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Can coppicing planted saplings improve the growing position of mid-tolerant northern hardwood tree species in harvest gaps?

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ABSTRACT

Group harvesting is often used to regenerate mid-tolerant tree species. However, in managed northern hardwood forests of the Great Lakes region, regeneration failures are common among mid-tolerant species regardless of gap size. Coppicing advance regeneration has the potential to alter recruitment patterns within harvest gaps, as some mid-tolerant species have large dormant season carbohydrate reserves in the root system. However, the comparative sprouting abilities of northern hardwood saplings are not well quantified. Furthermore, variation in light availability and chronic browsing from white-tailed deer may modify comparative sprouting abilities. In this study, we tracked the effects of dormant season coppicing and deer exclusion on the initial sprouting response and five-year survival, height growth, and final height of seven-year-old volunteer white ash saplings and planted yellow birch, paper birch, northern red oak, sugar maple, red maple, and American beech saplings across a gradient of harvest gap sizes (10–35 m diameter, <0.5–1.25 tree height) in a mature even-aged northern hardwood stand in northern Lower Michigan, USA. In addition, saplings were given a growing position ranking, which integrated sapling final height and survival status relative to competitors to evaluate the effects of coppicing and deer exclusion on sapling development. Overall, coppicing produced a strong initial sprouting response with nearly all red maple and northern red oak stems initially sprouting. In the absence of deer, appreciable differences in sprout survival and height growth occurred among mid-tolerant and intolerant species and contributed to changes in growing position. Northern red oak sprouts significantly gained growing position over all species through a combination of high survival and modest height growth across all gap sizes. In contrast, coppiced yellow birch and paper birch sprout survival was significantly lower than uncoppiced stems, which contributed to declines in growing position for both species across all gap sizes. Coppicing in the absence of deer had less effect on the growing position of mid-tolerant red maple and white ash and shade tolerant sugar maple and American beech. Without deer exclusion, browsing limited the effectiveness of coppicing by reducing height growth and final height of all mid-tolerant species. Collectively, our results indicate that coppicing does not benefit mid-tolerant species equally and is unlikely to benefit browsing-preferred species in areas with high deer density. Nevertheless, in areas of lower deer density or in situations where sprouts can be protected, coppicing may improve the competitiveness of northern red oak saplings within harvest gaps.

1. Introduction

Canopy gaps provide crucial yet competitive environments for tree species recruitment in closed-canopy forests (Yamamoto 2000). Competition for growing space is thought to be affected by gap size and its corresponding influence on resource availability (Ricklefs 1977; Denslow 1980). Small gaps, created by the death of a single tree, modestly increase resource availability to the understory and potentially favor shade tolerant species (Schliemann and Bockheim 2011; Walters et al. 2016). Conversely, high resource availability in multi-tree gaps promotes fast growing, shade intolerant species (Leak and Filip 1977; Walters et al. 2014).

Foresters have utilized the traditional model of gap partitioning as the basis for determining gap size (Hawley 1937). Single tree harvest gaps have been used to promote sugar maple (*Acer saccharum* Marsh.), an economically valued, shade tolerant species, among uneven-aged northern hardwoods for decades in the Great Lakes region (Arbogast 1957; Tubbs 1977; Crow et al. 2002). Recently, in response to growing

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concern over diminishing resources for wildlife and declining forest resilience, management recommendations have shifted towards increasing species diversity through varying gap size (Lindenmayer and Franklin 2002; Kern et al. 2017). However, evidence indicates that species composition within harvest gaps of differing size does not correspond predictably with shade tolerance rankings, raising concerns over whether gap harvesting can reliably modify species composition (Webster et al. 2018).

Mid-tolerant tree species have been one of the more challenging functional groups to regenerate with harvest gaps (Shields et al. 2007; Matonis et al. 2011; Bolton and D'Amato 2011; Kern et al. 2013; Walters et al. 2016; Knapp et al. 2019). For example, although yellow birch (*Betula alleghaniensis* Britton.) advance regeneration can survive and develop into free-to-grow heights within small canopy gaps (100–400 m^2) (Webster and Lorimer 2005), it is less persistent beneath an undisturbed canopy compared to shade tolerant species (McClure et al. 2000) and is rarely found as a free-to-grow sapling within harvest gaps (Neuendorff et al. 2007; Matonis et al. 2011). Conversely, larger gaps can be dominated by shade intolerant species such as pin cherry (*Prunus pensylvanica* L.) and paper birch (*Betula. papyrifera* Marshall) (Nyland et al. 2007; Walters et al. 2014), or by advance regeneration of shade tolerant species (Bolton and D'Amato 2011; Forrester et al. 2014; Kern et al. 2017). Consequently, many mid-tolerant species fail to regenerate in harvest gaps (Walters et al. 2020).

Release treatments provide a potential management option for improving mid-tolerant species recruitment in harvest gaps. Herbicides have been shown to be effective at releasing mid-tolerant species from competition (Povak et al. 2008; Miller et al. 2017). However, the use of herbicides may be administratively limited (Thiffault and Roy 2011). Mechanical treatments provide another option for releasing mid-tolerant species (Ward 2013) but are often expensive and logistically difficult to implement (Bailey et al. 2011). As such, new cost-effective release treatments are needed to create opportunities for recruiting mid-tolerant species within harvest gaps.

Coppicing advance regeneration may be an effective release treatment. Although sprouting is common among temperate hardwood species (Del Tredici 2001), mid-tolerant species generally have larger carbohydrate reserves in their roots compared to tolerant or intolerant competitors (Canham et al. 1999; Kobe et al. 2010). For example, oaks (*Quercus* spp) have large carbohydrate reserves, recover rapidly from top-kill via vigorous sprouting and growth (Chapin et al. 1990; Kruger and Reich 1993, 1997; Bond and Midgley 2003; Brose et al. 2013; Keyser 2019), and are frequently found on dry sites where fire and drought are common (Frey et al. 2007). In contrast, other mid-tolerant species associated with productive sites, such as yellow birch, do not have large dormant season carbohydrate reserves in the root system (Gaucher et al. 2005) and may not recover from coppicing as rapidly as oak. Therefore, coppicing may only improve the growing position of some mid-tolerant species and particularly those adapted to drier, more fire prone sites. Regardless of specific predictions, little information exists describing the sprouting response of planted-advance regeneration of northern hardwood tree species following a coppice treatment in the dormant season.

