

EARLY STUMP SPROUTING AFTER CLEARCUTTING IN A NORTHERN MISSOURI BOTTOMLAND HARDWOOD FOREST

Matthew G. Olson and Benjamin O. Knapp¹

Abstract.—Midwestern bottomland hardwood forests are often composed of species that are capable of sprouting vigorously, yet relatively little is known about sprout development within these mixed-species systems. This study describes stump sprouting of midwestern bottomland hardwood species in the first 3 growing seasons after a clearcutting with reserves (~2.0 m²/ha of residual basal area) treatment. Our results revealed that sprout development varied between species and between small and large parent trees over the 3-year study period. Stumps of American sycamore (*Platanus occidentalis* L.), American elm (*Ulmus americana* L.), and green ash (*Fraxinus pennsylvanica* Marsh.) maintained higher than 80 percent survival; the cumulative survival of river birch (*Betula nigra* L.) was 13 percent by the third growing season. Our results did not support a growth tradeoff between dominant sprout height and the number of live sprouts produced. The variation in sprouting ability that we observed in this study confirms the importance of factoring in pretreatment stand structure and composition when deciding on silvicultural regeneration methods in these bottomland hardwood forests.

INTRODUCTION

Many hardwood tree species are capable of sprouting (del Tredici 2001). Sprouts often have a competitive advantage over other sources of regeneration after disturbances (Dietze and Clark 2008, Vickers et al. 2011, White 1991). The rapid early growth of sprouts is supported by an established root system with stored carbohydrates (del Tredici 2001). A rapid flush of sprouts after a major disturbance can lead to the initiation of stands that are composed mainly of sprout-origin stems. As a result, sprouting allows forests to recover quickly from disturbances and can maintain predisturbance species composition (Dietze and Clark 2008).

Understanding the sprouting potential of a stand can help forest managers design silvicultural prescriptions for many hardwood forest types. Past research has shown that sprouting is related to the age, size, and condition of the parent tree before a disturbance (del Tredici 2001) and that site factors (e.g., site quality) can also influence sprouting (Gould et al. 2007, Johnson 1977, Weigel and Johnson 1998). Much of our understanding of sprouting is, however, based on research in upland forests.

Research on the regeneration of midwestern bottomland hardwood forests has been limited, and forest managers are often challenged to successfully achieve regeneration objectives in this forest type. Bottomland forest ecosystems support species that are capable of sprouting vigorously (Burns and Honkala 1990), but sprouting dynamics in these mixed-species systems are poorly understood. This investigation evaluated the effects of species and parent tree size on stump sprouting of midwestern bottomland hardwood species during the first three growing seasons after clearcutting with reserves. We also tested the relationship between stem density and height growth of sprout clumps to determine if there was a tradeoff between these sprouting characteristics.

¹ Resource Scientist (MGO), Missouri Department of Conservation, 551 Joe Jones Blvd., West Plains, MO 65775; Assistant Professor (BOK), University of Missouri. MGO is corresponding author: to contact, call 417-255-9561 or email at matthew.olson@mdc.mo.gov.

METHODS

Study Site

This investigation is based on a silviculture experiment in a bottomland hardwood forest in northeastern Missouri. The study site is located in the Deer Ridge Conservation Area (CA), a public land area that is managed by the Missouri Department of Conservation. The experiment was established in 1993 in a mature bottomland forest remnant that is adjacent to a channelized segment of the North Fabius River in Lewis County, MO.

The silviculture experiment at the Deer Ridge CA includes a clearcutting treatment applied as one of three treatment levels. Treatments were assigned to 2.6- to 3.2-ha stands after a completely randomized design. A clearcutting with reserves (CCR) treatment was randomly assigned to eight stands, which were treated between summer 1999 and spring 2000. Before treatment, stands that were designated for clearcutting had a mean stem density and basal area of 465 tree/ha and 28 m²/ha, respectively (trees ≥ 11.4 cm diameter at breast height [d.b.h.]). The CCR treatment removed nearly all trees >2.5 cm d.b.h. On average, the CCR retained 20 trees/ha and 2 m²/ha of basal area in reserves. Silver maple (*Acer saccharinum* L.), the dominant species before treatment, was the most abundant species retained after clearcutting followed by oak species (*Quercus* L.), which were retained for habitat value and to encourage oak regeneration (Olson et al. 2015).

