Frequency and timing of stem removal influence *Corylus americana* resprout vigor in oak savanna

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ABSTRACT

Shrubs are an important component of many ecosystems, contributing to spatial and resource heterogeneity and adding to life form and species diversity. Many shrub species have adapted to regular disturbances such as fire by resprouting after stem removal. The relative vigor with which shrubs resprout influences post-disturbance size and density of individuals and thus, can alter community structure. However, little is known about how disturbance frequency and seasonality influence resprouting. We studied resprout vigor of the native shrub American hazel (*Corylus americana* Walter) in oak savanna in Minnesota, USA. We measured resprout growth of individual shrubs in response to the frequency and timing of clipping in relatively open and shaded conditions. We hypothesized that resprouting of *C. americana* would be negatively related to clip frequency, due to more rapid depletion of stored resources necessary for resprouting, and positively related to light availability. In 12 weeks following a single clipping, shrubs recovered 82% of the lost stem biomass in open savanna, but only 17% in shaded forest. In both open and closed sites, shrubs clipped three times or more resprouted only 10–15% as much biomass as those clipped once. Moreover, the timing of clipping had as large an effect on resprout potential as the number of clipping events, and small differences in timing were important. Plants clipped once in mid or late June or in July regrew 57, 17, and 8% as much biomass, respectively in the six weeks following clipping as those clipped in early June. These results illustrate that both the timing and number of disturbance events within a growing season can strongly influence shrub growth, which can have important implications for ecosystem structure, function, and management.

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1. Introduction

Shrubs (whether true shrubs or the shrub stage of species that can also become large trees) are an important and dynamic part of many ecosystems. Variation in shrub density occurs in response to a number of factors including climate variation (Archer et al., 1995), grazing (Asner et al., 2004) and fire (Briggs et al., 2002a,b; Peterson and Reich, 2001). These fluctuations change light and soil resource availability, affect community dynamics and alter ecosystem productivity (Berlow et al., 2003; Briggs et al., 2005; Coomes and Grubb, 2000; Van Auken, 2000). The ability to resprout plays an important role in shrub population dynamics.

Resprouting often occurs in woody species in environments with frequent top-killing disturbance events (Bazzaz et al., 1987; Bellingham and Sparrow, 2000; Bond and Midgley, 2001; Kruger and Reich, 1997a,b,c; Peterson and Reich, 2001). Sprouting provides a fast and predictable alternative to recolonizing by seed after top-killing disturbance and a means to tolerate herbivory (Best et al.,

2003; Bond and Midgley, 2001; Del-Val and Crawley, 2005). For many shrub species, vegetative resprouting after top-killing disturbance leads to regrowth of more biomass than was lost (Briggs et al., 2005; Hoffmann and Solbrig, 2003; Lopez-Pintor et al., 2006; Silva et al., 2001). In some cases, topkill can result in clonal spread, especially when disturbance regimes are altered or resources are plentiful (Buckman, 1964; Briggs et al., 2005; Brown and Archer, 1989; Drewa et al., 2002; Weyenberg et al., 2004).

Disturbance characteristics, plant physiological traits and plant size are likely determinants of individual shrub resprout vigor. Plant physiological attributes such as carbohydrate storage capacity, relative growth rate and photosynthetic rate all influence vegetative resprouting (Chapin et al., 1990; Keel et al., 2007; Kruger and Reich, 1997b; Mallik et al., 1997; McCarron and Knapp, 2003). After topkill, new shoots are produced using carbohydrates stored in roots or other surviving tissues (Bowen and Pate, 1993; Cruz et al., 2002; Kruger and Reich, 1993). More stem biomass can be resprouted in plants with higher tissue concentrations or larger whole-plant pools of stored carbohydrates (Kabeya and Sakai, 2005). In addition, larger plants may also have a larger budbank from which to resprout (Bond and Midgley, 2001). Resprouted stems can have increased biomass production, through higher photosynthetic rates

and more photosynthetic tissues compared to undisturbed stems of the same species (Huang et al., 2007; Kruger and Reich, 1993; Peña-Rojas et al., 2005). Plants with high growth rates may begin using new photosynthate and recoup stored carbon faster than slower growing plants (Bowen and Pate, 1993). In some cases, shrubs can regain pre-disturbance size within months after top-kill by the mobilization of stored resources, renewed canopy area, higher carbon assimilation rate, and altered carbon allocation.