Little is also known about how existing biotic and abiotic factors will impact the effectiveness of coppicing. Sprout vigor could be affected by gap size, as saplings growing in the low light environment of small gaps may have limited carbohydrate reserves to mobilize for sprouting and growth (Piper et al. 2009; Kobe et al. 2010). The effectiveness of coppicing may also be constrained by browsing pressure, as white-tailed deer (*Odocoileus virginianus* (Zimmerman)) have been shown to prefer sprouts over seed established stems (Moore and Johnson 1967; Harlow et al. 1997). Selective browsing could also provide a competitive advantage to less-preferred species such as American beech (*Fagus grandifolia* Ehrh) or white ash (*Fraxinus americana* L.) (Krueger et al. 2009; Forrester et al. 2014; Royo et al. 2016; Walters et al. 2016).

Sprouting has been recognized as an important regeneration method worldwide (Bond and Midgley 2001; Poorter et al. 2010). Previous studies have detailed how sprouting from harvested mature trees is altering species composition in Eastern North America (Gould et al. 2006; Fei and Steiner 2009; Keyser and Loftis 2015). However, to our knowledge, no studies have examined how coppicing affects planted-advance regeneration across a range of harvest gap sizes in the presence or absence of deer. To examine the effectiveness of this treatment, we recorded the influence of coppicing on seven northern hardwood tree species grown inside and outside of deer exclosures across a gradient of harvest gap sizes (10–35 m in diameter, <0.5–1.25 tree height) on a mesic site in an even-aged northern hardwood stand in northern Lower Michigan, USA. We predicted in the absence of browsing pressure (1) coppicing would improve the competitive position of fire adapted, mid-tolerant species in group sized harvest gaps but not in single tree gaps, (2) sprouting percentage and survival of all species will increase with gap size, (3) height growth of sprouts and uncoppiced stems of all species will increase with gap size, and (4) browsing pressure will override the effects of coppicing and gap size, as growing position ranks among species will correspond with differences in browsing preference when deer are not excluded. The results of this study will inform on whether coppicing can improve the growing position of planted-advance regeneration of mid-tolerant northern hardwood tree species in harvest gaps.

2. Methods

2.1. Study area

Our experiment was conducted in a18 ha stand in Emmet County, Michigan, USA (45°36′38.0″N, 84°53′40.6″W). Mean daily maximum temperatures in Emmet County range from −3.3 °C to 26.1 °C. Precipitation averages 81 cm of rain and 320 cm of snow annually (US Climate Data). Site quality, as defined by habitat type, ranged from very mesic, nutrient rich (*Acer-Fagus-Osmorhiza-Caulophyllum*) (AFOCa) to mesic, nutrient rich (*Acer-Fagus-Osmorhiza*) (AFO) (Burger and Kotar 2003). The stand was even-aged and likely 100–120 years-old based on structural data from other northern hardwood stands in the region (Henry and Walters unpublished data). Species composition was dominated by sugar maple (79%) with minor components (<10%) of basswood (*Tilia Americana* L.), white ash, and American beech. Deer density at the site averaged 10.4 deer/km^2 (Walters et al. 2016).

2.2. Experimental design

In winter 2006–2007, 39 harvest gaps ranging in size from 127-955 m^2 were established. The gaps were approximately 10–35 m diameter and <0.5–1.25 tree heights in size relative to the residual border trees. Each gap was separated by at least 30 m of unharvested buffer to reduce potential edge effects. Plots measuring 10 × 10 m were established in the center of each harvest gap, along with 4 unharvested areas. To exclude deer, we selected 30 plots to be fenced with 2.4 m tall mesh fencing (DeerBusters, Waynesboro, Pennsylvania, USA), while the residual 9 plots remained unfenced. Both fenced and unfenced treatments were randomly assigned to plots across the full range of gap size (Table 1). Within each plot, we established 16 subplots (4 m^2) in a square grid. Each subplot was separated by a 0.5 m buffer. In spring 2007, we planted 3–5-month-old yellow birch, northern red oak (*Quercus rubra* L.), red maple (*Acer rubrum*), American beech, paper

Table 1
The number of fenced and unfenced single tree, small group, and medium group sized harvest gaps used in this study.

Treatment	Single tree gaps (10.0–14.9 m diameter)	Small group sized gaps (15.0–29.9 m diameter)	Medium group sized gaps (30.0–35.0 m diameter)
Fenced	10	15	5
Unfenced	5	2	2

birch, and sugar maple seedlings in the subplots. The seedlings were germinated in containers and grown in a lath house at the Michigan State University Tree Research Center. Prior to planting the seedlings were removed from containers, washed, and planted as bare root seedlings. All seedlings lacked branching and were between 10 and 60 cm in height. In addition to the planted seedlings, first-year volunteers of white ash were also retained in the subplots. All other naturally established advance regeneration was removed from the subplots prior to study initiation. After planting, each subplot contained at least one seedling of each species. Weeding was periodically performed to reduce herbaceous competition on seedlings through 2013. Prior to the initiation of this experiment, we intermittently removed planted saplings and retained volunteers from the subplots to prevent overcrowding. The goal of the removals was to reduce competition among saplings, create a uniform growing environment within the subplot, and maintain species diversity. All removals were made without size bias. For further information on the sapling removals see Walters et al. (2016).

At the end of the 2013 growing season, we randomly selected three planted subplots in each plot for coppicing. Planted saplings and retained volunteers in the other two subplots remained uncoppiced. Each plot contained between 3 and 7 species; and all stems had lost nearly all leaves from autumn leaf abscission. Coppiced saplings were cut at the root collar with hand shears. No stems outside the subplots were coppiced.

2.3. Field measurements

All planted saplings were measured for height and ground line diameter prior to coppicing. Each coppiced and uncoppiced subplot was remeasured in the fall of 2014, 2015, and 2018. In coppiced subplots, individual saplings were measured for sprouting response, height, survival, and growing position rank relative to other sprouts. Height was assessed on the dominant stem when coppiced saplings produced multiple sprouts. Stems in uncoppiced subplots were measured for height, survival, and growing position rank relative to other uncoppiced stems. Light availability was estimated as a percentage of canopy openness from hemispherical photographs taken from the center of each subplot in July 2013; see Walters et al. (2014) for further information on how canopy openness corresponded with gap size. In uncoppiced subplots, stems exceeding 2 m in height were bent down prior to taking the photograph in order to quantify the effect of canopy trees on light availability. Black and white threshold values were derived from Sidelook software (Nobis and Hunziker 2005). The photos were then analyzed with Gap Light Analyzer v 2.0 (Frazer et al. 1999) parameterized with a custom lens distortion correction obtained from the Sigma Corporation.