Sampling Design and Analysis

After the harvest in 2000, stump sprouting of all trees ≥ 11.4 cm d.b.h. (large stumps) was tracked in two, 0.2-ha circular plots within each CCR stand. Stems <11.4 cm d.b.h. (small stumps) were also tracked. Before treatment, 15 small silver maple stumps and 15 small American elm (*Ulmus americana* L.) stumps were identified in each stand to track sprouting. Small stumps of other common species and groups, including American sycamore (*Platanus occidentalis* L.), boxelder (*A. negundo* L.), hackberry (*Celtis occidentalis* L.), eastern cottonwood (*Populus deltoides* Bartr. Ex Marsh. var. *deltoides*), hickory spp. (*Carya* Nutt.), river birch (*Betula nigra* L.), and green ash (*Fraxinus pennsylvanica* Marsh.), were also tracked but at lower sampling intensity. As many as 100 small stumps of each species were initially marked and tracked in all CCR stands combined.

Several attributes of each sprout clump were recorded, including the number of live sprouts and height of the dominant sprout. Sprouting information was collected following the first (2000), second (2001), and third (2002) growing seasons.

A repeated measures analysis of variance (ANOVA) was used to assess the effects of species and parent tree size (large versus small stumps) on the cumulative survival (i.e., survival based on the initial population) of stumps, number of live sprouts/stump, and height of the dominant sprout within a sprout clump over the first three growing seasons following clearcutting (2000–2002). ANOVA models were based on a completely randomized split-plot design. Species (whole-plot factor) and parent tree diameter class (split-plot factor) were included as fixed effects, and stand was included as a random effect. Response variables were summarized at the stand level before analysis. Low sample sizes for some species limited the number of species included in ANOVA models. ANOVA was performed using PROC MIXED in SAS (SAS Institute Inc., Cary, NC; version 9.2). Data were transformed to improve normality and homogeneity of residuals when warranted. Mean separation of significant sources of variation (SVs) was performed using Tukey's honestly significant difference. Significant interactions were examined using the SLICE option. Significance was assessed at $\alpha = 0.05$.

To test for a tradeoff between the height and stem density of sprout clumps, the relationship between dominant sprout height and the number of live sprouts after the first growing season was tested using simple linear regressions built individually for each species. After inspecting scatterplots and linear regression results, we refit models for species with positive slopes from linear regression using a power function:

$$y = a \times x^b \quad (1)$$

Where

y = dominant sprout height,

x = number of live sprouts, and

a and b are estimated parameters.

For species with a negative slope in the linear regressions, models were refit with a negative exponential function:

$$y = a \times e^{(-b \times x)} \quad (2)$$

All models were fit using PROC MODEL in SAS, and significance was assessed at $\alpha = 0.05$.

Table 1.—ANOVA table for analysis of cumulative stump survival, density of sprouts/stump, and dominant stump sprout height for sprouts originating off of large and small stumps (dbh ≥ 11.4 and < 11.4 cm, respectively). Sources of variation (SV) are species (S), diameter class (D), year (Y), and interactions among the three.