Disturbances vary in type, timing, and frequency, each potentially resulting in different species-specific responses. For example, wildfire or browse during a dormant season can result in rapid and vigorous resprouting during the subsequent growing season, as plants have invested little stored reserves in new aboveground biomass (Drewa et al., 2002; Johnson, 1992; Kruger and Reich, 1993; Matlack et al., 1993). Vigorous resprouting is most likely to occur if carbohydrate reserves remain plentiful enough to replace lost stems and fuel the rapid recovery of leaf area along with increased photosynthetic rates. While the effects of disturbance characteristics and physiological traits on resprouting have been tested across multiple growing seasons, relatively little is known about how the number and timing of top-killing events within a growing season influence resprout growth. Better understanding of this process would advance ecophysiological science as well as inform ecosystem management of shrubs since manipulation of the timing and frequency of stem removal can be used to achieve management objectives.

To address the issues above, we conducted mechanical removal experiments in oak savanna and adjacent closed-canopy oak forest in east central Minnesota. Both habitats had understory dominated by *Corylus americana* Walter (American hazel), a native rhizomatous, resprouting shrub. We addressed the following questions: (1) does increased frequency of stem removals via clipping reduce *C. americana* resprout vigor? (2) how does timing of stem removal in the middle of growing season affect *C. americana* resprout vigor? and (3) how does the response of *C. americana* to number and timing of clip treatments differ between oak savanna and closed-canopy oak forest? We expected resprout biomass would decline with more frequent clipping because repeated stem removal depletes stored carbohydrate reserves, necessary for resprouting, faster than photosynthesis can replenish them. We expected resprout vigor to be lower in closed forest because low light reduces the capacity for resprouts to replenish stored reserves and supply new stems with carbon and energy. Finally, we expected that resprout vigor might change with timing of disturbance for a variety of reasons – including changing photoperiod, light availability, moisture and nutrient supply and shoot ontogeny – but that the effect of timing would be modest compared to that of light availability or number of clippings. Variation in the timing of clipping during the growing season likely has a small effect on resources accumulated prior to or available following clipping compared to different numbers of clippings or different light environments.

2. Materials and methods

2.1. Study area

Two experiments were conducted in 2006 and 2007 at Cedar Creek Ecosystem Science Reserve (CCESR) a Long Term Ecological Research (LTER) site in central MN (45°40′N, 93°20′W, elevation 270 m). The climate is temperate with a mean annual temperature of 6.7 °C and a mean annual precipitation of 801 mm with approximately 500 mm falling during the May through September growing season. The soils of the area are glacial outwash of the Zimmer-

man and Sartell series, with low water holding capacity and limited nutrient availability (Grigal et al., 1974).