2.4. Statistical methods

2.4.1. Sprouting, survival, growth, and final height of planted stock

We used generalized linear mixed models (ANOVA) to examine factors influencing the sprouting of coppiced saplings and the survival of coppiced and uncoppiced stems. In both analyses, a binomial distribution with a logit link was used to model residual errors. A Kenward-Roger approximation of the denominator degrees of freedom was used in both analyses to account for imbalance in the experimental design. Preliminary analyses yielded a strong species effect prompting us to run species-specific models. Sprouting was analyzed on individual saplings in a completely random design. Deer exclusion (fenced or unfenced) was considered a categorical, fixed effect, while canopy openness was considered a continuous, fixed effect. Subplot was considered a categorical random effect. For red maple, northern red oak, white ash, and yellow birch, the full model included the main effects of canopy openness, deer exclusion, and their interaction. Due to limited replication outside the deer exclosures ($n < 6$ saplings), the full model for American beech, paper birch, and sugar maple was restricted to canopy openness and subplot. Model selection was accomplished through backward selection. Preliminary model runs producing interaction terms above the recommended threshold for pooling ($P > 0.25$) resulted in the elimination of the highest-order interaction term exceeding the pooling threshold (Bancroft 1964). Backward selection ceased once all interaction terms fell below the recommended pooling threshold or were eliminated from the model. Factors and interactions remaining in the model were considered significant ($\alpha = 0.05$) and further explored through Tukey-Kramer post-hoc tests. All statistical procedures were conducted with SAS Version 9.4 (PROC GLIMMIX) (SAS Institute, Cary, NC, U.S.A.).

Survival was analyzed under a split-plot design. Deer exclusion served as the whole-plot factor, while coppicing (coppiced or uncoppiced) served as the split-plot factor. Deer exclusion and coppicing were considered categorical, fixed effects, while canopy openness was considered a continuous, fixed effect. The interaction between gap and deer exclusion was considered a random effect. The full model for red maple, northern red oak, white ash, and yellow birch included the fixed main effects of canopy openness, coppicing, and deer exclusion, two-way interactions between canopy openness × coppicing and deer exclusion × coppicing, a three-way interaction between canopy openness, deer exclusion, and coppicing, and the random interaction between gap and deer exclusion. Low replication required the use of smaller initial models for paper birch, American beech, and sugar maple. For paper birch, the full model included only the fixed main effects of coppicing, canopy openness, deer exclusion, and the random interaction between gap and deer exclusion. The full model for sugar maple and American beech was limited to the fixed main effects of canopy openness, coppicing, and the random interaction between gap and deer exclusion. All other protocols followed the procedures described in the sprouting analysis.

Five-year height growth (2013–2018) and final height (2018) were analyzed under the previously described split-plot design using generalized linear-mixed models (ANOVA) (PROC MIXED). Growth was determined for uncoppiced stems by subtracting the pre-treatment sapling height measured in 2013 from the final height recorded in 2018. For coppiced stems, growth was identical to final height. The individual species models were identical to those described in our survival analysis. All coppiced and uncoppiced stems recorded as living in 2018 were included in both analyses.

2.4.2. Relative growing position of planted stock

Three separate analyses were conducted to evaluate competitive hierarchies among planted saplings within each treatment combination: deer excluded + coppiced, deer excluded + uncoppiced, unexcluded + coppiced, unexcluded + uncoppiced. Due to experiment-long effects on survival, species were unevenly distributed between and within subplots. Thus, subplots containing less than three species at the beginning of the experiment were excluded from all ranking analyses. Response to treatment in the first analysis was quantified by assigning sprouts and uncoppiced planted stems a growing position rank that integrated survival and final height (2018) at the subplot level. All living stems were ranked sequentially by their final height, with the tallest sapling receiving a ranking of one. Mortality was accounted for by assigning deceased saplings a ranking equal to the original number of saplings recorded in the plot (e.g., a deceased coppiced or uncoppiced stem in a subplot that contained 5 saplings in 2013 would be ranked 5 in 2018). Stems with identical final heights (or multiple deceased stems) received the same growing position rank. Differences in species average ranking were then compared within each treatment with a Kruskal-Wallis test ($\alpha = 0.05$). Significant treatment differences were further explored with Steel-Dwass all pairs multiple comparison tests.

The second analysis examined how the response of species to treatment changed over time. Change in growing position was calculated as the difference between initial (2013) and final (2018) growing position rank. All other procedures were identical to the previously described

analysis.

The third analysis examined change in growing position within deer exclosures in different light environments. Harvest gaps were classified as single-tree (10.0–14.9 m diameter, < 10% canopy openness) or small-to-medium group sized harvest gaps (15.0–35.0 m diameter, 10–32%) based upon percent canopy openness values presented in Walters et al. (2016). Treatments without deer exclusion were not included in this analysis due to low replication. All other procedures were identical to the previously described analyses.

3. Results

3.1. Sprouting of planted stock

Overall, 88% of coppiced saplings sprouted, with nearly all red maple and northern red oak initially sprouting (Table 2). American beech and yellow birch were significantly less likely to sprout than red maple and northern red oak (Table 2). Neither deer exclusion, canopy openness, nor their interaction significantly affected sprouting for any species (Table 3).

3.2. Survival of planted stock

For all species, the average survival of uncoppiced stems (77%) was higher than sprouts (71%). Northern red oak sprout and uncoppiced stem survival was higher when deer were excluded, but deer exclusion produced no statistically significant differences for all other species (Tables 3 and 4). Yellow birch and paper birch sprout survival was significantly lower than uncoppiced stems (Tables 2 and 3). Survival was not significantly associated with canopy openness for any species (Table 3). However, uncoppiced northern red oak stems survived better than sprouts at higher levels of canopy openness (Table 3) (data not shown). No investigated factors or interactions significantly influenced survival for red maple, white ash, American beech, or sugar maple (Table 3).