SV	Stump survival				Sprouts/stump				Dominant height			
	Ndf	Ddf	F	P > F	Ndf	Ddf	F	P > F	Ndf	Ddf	F	P > F
S	7	62.3	6.27	<0.001	4	44.4	5.49	0.001	4	39.3	7.72	<0.001
D	1	14.1	12.55	0.003	1	15.1	23.60	0.002	1	13.5	0.09	0.773
S*D	7	62.3	1.60	0.1523	4	44.4	1.07	0.3840	4	39.3	0.95	0.444
Y	2	140	17.27	<0.001	2	101	33.77	<0.001	2	95.2	53.71	<0.001
S*Y	14	140	1.79	0.045	8	101	4.71	<0.001	8	95.2	4.70	<0.001
D*Y	2	140	1.44	0.241	2	101	1.26	0.288	2	95.2	0.48	0.620
S*D*Y	14	140	1.50	0.118	8	101	1.04	0.409	8	95.2	0.69	0.699

RESULTS

Species, year, and the interaction of species and year were significant SVs in ANOVA models for stump survival, sprouts per stump, and dominant sprout height for all stumps (large and small) in the CCR treatment (Table 1). Diameter class of stumps (large versus small stumps) was also a significant SV in models for stump survival and sprouts per stump.

Averaging across diameter classes, mean cumulative stump survival exceeded 80 percent for American elm, green ash, American sycamore, and hackberry after the first growing season and remained higher than 80 percent for American elm, green ash, and American sycamore by the end of the third season (Fig. 1A). In contrast, river birch survival was 22 percent after the first season and dropped to 13 percent by the end of the second and third seasons, which was significantly lower than several species in all years. Survival significantly decreased for hackberry (years 1 and 2 > year 3) and green ash (year 1 > years 2 and 3), but we saw no difference in survival for the other species. When averaged across species and time, mean cumulative survival of small stumps (80 percent) was significantly greater than large stumps (56 percent) (Fig. 2A).

The mean number of sprouts per stump, when averaged across diameter classes, differed between species only after the first growing season (Fig. 1B). American elm and hackberry stumps supported a significantly greater number of sprouts than silver maple, green ash, and American sycamore, with three, five, and four more sprouts per stump on average, respectively. Mean sprouts per stump for all species declined steadily and significantly over 3 years (i.e., year 1 > year 2 > year 3). Most notable were significant decreases in the number of sprouts for American elm (year 1 > years 2 and 3) and hackberry (year 1 > year 2 > year 3). When averaged across species and time, the mean number of sprouts/stumps was significantly greater for large stumps (nine sprouts) than small stumps (six sprouts) (Fig. 2B).

The mean dominant sprout height did not differ among species after the first growing season but did by the end of the second and third seasons (Fig. 1C). Dominant sprouts of American sycamore were significantly taller (3.8 m) than green ash and hackberry after the second season, and American sycamore was taller (5.3 m) than all species considered after the third season. By the end of the third season, dominant American sycamore sprouts had, on average, a height advantage over dominant sprouts of silver maple, American elm, green ash, and hackberry of 1.3 m, 1.2 m, 2.0 m, and 2.1 m, respectively.