2.2. Experiment 1: clip frequency

We selected 192 *C. americana* shrubs, split between two relatively open oak savanna sites and two closed-canopy oak forest sites ($n = 96$ individuals per habitat type). The sites were nearby (within ≈ 2 km) but not adjacent (separated by at least 500 m), had very similar climate and soil but differed in fire history. The open savanna sites had been prescriptively burned approximately one in three years for the past 45 years, resulting in relatively high understory light availability. Basal area of woody stems >10 cm DBH averaged 14.8 m^2 ha^{-1} and stem density averaged 310 stems ha^{-1} (Peterson and Reich, 2001). The closed-canopy oak forest sites had not burned during that time period, resulting in relatively low light availability, higher basal areas (25.2 m^2 ha^{-1}) and stem densities (579 stems ha^{-1}; Peterson and Reich, 2001; Reich et al., 2001). We refer to the former habitat as "open savanna" and the latter habitat as "closed forest". To capture the light heterogeneity within the sites we selected shrubs exposed to a range of light conditions in each study area. The multi-stemmed rhizomatous nature of *C. americana* makes it difficult to delineate individuals, especially in dense stands. To increase the likelihood of selecting stems from a single, genetically distinct individual, we identified shrubs isolated from the next nearest *C. americana* shrub by a meter or more (common in closed forest) or on edges of large patches (common in open savanna). We treated stems in a 1.5 m diameter plot (1.77 m^2) and sampled a center 0.5 m diameter subplot (0.196 m^2) to further limit the potential effects of multiple individuals in a sampling area. To begin each treatment, we removed standing biomass by clipping all biomass within the 1.77 m^2 treatment plot, leaving 10 cm tall "stumps" of *C. americana* in the inner 0.196 m^2 sampling subplot. For the remainder of the manuscript we will refer to plot or subplot as our sample unit assuming that each represents a sample from a genetically distinct multi-stemmed individual (i.e. genet). We note that is it likely that individual genets in the open savanna habitat were larger than our sample plot (Cheyney, 1928).

Clipping treatments began in mid-May 2006 and lasted for 12 weeks, terminating in mid-August 2006. We randomly assigned each plot to one of four clipping frequency treatments: unclipped (*control*), clipped one time (1×), clipped three times (3×), or clipped six times (6×). Treatments were evenly spaced across 12 weeks such that 3× treatments were monthly, and 6× treatments were bi-weekly. On the first sampling date, we removed aboveground biomass from all but the control plots. For control plots, we measured average stem length and diameter of stems within the sampling subplot. On each subsequent clip date, we removed and measured all resprouted *C. americana* stems within the sampling subplot and clipped the remaining stems in the larger treatment plot. We counted total resprout stem number and measured the length and diameter of a representative subsample of five new stems. Any herbivory or other disturbance to the shrub stems was also noted. All clipped biomass from within the sampling subplot was oven dried for seven days at 55 °C and weighed.

To assess the long-term legacy effect of the treatments, we measured biomass one year after the clip treatments ended. In late July 2007, we harvested all aboveground biomass in the sampling subplot, dried the biomass for 14 days at 55 °C and weighed it. We note that both open savanna study areas were prescriptively burned in the spring of 2007, while the closed forest study areas remained unburned. This decoupled our comparison of legacy effects between habitat types since half of the plots were essentially "clipped" by fire in spring 2007 and half were not. Therefore, we restrict any discussion of legacy effects to comparisons among clipping treatments within a habitat type.

Table 1
Measures of initial size of *Corylus americana* in open savanna and closed forest habitats at Cedar Creek Ecosystem Science Reserve in east central Minnesota, USA. Means and standard errors (in parentheses) are for stems in 0.5 m radius plots. Closed forest that had not been burned in the past 45 years and open savanna had been burned once every three years. Asterisks (*) indicate significance at the 0.05 level for two-tailed *t*-tests.

	Open savanna	Closed forest
n	72	72
Mean number of stems	11.3 (0.66)	3.0 (0.22)*
Total stem biomass (g)	92.5 (10.3)	74.9 (7.3)
Mean stem length (cm)	74.7 (2.6)	99.0 (5.2)*
Mean stem diameter (cm)	0.60 (0.014)	0.77 (0.029)*
Mean biomass per stem (g)	7.9 (0.64)	29.5 (3.2)*

Percent diffuse transmittance of photosynthetically active radiation (PAR) was assessed once at every plot in mid-summer 2006 using a Decagon Sunfleck Ceptometer (Decagon Devices, Pullman, WA). We calculated percent diffuse transmittance (%T) as the percent of PAR above the forest canopy arriving at each plot below the forest canopy. All measurements were made under diffuse light conditions. We measured above-canopy PAR in a nearby open field and below canopy PAR at either 100 cm above ground level or at the top of the standing *C. americana* stems, whichever was higher.