3.3. Height growth of planted stock

After five years (2013–2018, since coppice treatment), sprout average height growth (115 cm, all species considered) exceeded that of uncoppiced stems (71 cm). The five-year growth of paper birch, red maple, and northern red oak sprouts significantly exceeded their uncoppiced stems (Tables 2 and 3). Deer exclusion produced significantly greater five-year growth for red maple, northern red oak, yellow birch, and paper birch sprouts and uncoppiced stems compared to where deer were not excluded (Tables 3 and 4). Increasing canopy openness was associated with significantly greater five-year growth for red maple, northern red oak, American beech, and paper birch sprouts and uncoppiced stems (Fig. 1). Yellow birch five-year growth also increased at higher levels of canopy openness, but uncoppiced stem growth exceeded that of sprouts (Fig. 2). No examined factor or interaction significantly affected white ash or sugar maple five-year growth (Table 3).

3.4. Final height of planted stock

The average final height of uncoppiced stems (2008–2018) (168 cm all species considered) exceeded that of sprouts (2013–2018) (115 cm). Uncoppiced stems of American beech, paper birch, red maple, and white ash were significantly taller compared to their sprouts (Table 2). Deer exclusion resulted in significantly taller sprouts and uncoppiced stems of red maple, northern red oak, yellow birch, and paper birch compared to where deer were not excluded (Tables 3 and 4). Increasing canopy openness was associated with significantly greater final height for red maple, northern red oak, American beech, and paper birch sprouts and uncoppiced stems (Fig. 1) (Table 3). The final height of yellow birch also increased with canopy openness, but uncoppiced stems were taller than sprouts at higher levels of canopy openness (Fig. 2). No examined factor significantly influenced the final height of sugar maple (Table 3).

3.5. Relative growing position of planted stock

Averaged across all gap sizes, final growing position ranking varied significantly among species (metric integrating final height and survival) where deer were excluded and stems were coppiced ($P = 0.0029$) (Fig. 3). In the absence of deer, northern red oak sprouts received the highest average growing position rank and occupied significantly better growing position than sugar maple, red maple, American beech, and paper birch (Fig. 3). Where deer were excluded but stems were not coppiced ($P < 0.0001$), yellow birch received the highest growing position ranking and occupied significantly better growing position than any other species (Fig. 3). In contrast, both sprouts and uncoppiced sugar maple stems received the lowest growing position ranking where deer were excluded (Fig. 3). No significant differences in growing position rank were detected among species without deer exclusion (Coppiced: $P = 0.0750$, Uncoppiced: $P = 0.1218$) (Fig. 3).

Significant differences in growing position change were also found among species in coppiced subplots with deer exclusion ($P < 0.0001$) (Fig. 2). Averaged across all gap sizes with deer exclusion, the four initially tallest species lost growing position as sprouts, while sprouts from the three shortest species gained growing position (Fig. 4). Northern red oak sprouts benefited most from deer exclusion, and significantly gained growing position compared to all other species (Fig. 4). The general pattern of sprout growing position change in the presence of deer was similar to that observed when deer were excluded ($P = 0.0029$) (Fig. 4). However, in the presence of deer, red maple sprouts benefited most from coppicing, and significantly gained growing position compared to paper birch and yellow birch (Fig. 4). Trends in uncoppiced stem growing position change with ($P = 0.0564$) and without ($P = 0.7280$) deer exclusion were less consistent and not statistically significant (Fig. 4).

Trends in growing position change in single tree (10.0–14.9 m diameter, < 0.5 tree height) and group sized gaps (15.0–35.0 m diameter, 0.5–1.25 tree height) with deer exclusion mirrored previous

Table 2
Estimated average sprouting (±1 SE), survival, five-year height growth, and final height of coppiced and uncoppiced saplings. Species with differing letters were found to have a significantly different probability of sprouting (Tukey-Kramer) ($\alpha = 0.05$). Bold text indicates a significant difference between coppiced sprouts and uncoppiced stems in survival, growth, or final height.

	Coppiced					Uncoppiced			
Species	N	Sprouting (%)	Survival (%)	Height growth (cm)	Total height (cm)	N	Survival (%)	Height growth (cm)	Total height (cm)
American beech	25	67 (10)^{b}	71 (27)	59.7 (13.2)	62.8 (18.8)	21	98 (6)	68.1 (10.1)	**144.2 (13.4)**
Paper birch	47	88 (5)^{ab}	28 (14)	**126.6 (26.2)**	115.0 (44.2)	23	**72 (15)**	57.3 (29.5)	**251.4 (46.1)**
Red maple	96	98 (1)^{a}	77 (5)	**77.8 (8.0)**	72.4(10.9)	100	77 (5)	30.0 (8)	**105.0 (10.9)**
Northern red oak	129	97 (1)^{a}	75 (7)	**83.9 (8.3)**	78.6 (10.8)	94	76 (6)	38.2 (8.9)	104.3 (11.6)
Sugar maple	32	84 (7)^{ab}	53 (14)	71.8 (11.9)	88.3 (14.2)	21	61 (12)	38.1 (12.4)	73.4 (13.7)
White ash	52	85 (5)^{ab}	82 (8)	122.4 (21.0)	117.7 (27.6)	46	75 (8)	86.0 (19.6)	**200.2 (26.4)**
Yellow birch	71	72 (7)^{b}	45 (11)	106.6 (22.6)	79.6 (41.5)	25	**94 (5)**	138.8 (18.8)	301.5 (34.3)

Table 3
Results of generalized linear mixed models and general linear mixed models (ANOVA) examining factors influencing the initial sprouting response of coppiced stems and the survival, five-year height growth, and final height of all living coppiced and uncoppiced stems of volunteer white ash (WA) and planted red maple (RM), northern red oak (RO), yellow birch (YB), American beech (AB), sugar maple (SM), paper birch (PB) saplings. The initial model for sprouting included the fixed main effects of canopy openness, the interaction between deer exclusion and canopy openness, and the random effect of subplot. For the survival, height growth, and final height analyses, the initial model included the fixed main effects of canopy openness, deer exclusion, coppicing, two way interactions between canopy openness (CO) × coppicing (C) and coppicing × deer exclusion (DE), the three-way interaction between canopy openness, deer exclusion, and coppicing, and the random interaction of gap and deer exclusion. Bolded main effects and interactions were considered significant at $\alpha = 0.05$.