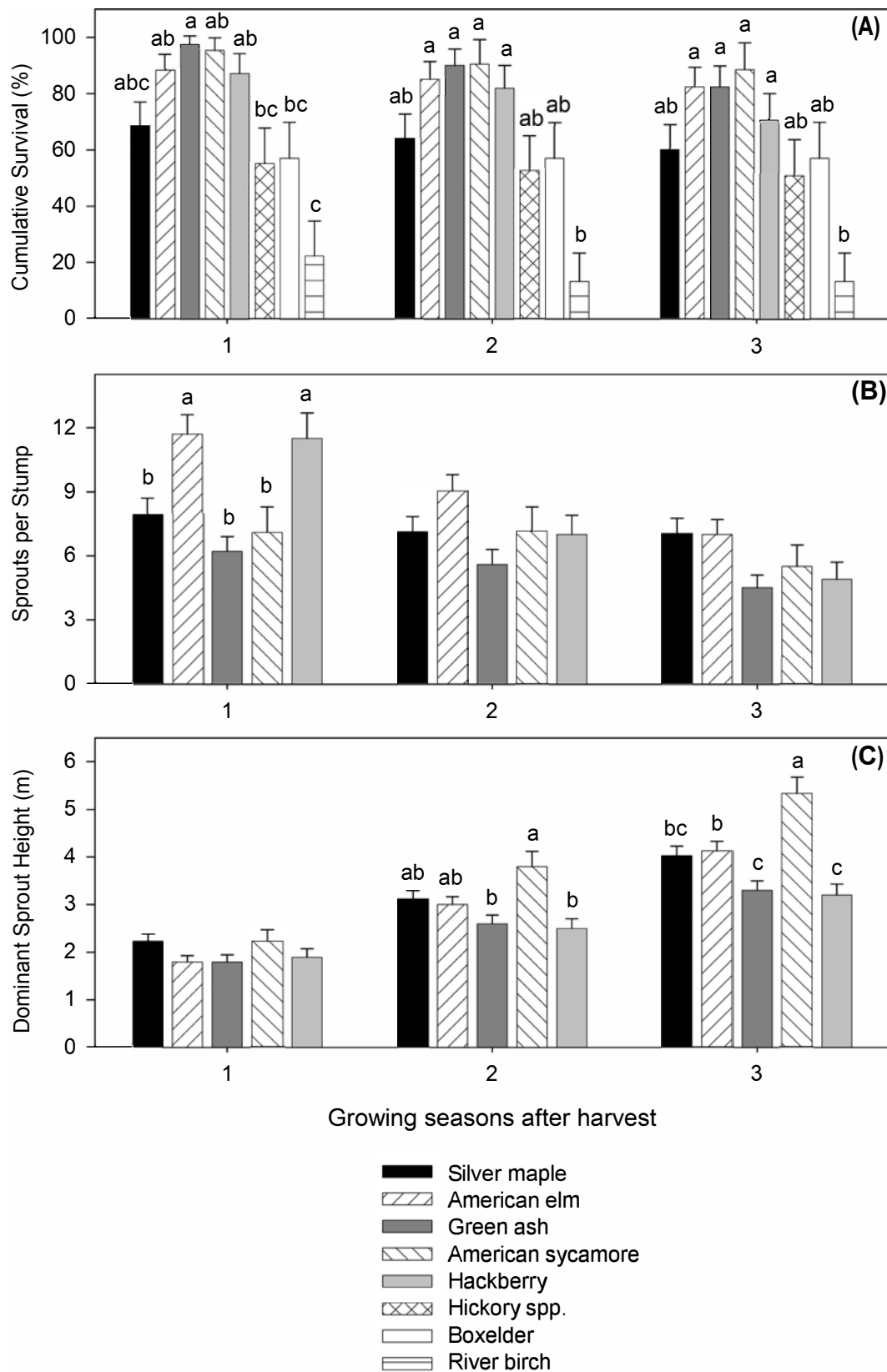


Figure 1.—Least squares means of cumulative stump survival (A), number of sprouts/stump (B), and dominant stump sprout height (C) for bottomland hardwood species over three growing seasons after harvest. Fewer species were included in analysis of variance models for sprouts/stump and dominant sprouts because of low sample size. Different letters indicate significant differences between species within each respective year ($p < 0.05$).

Table 2.—Regression results for number of sprouts at the end of year 1 and sprout height at the end of year 1

Species	<i>a</i>	<i>b</i>	p-value	<i>r</i> ²
American elm ^a	1.63	0.05	0.0326	0.0123
American sycamore ^a	1.74	0.17	<0.0001	0.2666
Boxelder ^a	1.91	0.16	0.0037	0.1539
Eastern cottonwood ^b	1.53	0.01	0.8552	0.0011
Green ash ^b	1.87	0.01	0.4520	0.0051
Hackberry ^a	1.53	0.10	0.0339	0.0442
Hickory spp. ^a	1.08	0.04	0.6108	0.0039
Oak spp. ^b	2.11	0.01	0.6773	0.0163
River birch ^a	1.60	0.15	0.2287	0.0840
Silver maple ^a	1.73	0.19	<0.0001	0.2208