2.3. Experiment 2: timing of clipping

In 2007, we examined the effect of disturbance timing within the growing season on *C. americana* resprout vigor. We sampled hazel in the same closed forest site as experiment one, but due to the CCESR prescribed burning schedule, we sampled a different open savanna site, with a similar fire frequency (burned every four years versus every three). We tested the effect of seasonality on shrub resprout vigor by clipping 60 randomly chosen *C. americana* shrubs one time during the summer in a temporally staggered design. Individuals were randomly assigned a clip date. On each of six days (28 May, 5 June, 11 June, 25 June, 9 July, 23 July), we clipped five shrubs in open savanna and five in closed forest (6 dates × 2 overstory × 5 individuals = 60 individuals total). We hereafter refer to groups of shrubs by their clip date. On each clip date, we removed standing biomass of the shrubs in the same fashion as the first experiment, by clipping all biomass within a 1.5 m diameter plot and leaving 10 cm tall "stumps" of *C. americana* in the inner 0.5 m diameter sampling subplot. We non-destructively measured stem length on a subsample of three resprouted stems within the sampling subplot every two weeks. On the sixth week following each clip event, all resprouted biomass was harvested from within the sampling subplot. We measured stem length on a random subsample of these stems and then oven-dried the biomass for 7 days at 55 °C.

2.4. Statistical analysis

We analyzed the effects of clip treatments and habitat on resprout characteristics using analysis of variance (ANOVA), linear regression and multivariate modeling in JMP 6.0.3 software (SAS Institute, Cary, NC, USA). Because shrubs differed in initial size (Table 1), initial aboveground biomass was used as covariate in the ANOVA models. Measured parameters for resprout vigor included standing biomass, mean stem length, and mean stem diameter. We focused on biomass production as our key growth response variable because it integrates whole plant function. In some cases, we examined mean stem length to better understand the components that contribute to biomass responses. We used the Tukey HSD to test for significant differences in response among specific treatments. Where necessary, we log transformed our data to fit assumptions of normality.

Table 2
Mixed model of cumulative biomass production of *Corylus americana* as a function of clip frequency, habitat, and natural log of initial biomass. The study occurred over 12 weeks (May to August) at Cedar Creek Ecosystem Science Reserve in east central Minnesota, USA. Habitats included closed forest that had not been burned in the past 45 years and open savanna, burned once every three years. Clip frequencies were either none, once (early season), monthly or bi-weekly.

| Factor	df	SS	F	P
Habitat	1	4205.11	46.28	<0.0001
Clip frequency	3	5856.54	32.23	<0.0001
Habitat × clip frequency	2	4277.31	23.54	<0.0001
ln (initial biomass)	1	505.20	5.560	0.0198
Error	137	12449.2	–	–

3. Results

3.1. Experiment 1: effects of habitat and clip frequency

As expected, light availability was strongly related to habitat ($F_{3,183} = 116.2$, $P < 0.0001$) – shrubs in closed forest received $6.8\% \pm 2.6$ (*SD*) of above canopy PAR on average, while those in open savanna received $53.1\% \pm 24.4$. Habitat and clipping frequency significantly influenced resprout growth (Table 2). Log transformed initial biomass was a significant covariate; large shrubs produced more biomass. Regardless of clip frequency, plants in open savanna sprouted more vigorously than those in closed forest. In both habitats, cumulative resprout biomass declined significantly as clip frequency increased (Fig. 1). In each habitat, plants clipped once produced eight times more biomass over the 12-week period than those clipped three or six times; the latter were similar. In open savanna, plants clipped once regained >80% of their initial aboveground biomass compared to <20% regained for plants in closed forest (Fig. 2). A significant interaction occurred between habitat and clip treatments. Since habitats differed in light availability, this interaction was likely due to greater absolute cumulative biomass in the high light conditions of open savannas compared to closed forests. The relative differences among clip treatments within the two habitats were similar (Figs. 1 and 2). Greater cumulative biomass in high light conditions was due to higher individual stem biomass; resprouted stem numbers did not differ between habitats (data not shown).