Response		RM			RO			YB			WA			AB			SM			PB			
	Model	DF	DDFM	F Ratio	Prob > F	DDFM	F Ratio	Prob > F	DDFM	F Ratio	Prob > F	DDFM	F Ratio	Prob > F	DDFM	F Ratio	Prob > F	DDFM	F Ratio	Prob > F	DDFM	F Ratio	Prob > F
Sprouting	Canopy openness	1	66.55	1.72	0.1942	91.23	0.29	0.5882	28.56	0.55	0.2269	49.00	0.73	0.3958	22.00	4.06	0.0625	18.21	0.05	0.4793	45.00	0.05	0.4870
	Deer exclusion	1	77.43	2.47	0.1201	81.36	1.23	0.2666	11.03	0.75	0.3874	49.00	0.38	0.5416	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
	CO*DE	1	66.55	2.61	0.1108	91.23	1.96	0.1617	n/a	n/a	> 0.25	n/a	n/a	> 0.25	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
Survival	Canopy openness	1	152.00	0.31	0.5767	161.00	3.08	0.0812	26.00	2.13	0.1569	47.00	1.47	0.2322	10.00	0.05	0.4950	15.00	1.26	0.2608	28.00	3.78	0.6210
	Deer exclusion	1	31.00	1.69	0.2034	33.00	8.96	**0.0052**	31.00	1.86	0.1819	32.00	0.81	0.3742	n/a	n/a	n/a	n/a	n/a	n/a	29.00	2.66	0.1135
	Coppice	1	152.00	0.03	0.8624	161.00	3.85	0.0652	26.00	7.87	**0.0094**	47.00	0.41	0.5245	10.00	1.14	0.3116	15.00	0.13	0.7231	28.00	4.66	**0.0397**
	CO*C	1	n/a	n/a	> 0.25	161.00	4.70	**0.0316**	n/a	n/a	> 0.25	n/a	n/a	> 0.25	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
	DE*C	1	n/a	n/a	> 0.25	n/a	n/a	> 0.25	n/a	n/a	> 0.25	n/a	n/a	> 0.25	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
	CO*DE*C	2	n/a	n/a	> 0.25	161.00	1.88	0.1555	n/a	n/a	> 0.25	n/a	n/a	> 0.25	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
Height growth	Canopy openness	1	26.50	10.89	**0.0028**	23.10	74.05	**<0.0001**	25.60	15.74	**0.0005**	36.90	0.20	0.6551	15.40	9.82	**0.0017**	13.60	0.09	0.7668	15.30	24.18	**<0.0001**
	Deer exclusion	1	22.70	20.32	**0.0002**	26.80	22.83	**<0.0001**	21.00	13.16	**0.0016**	15.80	2.31	0.1484	n/a	n/a	n/a	n/a	n/a	n/a	14.40	9.96	**0.0035**
	Coppice	1	132.00	35.78	**<0.0001**	146.00	22.75	**<0.0001**	32.80	5.53	0.0648	59.60	2.41	0.1258	14.40	0.48	0.4983	12.10	3.73	0.0663	16.70	4.90	**0.0341**
	CO*C	1	n/a	n/a	>0.25	n/a	n/a	>0.25	31.10	11.65	**0.0018**	n/a	n/a	> 0.25	n/a	n/a	n/a	n.a	n/a	n/a	n/a	n/a	n/a
	DE*C	1	n/a	n/a	>0.25	n/a	n/a	> 0.25	n/a	n/a	>0.25	n/a	n/a	> 0.25	n/a	n/a	n/a	n.a	n/a	n/a	n/a	n/a	n/a
	CO*DE*C	2	n/a	n/a	>0.25	n/a	n/a	>0.25	n/a	n/a	>0.25	n/a	n/a	>0.25	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	**n/a**
Final height	Canopy openness	1	29.70	11.48	**0.0020**	23.80	69.31	**<0.0001**	24.40	8.66	**0.0070**	33.20	0.38	0.5401	12.30	10.52	**0.0068**	14.20	1.96	0.3080	15.70	8.58	**0.0100**
	Deer exclusion	1	25.40	20.60	**0.0001**	28.90	21.94	**<0.0001**	18.50	0.12	**0.0052**	17.80	2.37	0.1412	n/a	n/a	n/a	n/a	n/a	n/a	14.20	6.0.25	**0.0379**
	Coppice	1	133.00	9.00	**0.0032**	144.00	0.01	0.9156	27.80	0.12	0.7368	52.70	9.76	**0.0029**	19.70	17.99	**0.0004**	11.80	1.64	0.4616	16.10	19.42	**0.0004**
	CO*C	1	n/a	n/a	>0.25	n/a	n/a	> 0.25	26.10	4.82	**0.0372**	n/a	n/a	> 0.25	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
	DE*C	1	n/a	n/a	> 0.25	n/a	n/a	> 0.25	n/a	n/a	> 0.25	n/a	n/a	> 0.25	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
	CO*DE*C	2	n/a	n/a	> 0.25	n/a	n/a	>0.25	n/a	n/a	>0.25	n/a	n/a	>0.25	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a

Only the main effects of canopy openness were included in the sprouting model for American beech, sugar maple, and paper birch due to low coppicing replication outside of deer exclosures.
Low replication limited the full model for survival, five-year height growth, and final height for American beech and sugar maple to the main effects of canopy openness and coppicing.
Low replication limited the full model for survival, five-year growth, and final height for paper birch to the main effects of canopy openness, coppicing, and deer exclusion.
Interaction terms exceeding the P > 0.25 threshold were removed from the model and pooled into the error term (Bancroft 1964).

Table 4
Estimated average survival (±1 SE), five-year height growth, and final height of volunteer white ash and planted paper birch, red maple, northern red oak, and yellow birch coppiced and uncoppiced stems with and without deer exclusion. Bolded text represents a statistically significant difference between deer exclusion and deer presence (α = 0.05) (Tukey-Kramer).

	Deer Excluded				Deer Unexcluded			
Species	N	Survival (%)	Height growth (cm)	Total height (cm)	N	Survival (%)	Height growth (cm)	Total height (cm)
Paper birch	51	74 (10)	**165.0 (18.8)**	**272.1 (26.3)**	10	26 (21)	18.8 (43.7)	94.3 (81.4)
Red maple	142	81 (4)	**85.4 (6.7)**	**132.2 (9.1)**	46	71 (8)	22.3 (12.2)	45.2 (16.8)
Northern red oak	151	92 (3)	**94.9 (5.6)**	**134.1 (7.1)**	50	44 (11)	27.1 (13.1)	48.7 (16.9)
White ash	60	84 (72)	129.6 (15.3)	195.6 (20.7)	23	72 (12)	78.8 (29.5)	122.3 (42.6)
Yellow birch	44	94 (5)	**180.4 (15.6)**	**301.5 (34.3)**	17	45 (11)	65 (28.8)	79.6 (41.5)

Low replication of saplings outside the deer exclosures prevented the estimation of browsing effects on sugar maple and American beech.

