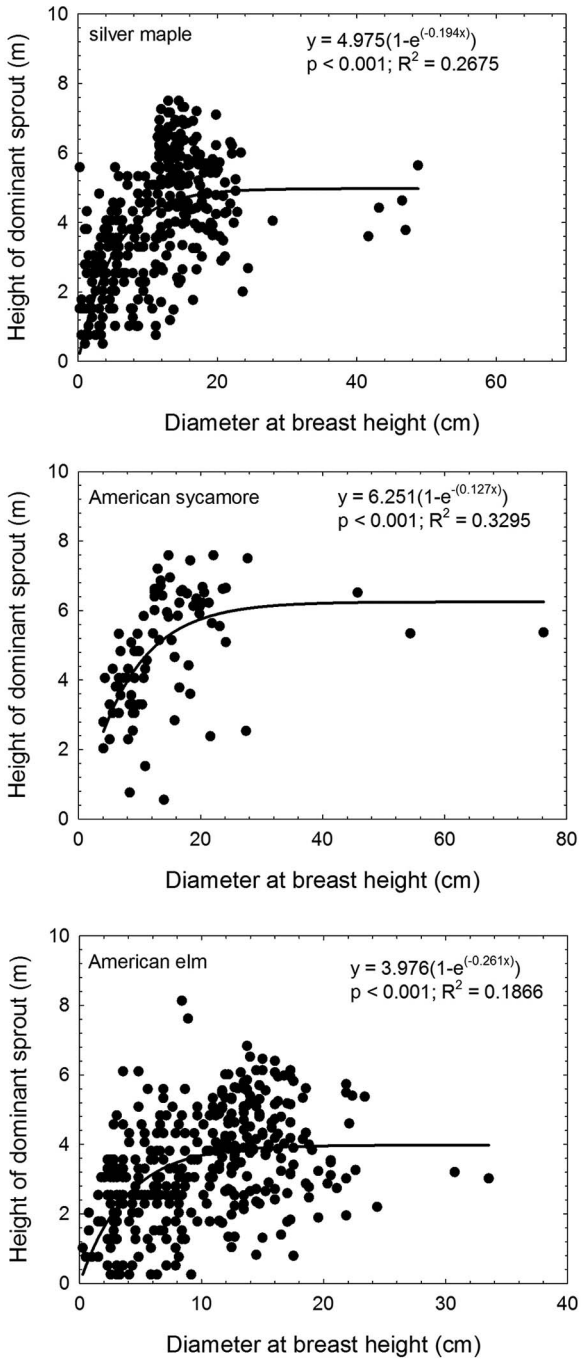

Figure 6. Nonlinear relationships between parent tree dbh (cm) and height of the dominant sprout for silver maple, American sycamore, and American elm.

positive relationships between sprout height and parent tree dbh across the range of parent tree sizes examined for yellow-poplar (*Liriodendron tulipifera* L.), silverbell (*Halesia tetraptera* Ellis), and white basswood (*Tilia heterophylla* Vent.) in the southern Appalachians. Similar to our results, however, these studies observed high variability in the relationships.

Previous studies have found few effects of silvicultural treatment (e.g., residual stand density or type of regeneration harvest) on the production of stump sprouts for bottomland hardwoods (Gardiner and Helmig 1997, Lockhart and Chambers 2007) or for upland oaks and other upland hardwoods (Dey and Jensen 2002, Keyser and Zarnoch 2014). However, the survival of sprouts after harvest has been found to be lower with greater canopy retention (Atwood et al. 2009, Keyser and Zarnoch 2014). Ten years after regeneration harvest in the Missouri Ozark Highlands, Dey et al. (2008) reported that single-tree selection significantly reduced stump survival of upland oak species compared with group selection and clearcutting. For plantations of cherrybark oak and water oak, heavy silvicultural thinning treatments resulted in greater sprout survival than light thinning treatments (Gardiner and Helmig 1997, Lockhart and Chambers 2007). Our logistic models indicated that greater canopy retention reduced the presence of sprouts for silver maple after the first growing season and for silver maple, American elm, and hackberry after three growing seasons, although we found no statistically significant differences in sprout survival between harvest treatments.

Canopy retention during regeneration harvest has been found to reduce the subsequent growth rate of regenerating hardwoods across species in upland (Vickers et al. 2014) and bottomland (Oliver et al. 2005) forest ecosystems. Similar findings have been consistently reported for growth rates of stump sprouts (Gardiner and Helmig 1997, Lockhart and Chambers 2007, Dey et al. 2008, Keyser and Zarnoch 2014). Our study corroborates these findings, with growth reductions of all species by the end of the third growing season, after which sprouts in the BAR treatment were on average approximately 1 m shorter than those in the CCR treatment. Similar to thinning studies in bottomland oak plantations (Gardiner and Helmig 1997, Lockhart and Chambers 2007), we found no effects of canopy density on the number of sprouts per stump. Additional research is warranted to further develop our understanding of sprouting response to silvicultural treatments in bottomland hardwood forests, including effects of greater canopy retention, harvest season, and long-term temporal patterns in sprout growth and survival.

Management Implications

Sprouting dynamics play an important role in the development of regenerating forests because sprouts can provide a regeneration source with rapid growth supported by the root system of the parent tree. Several studies have documented the major contribution of sprouts as a regeneration source within upland (Beck and Hooper 1986, Arthur et al. 1997, Dietze and Clark 2008) and bottomland (Johnson and Deen 1993) forests. Both sprout presence, through initial sprout production and subsequent survival, and the growth rates of surviving sprouts contribute to the likelihood of sprout-origin stems becoming future canopy trees (Dey et al. 1996a, Gould et al. 2007). Our results indicated species-specific relationships between parent tree dbh and both sprouting occurrence and persistence through three growing seasons. In particular, American sycamore sprouted vigorously, especially for large parent trees. After three growing seasons the bottomland hardwood species in this study demonstrated evidence of height differentiation, with height growth of American sycamore exceeding that of all other species. Through time, it is probable that height differentiation would continue, with dominance of American sycamore, as well as silver maple and American elm, increasing in the regenerating stands.

Regeneration of oak species is often a management objective in bottomland hardwood ecosystems. Advance reproduction and sprouting are considered the primary regeneration sources, and recommendations for successfully regenerating oak include releasing advance reproduction and initiating stump sprouting through harvest (Clatterbuck and Meadows 1993, Meadows and Stanturf 1997, Oliver et al. 2005, Motsinger et al. 2010). However, the sprouting

rates of oak species in our study were relatively low, with white oaks showing the lowest sprout rate among all species at the end of the first growing season. Moreover, the average dominant height of pin oak after three growing seasons was near the lowest of any species. These findings suggest that the sprouting characteristics of oak species in this study provided little competitive advantage over those of associated species in the first few growing seasons, supporting the importance of oak advance reproduction over stump sprouting for regeneration success in bottomland forests (Motsinger et al. 2010).

This study provides information on the sprouting characteristics of common bottomland hardwood species, many of which have not been previously studied in detail. The high sprouting probability of American sycamore and the extremely rapid growth rates of its sprouts suggest it will be favored by coppice regeneration. In contrast, the sprouting characteristics of river birch and eastern cottonwood highlight the importance of regeneration from other sources, such as seed, for these species. With their relatively low sprouting probabilities and slow sprout growth rates, our results suggest that sprouting may not be a reliable regeneration source for bottomland oaks species in stands with abundant American sycamore, American elm, or silver maple in the midwestern United States.

Endnote

1. For more information, see https://www.ncdc.noaa.gov/cdo-web/datasets/GHCND/stations/GHCND:USC00234544/detail.

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