Measurement one year following treatments revealed some legacy effects. In the open savanna sites, the average proportion of 2006 initial standing biomass regrown was highest in the once-clipped treatment ($F_{2,97} = 3.5$, $P = 0.035$) followed by 3× and 6×, which differed modestly from each other (data not shown). By July 2007, shrubs clipped once in 2006 in open savannas produced an average of 86% of the 2006 initial standing biomass while shrubs clipped three times produced 49%. This regrowth occurred despite experimental clipping in 2006 (and a uniform prescribed surface fire in spring 2007, which burned the 2006 stem regrowth). In contrast, there were no significant differences among clip treatments in closed forest: all treatments resulted in regrowth of less than 20% of initial biomass by July 2007.

3.2. Experiment 2: effects of clip timing

The amount of biomass regrown in the first six weeks after a single clipping varied markedly with time ($F_{5,138} = 3.94$, $P = 0.005$; Fig. 3). Biomass produced during the six week period following clipping was highest when clipping occurred in early June; was only about half as great when clipping was done one week earlier or one week later; and was much lower when it was done in late June or anytime in July (Fig. 3). Differences in final biomass regrown were due both to a longer delay in the onset of regrowth in shrubs clipped later in the season and a shallower regrowth response per unit time
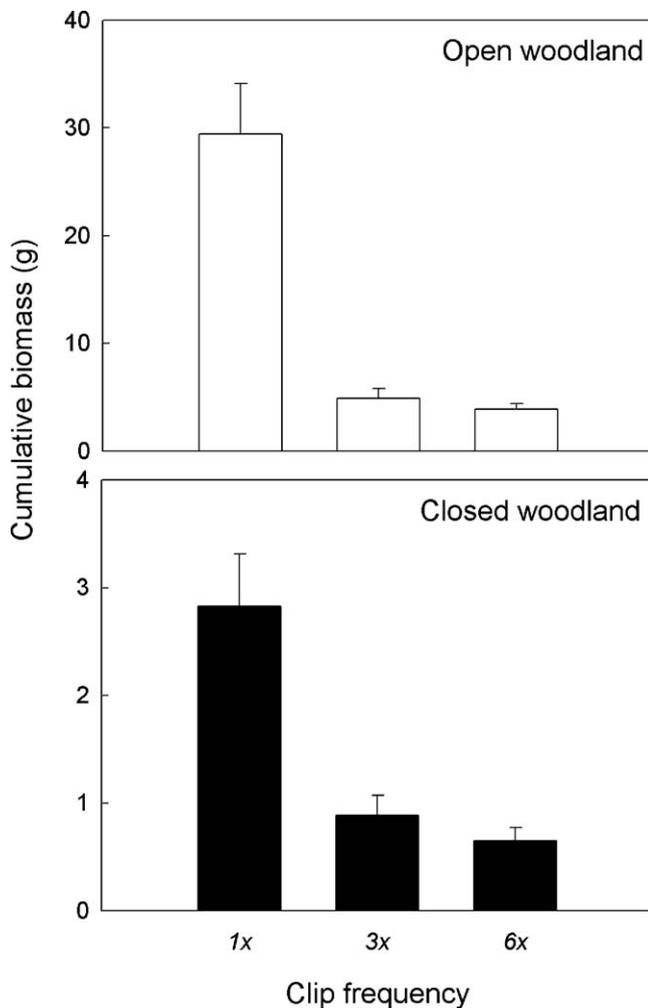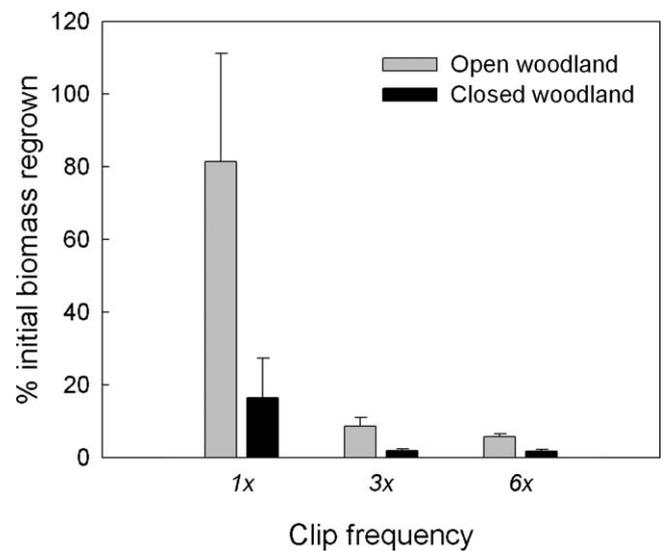
Fig. 1. Mean (±SE) cumulative biomass (g) produced in a 12 week study (mid-May to mid-August 2006) by *Corylus americana* in open and closed-canopy oak-dominated woodlands at Cedar Creek Ecosystem Science Reserve in east central Minnesota, USA under three clipping regimes. All stems within a sampling area were mechanically removed once at the start of the experiment (1×), monthly (3×), or bi-weekly (6×). Open savannas were maintained by prescribed fire approximately once every three years during the 40 years leading up the experiment, in closed-canopy forests fire was excluded.