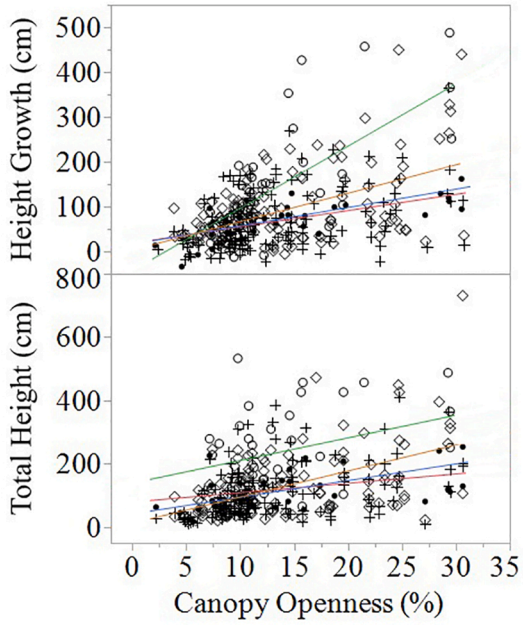

Fig. 1. The effects of canopy openness on five-year height growth and total height of sprouts and uncoppiced stems of planted American beech (filled circles) (red), paper birch (open circles) (green), red maple (plus signs) (blue), and northern red oak (open diamonds) (orange). Canopy openness was found to be significant (α = 0.05) and did not significantly interact with any other factor for each species. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

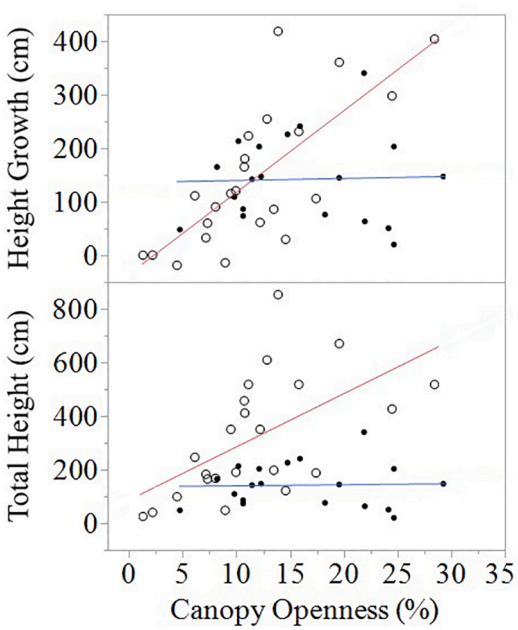

Fig. 2. The interacting effects of canopy openness and coppicing on the five-year height growth and final height of yellow birch sprouts (filled circles) (blue) and uncoppiced stems (open circles) (red). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

ranking analyses (Fig. 5). In both single tree and group sized gaps with deer exclusion (P < 0.0001), northern red oak sprouts significantly gained growing position compared to paper birch and yellow birch (Fig. 5). Northern red oak sprouts also gained growing position relative to white ash and American beech when deer were excluded, but only significantly so in single tree gaps (Fig. 5). With deer exclusion, red maple benefited from coppicing in group sized gaps and significantly gained growing position compared to paper birch and yellow birch (Fig. 5). However, red maple sprouts lost growing position in single tree gaps where deer were excluded (Fig. 5). No statistically significant changes in growing position were detected among uncoppiced stems in single tree (P = 0.4477) or group sized gaps (P = 0.0742) where deer were excluded (Fig. 5).

4. Discussion

4.1. Deer exclusion

Multiple studies have demonstrated that increasing light availability alone is unlikely to improve the regeneration of mid-tolerant species in managed northern hardwood forests of the Great Lakes region (Bolton and D'Amato 2011; Kern et al. 2013; Poznanovic et al. 2013). This calls for novel silvicultural approaches to overcome the interacting factors constraining species diversity (Kern et al. 2017; Webster et al. 2018). Our results indicate that coppicing advance-planted saplings within harvest gaps had a mixed-effect on the competitiveness of mid-tolerant species when deer were excluded. However, coppicing was not successful when deer were present. This confirms that chronic browsing is not only limiting natural regeneration of browsing-sensitive species (Matonis et al. 2011; White 2012; Vickers et al. 2019; Walters et al. 2020) but may also overwhelm silvicultural efforts to increase the presence of browsing-preferred species. While fencing to exclude deer is not a realistic option in most situations, our discussion on the effects of coppicing in the absence of deer may be informative to management in locations with lower deer densities or where hunting can be used to periodically reduce deer populations (Sage et al. 2003).

4.2. Coppicing

Nearly all temperate hardwood tree species can survive top kill through sprouting (Del Tredici 2001). However, differences in growth strategies suggest that certain species may sprout more vigorously than others (Crow 1988; Keyser and Loftis 2015; Keyser 2019). Based on growing position rankings, northern red oak benefited most from

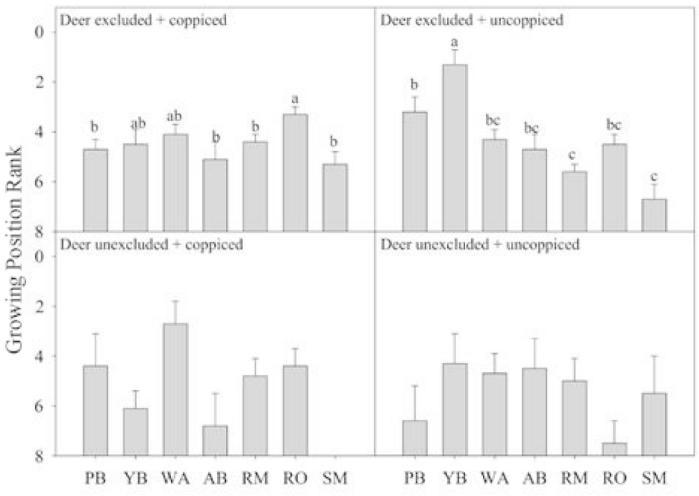

Fig. 3. Final growing position ranking (±1 SE) among species in each unique combination of coppicing and deer exclusion treatments. Species acronyms are American beech (AB), paper birch (PB), red maple (RM), northern red oak (RO), sugar maple (SM), white ash (WA), and yellow birch (YB). Bars with different letters were found to be significantly different $\alpha = 0.05$ with Steel-Dwass all pairs multiple comparison tests. Species missing within treatments were excluded due to low sample size ($n < 3$). *Deer excluded + coppiced sample size - AB-15, PB-37, RM-61, RO-75, SM-27, WA-37, YB-32. *Deer excluded + uncoppiced sample size - AB-15, PB-18, RM-51, RO-46, SM-16, WA-32, YB-18. *Unexcluded + coppiced sample size- AB-5, PB-5, RM-18, RO-17, SM-N/A, WA-9, YB-15. *Unexcluded + uncoppiced sample size- AB-6, PB-5, RM-11, RO-15, SM-4, WA-15, YB-6.