^aModel form $y = a \times x^b$

^bModel form $y = a \times e^{(-b \times x)}$

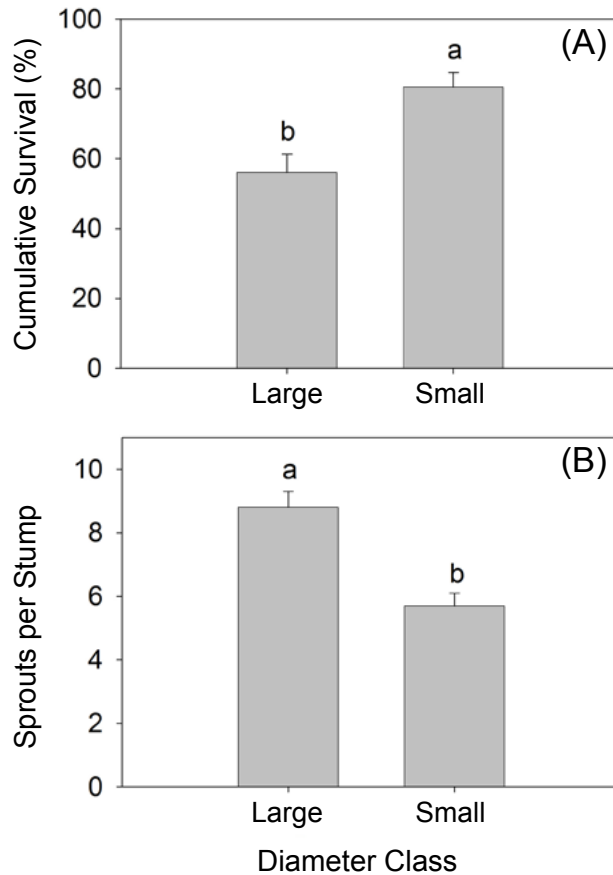


Figure 2.—Least squares means of cumulative stump survival (A) and number of sprouts/stump (B) for large and small stumps (d.b.h. ≥ 11.4 and < 11.4 cm, respectively) of bottomland hardwood species over three growing seasons after harvest. Different letters indicate significant differences between diameter classes ($p < 0.05$).

Simple linear regression of first year dominant sprout height predicted from the first year number of live sprouts per stump produced species-level models with positive and negative slopes. The nonlinear regression models resulted in significant models for American elm, American sycamore, boxelder, hackberry, and silver maple (Table 2). The strongest relationships between number of sprouts and dominant sprout height from significant models were for American sycamore (Fig. 3B) and silver maple (Fig. 3E), with r^2 values of 0.2666 and 0.2208, respectively.