*Deer excluded + coppiced sample size - AB-15, PB-37, RM-61, RO-75, SM-27, WA-37, YB-32

*Deer excluded + uncoppiced sample size - AB-15, PB-18, RM-51, RO-46, SM-16, WA-32, YB-18

*Unexcluded + coppiced sample size- AB-5, PB-5, RM-18, RO-17, SM-N/A, WA-9, YB-15

*Unexcluded + uncoppiced sample size- AB-6, PB-5, RM-11, RO-15, SM-4, WA-15, YB-6

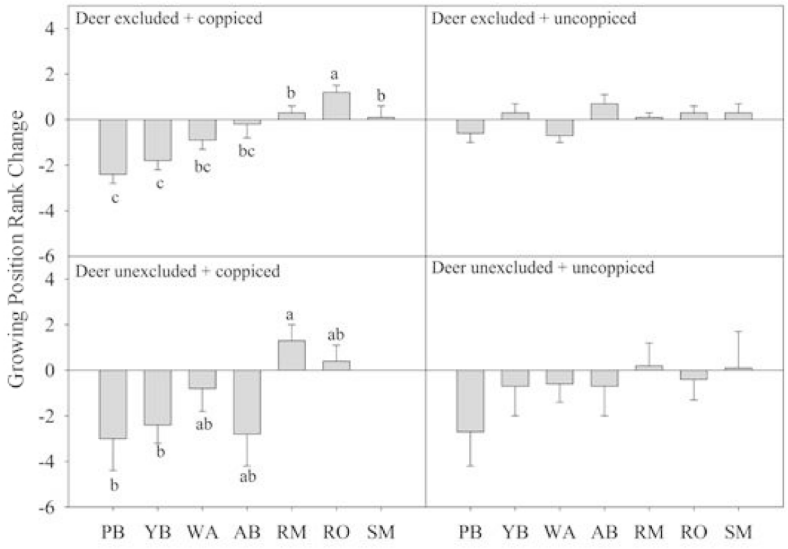

Fig. 4. Growing position rank changes (±1 SE) among species in each unique combination of coppicing and deer exclusion treatments. The zero line represents the average species growing position rank in 2013, while the bars represent whether growing position was gained (+) or lost (−) when measured in 2018. See Fig. 3 for other legend details. * Deer excluded + coppiced sample size - AB-15, PB-37, RM-61, RO-75, SM-27, WA-37, YB-32. * Deer excluded + uncoppiced sample size - AB-15, PB-18, RM-51, RO-46, SM-16, WA-32, YB-18. * Unexcluded + coppiced sample size- AB-5, PB-5, RM-18, RO-17, SM-N/A, WA-9, YB-15. * Unexcluded + uncoppiced sample size- AB-6, PB-5, RM-11, RO-15, SM-4, WA-15, YB-6.

* Deer excluded + coppiced sample size - AB-15, PB-37, RM-61, RO-75, SM-27, WA-37, YB-32

* Deer excluded + uncoppiced sample size - AB-15, PB-18, RM-51, RO-46, SM-16, WA-32, YB-18

* Unexcluded + coppiced sample size- AB-5, PB-5, RM-18, RO-17, SM-N/A, WA-9, YB-15

* Unexcluded + uncoppiced sample size- AB-6, PB-5, RM-11, RO-15, SM-4, WA-15, YB-6

coppicing. This result corresponds with northern red oak's adaptation to sprout after fire (Chapin et al. 1990; Abrams 1992). It also aligns with reports that northern red oak has larger dormant season carbohydrate reserves in the root system than many northern hardwood tree species (Canham et al. 1999; Kobe et al. 2010). However, unlike a previous study following sprout performance after prescribed fire (Kruger and Reich 1997), the 5-year height growth of northern red oak sprouts did not exceed that of most other species, Rather, the growing position of northern red oak sprouts improved more in single tree gaps, where height growth of all species was constrained. Thus, we believe that the improved growing position of northern red oak sprouts was primarily due to a strong initial sprouting response and high sprout survival, and not to longer term height growth.

While northern red oak benefited from coppicing, yellow birch and paper birch sprouts lost growing position. This trend was best illustrated by yellow birch, which, in the absence of deer, occupied dominant

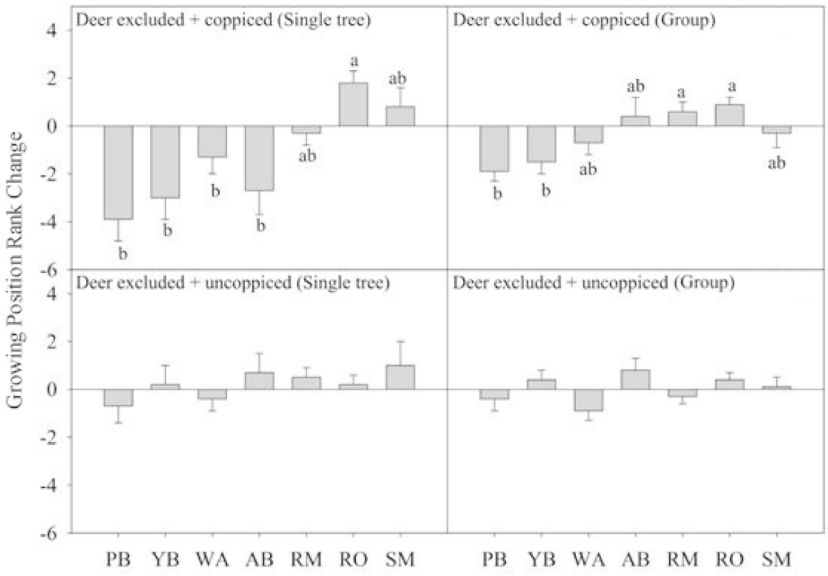

Fig. 5. Growing position rank changes among species in each unique combination of coppicing and deer exclusion treatments established within single tree (ST) (10–14.9 m diameter, < 10% canopy openness) and group sized(GS) (15.0–35.0 m diameter, 10–32% canopy openness) harvest gaps ± 1 SE. See Figs. 3 and 4 for other legend details. *Group sized harvest gaps, Deer excluded + coppiced sample size - AB-9, PB-29, RM-39, RO-48, SM-18, WA-24, YB-25. *Group sized harvest gaps, Deer excluded + uncoppiced sample size sample size - AB-9, PB-9, RM-28, RO-25, SM-12, WA-17, YB-12. *Single harvest tree gaps, Deer excluded + coppiced sample size - AB-6, PB-8, RM-22, RO-27, SM-9, WA-13, YB-7. *Single harvest tree gaps, Deer excluded + uncoppiced sample size – AB-6, PB-9, RM-23, RO-21, SM-4, WA-15, YB-6.

*Group sized harvest gaps, Deer excluded + coppiced sample size - AB-9, PB-29, RM-39, RO-48, SM-18, WA-24, YB-25
*Group sized harvest gaps, Deer excluded + uncoppiced sample size sample size - AB-9, PB-9, RM-28, RO-25, SM-12, WA-17, YB-12
*Single harvest tree gaps, Deer excluded + coppiced sample size - AB-6, PB-8, RM-22, RO-27, SM-9, WA-13, YB-7
*Single harvest tree gaps, Deer excluded + uncoppiced sample size – AB-6, PB-9, RM-23, RO-21, SM-4, WA-15, YB-6

growing positions as an uncoppiced stem but average growing positions as a sprout. Unlike northern red oak, yellow birch is generally associated with mesic soils where fire is rare and competition for light is the primary factor influencing survival (Tubbs 1977; Perala and Alm 1990; Ashton et al. 1998). Indeed, yellow birch is not known to have large dormant season carbohydrate reserves in its root system (Gaucher et al. 2005) or reliably sprout in response to disturbance (Solomon and Blum 1967; Hughes and Fahey 1991). Poor sprout survival for yellow birch also supports the notion that carbohydrate storage can act as a buffer against disturbance (Canham et al. 1999; Poorter and Kitajima 2007). In addition, coppicing may have negatively influenced height growth, as yellow birch sprouts grew less than uncoppiced stems at higher levels of canopy openness. Sprout growth of yellow birch may have been limited by increased competition for light, which likely resulted from an early loss of growing position to vigorously sprouting competitors in coppiced subplots. In contrast, yellow birch stems on average occupied dominant growing positions in uncoppiced subplots, and thus likely experienced less competition for light at a given gap size compared to yellow birch sprouts. Nevertheless, we cannot discount the possibility that coppicing may have negatively impacted the growth potential of yellow birch.

In contrast to yellow birch, sprouting is regarded as a viable means to regenerate paper birch (Hutnik and Cunningham 1961; Perala and Alm 1989). The reasonably strong initial sprouting response of coppiced paper birch stems supports this view; however, paper birch sprouts also had the lowest survival. This result may be related to a lack of shade tolerance (Kobe and Coates 1997; Kneeshaw et al. 2006), as paper birch sprouts survived better at higher levels of canopy openness. Moreover, the growing position of paper birch sprouts declined less in group sized gaps compared to single tree gaps. High sprout mortality could also be attributed to the timing of the coppicing treatment, as paper birch is known to have a larger percentage of its carbohydrate reserves remaining in its branches and stems in the dormant season than other northern hardwood tree species (Furze et al. 2019).

Of the mid-tolerant species, red maple and white ash were least affected by coppicing. Consistent with previous studies (Solomon and Blum 1967; Brown 1994; Fei and Steiner 2009; Petrice and Haack 2011), the initial sprouting response and sprout survival was high for both species and unaffected by any examined factor. For red maple, this finding is consistent with its wide ecological amplitude and reputation as a generalist tree species (Abrams 1998). The modest response of white ash is somewhat surprising given its common association with mesic soils and rapid early growth rate (Schreeg et al., 2005). However, unlike yellow birch, white ash does have relatively large sugar reserves in its root system (Furze et al.2019), which may explain why coppicing had opposing effects on these species. What remains unknown is why white ash and yellow birch have differing storage patterns given their otherwise similar life history characteristics.

5. Conclusions

Nearly all temperate hardwood tree species sprout (Del Tredici 2001). However, coppicing will benefit some species more than others. Regeneration failures of mid-tolerant tree species within harvest gaps are common in managed northern hardwood forests (Neuendorff et al. 2007; Matonis et al. 2011). Yet, certain mid-tolerant species are known to have relatively large dormant season carbohydrate reserves in the root system; and thus, may gain growing position in harvest gaps if the advance regeneration layer was coppiced (Canham et al. 1999; Kobe et al. 2010). Our findings generally support this notion, as white ash volunteers and planted northern red oak, yellow birch, and red maple saplings had a strong initial sprouting response and high sprout survival. Northern red oak benefited most from coppicing and gained growing

position in all gap sizes when deer were excluded. In contrast, yellow birch is not known to have large dormant season carbohydrate reserves in the root system and had a lower initial sprouting response, poor sprout survival, and lost growing position in all gap sizes regardless of deer exclusion. Collectively, these results suggest that coppicing has the potential to improve the growing position of mid-tolerant saplings but only for those species that maintain large dormant season carbohydrate reserves in the root system. Nevertheless, it should be recognized that deer browsing overwhelmed the effects of coppicing outside the exclosures, which suggests that coppicing may only benefit browsing-preferred, mid-tolerant species in locations with low deer populations or where deer can be excluded.

It should also be recognized that improved growing position does not guarantee successful regeneration. With the exception of northern red oak, the sprouts of each species were on average shorter than uncoppiced stems. Reduced advance regeneration height has potential negative implications for the recruitment of mid-tolerant species to the canopy, as the lateral expansion of branches from edge trees will diminish light availability. The relatively short time frame of this study only allows us to speculate on whether mid-tolerant sprouts will be able to persist in a reduced light environment. However, given the average final height of coppiced stems, and the size of harvest gaps used in this study, it is likely that a second harvest will be needed to release the sprouts into the canopy.

CRediT authorship contribution statement

John L. Willis: Funding acquisition, Conceptualization, Formal analysis, Investigation, Writing-original draft. **Michael B. Walters:** Investigation, Writing-review & editing. **Evan J. Farinosi:** Investigation, Writing- review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this manuscript.

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