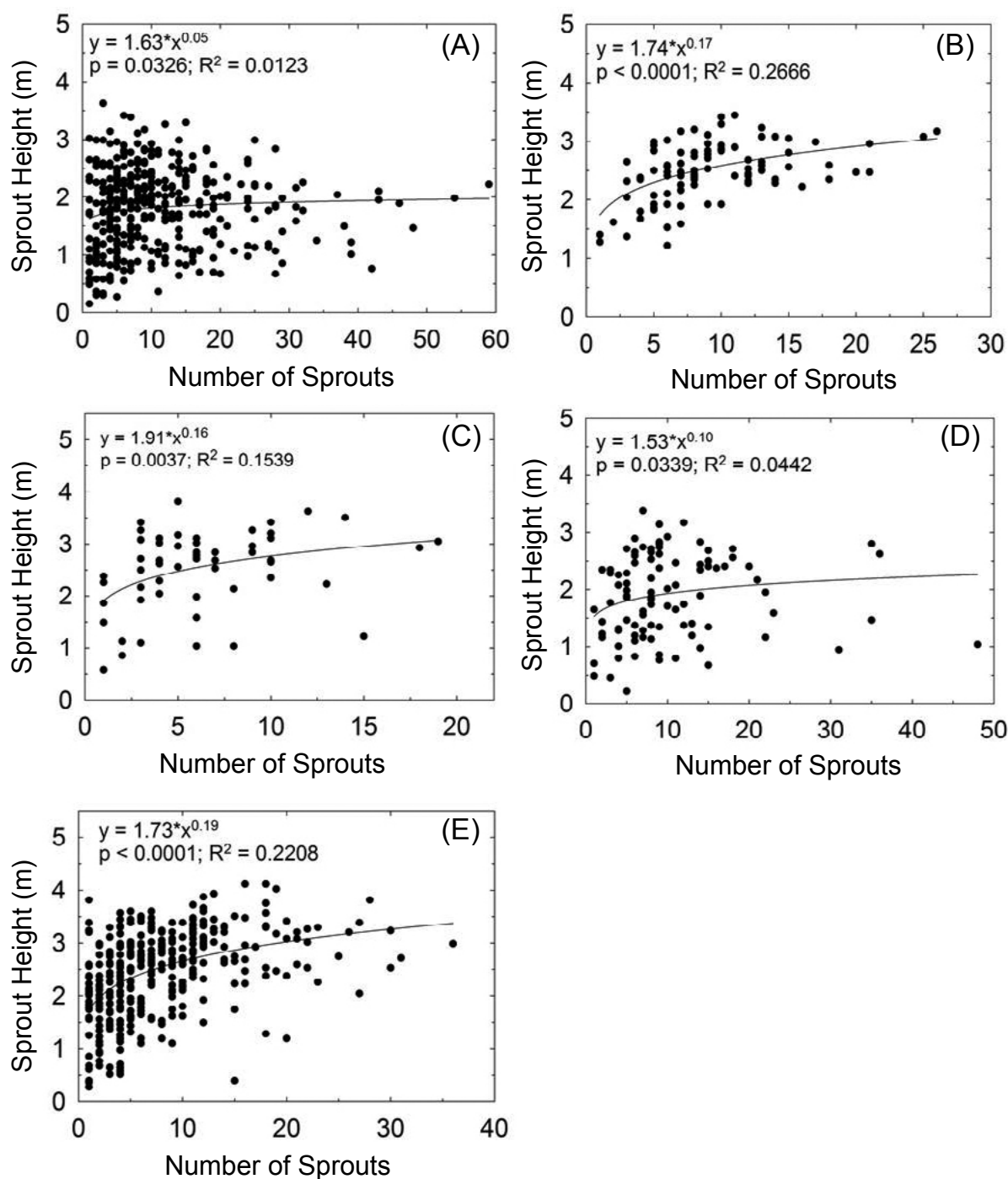


Figure 3.—Scatterplots and nonlinear regression models depicting the relationship between first-year dominant sprout height and the number of live sprouts for American elm (A), American sycamore (B), boxelder (C), hackberry (D), and silver maple (E).

DISCUSSION

Sprouting characteristics observed in this study varied by species. Three-year cumulative survival ranged from a low of 13 percent for river birch to greater than 80 percent for American elm, American sycamore, and green ash. Sprout clumps are generally expected to have high survival because of the initially rapid growth that enables sprouts to assert early dominance (Gould et al. 2007, McQuilkin 1975) that may persist for several decades after overstory removal (Johnson 1975, Roth and Hepting 1943, Wendel 1975). Low survival of river birch sprouts could be linked to this species' pioneer strategy. River birch frequently produces large crops of light, wind-dispersed seed, and it is capable of producing abundant seedlings, particularly on recently disturbed sites (Grelen 1990). Because of this ability to establish numerous seedlings after disturbance, river birch may be less dependent on vegetative reproduction than co-occurring species in these floodplain systems.

Interspecific variability in height growth during early stand development is a common pattern of mixed-species stand dynamics after a major disturbance (Oliver and Larson 1996), particularly under open conditions where species can express their growth potential (Vickers et al. 2014). In this study, dominant sprouts of American sycamore were significantly taller than all other species by the end of the third growing season and were, on average, more than 1 m taller than the next tallest species (American elm). American sycamore is one of the fastest growing tree species in North America and is a vigorous stump sprouter (Wells and Schmidting 1990). Silver maple and American elm had similar dominant sprout heights, and both species had a height advantage over several other species by year 3. Rapid growth and vigorous sprouting are also attributes of silver maple and American elm (Bey 1990, Gabriel 1990). Rapid sprout growth enables species such as American sycamore, silver maple, and American elm to aggressively recolonize recently disturbed floodplain sites after top-killing disturbances.

Johnson (1975) and Roth and Hepting (1969) reported that sprout clump densities follow a pattern of rapid decline during the first decade followed by a gradual decline over subsequent decades. Stumps of American elm and hackberry supported more live sprouts than other species before the start of the second growing season, but their stem densities declined rapidly during year 2. This decline in density could be related to a variety of biotic and abiotic factors that affect these floodplain forests. From a stand development perspective, this pattern could represent the early transition from the stand initiation stage to the stem exclusion stage. For example, the large flush of American elm and hackberry sprouts initiated by clearcutting (i.e., stand initiation) was followed by early onset of intense competition within sprout clumps and with neighboring plants (i.e., the start of stem exclusion) in the open conditions created by the CCR treatment. Because stand development is a continuous process, transition from one stage to the next occurs continuously with rate changes driven by internal and external factors that either slow or hasten the process.

Within the data range of our study, our findings supported the expectation that parent tree size would influence sprouting characteristics. We observed more live sprouts on large stumps than on small stumps. A higher density of sprouts developing off large stumps was likely due to a larger bank of dormant buds accumulated by larger, and presumably older, trees before harvest (Johnson 1975, Kozlowski et al. 1991). The higher sprout density could also be related to a greater perimeter of cambium for adventitious bud development (Kozlowski et al. 1991). Cumulative survival of sprout clumps was higher for small stumps than for large stumps, which is similar to the commonly reported inverse relationship between sprouting probability and parent tree size (del Tredici 2001). Although we did not detect an effect of stump size on

dominant sprout height, differences in sprout density and survival of sprout clumps between small and large stumps could convey competitive advantages onto each. For example, higher survival of small stumps could translate into a survival advantage over sprout clumps that develop from large stumps, whereas a higher density of sprouts from surviving large stumps could increase the likelihood that at least one sprout will secure a position in the developing canopy. The latter situation could result from a buffering effect of larger sprout clumps that protects interior sprouts from competition from neighboring sprout clumps.

Theoretically, stumps that produce many sprouts have less to invest in individual sprout growth than those that produce fewer sprouts. This scenario represents a growth tradeoff in how live stumps allocate finite resources to sprout production and would be supported by a negative relationship between sprout height and number of live sprouts. Regression relationships between dominant sprout height and the number of live sprouts after the first growing season, however, indicated that few species displayed patterns of a negative relationship, none of which were statistically significant. This result does not support a simple growth tradeoff between sprout height and density. A significant positive relationship was detected for several species, although the r -squared values were greater than 0.2 for only American sycamore and silver maple. The power function used to describe this relationship suggests that dominant sprout height reaches either a peak or a plateau with an increasing number of live sprouts. This pattern is biologically logical because there is likely a limit to maximum sprout height in a 3-year period. Moreover, stumps that produce low numbers of sprouts may be of low vigor, resulting in poor subsequent growth of the sprouts. Including additional covariates, such as size and vigor of the parent tree, may also help to shed light on growth tradeoffs in sprout production.

CONCLUSIONS

Our study provides evidence that sprouting is common to bottomland hardwood species, and the interspecific variation in sprouting ability suggests the importance of factoring in pretreatment composition when deciding on silvicultural regeneration methods in these hardwood forests. For example, even-aged regeneration methods applied to stands composed of species with a strong sprouting ability, such as American sycamore and American elm, are more likely to stimulate sprouts that capture a dominant position in the regenerating cohort than stands composed of species with relatively poor sprouting ability, such as river birch. In this study, however, we considered only sprout-origin regeneration. Additional research is needed to determine the contribution of sprouting to stand initiation in this mixed-species forest type.

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