Fig. 2. Mean (±SE) percent of initial biomass produced in a 12 week study (mid-May to mid-August 2006) by *Corylus americana* in open and closed-canopy oak-dominated woodlands at Cedar Creek Ecosystem Science Reserve in east central Minnesota, USA under three clipping regimes. All stems within a sampling area were mechanically removed once at the start of the experiment (1×), monthly (3×), or bi-weekly (6×). Open savannas were maintained by prescribed fire approximately once every three years during the 40 years leading up the experiment, in closed-canopy forests fire was excluded.

about effects of habitat and clip frequency were supported: shrubs in open sunlit conditions had more vigorous resprouting than in shaded sites, while increased clip frequency reduced resprout biomass in both habitats. The magnitude of impact of the timing of clipping during the growing season was much greater than anticipated. Modest differences in the timing of clip treatments markedly affected resprout vigor: shrubs clipped later resprouted more slowly and to a lesser extent. These effects were as large as those among light environments or among clip frequency treatments and suggest that resprout vigor results from the joint impact of frequency and timing.

(Fig. 4). Stem length produced during the six week period following clipping was highest and recovered most rapidly when clipping occurred early in the growing season (late May to early June); was only about half as great when clipped in late June; and was much lower and slower when clipped in late July (Fig. 4). Responses were similar in both open and shaded habitats, although regrowth biomass was greater in the former. Since average initial biomass in both habitats was approximately 100 g, patterns of temporal variation in percent of initial biomass and final standing biomass are nearly interchangeable (data not shown but see Table 1 for initial size patterns for Exp. 1).
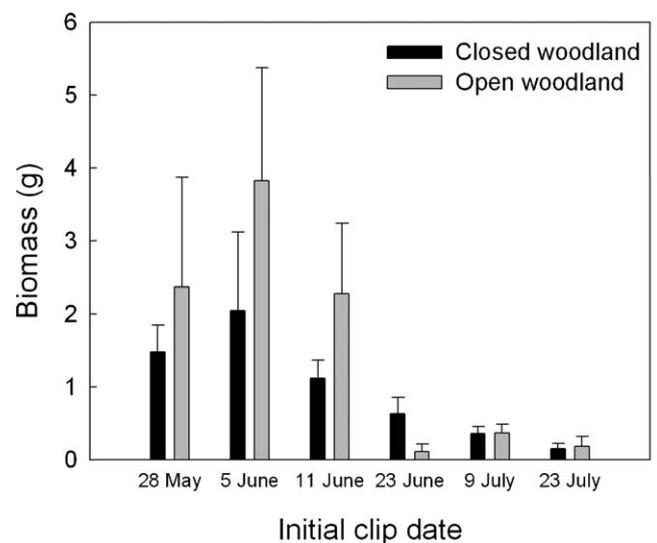
4. Discussion

Shrubs are found in many disturbance-prone ecosystems and individual shrub size and stem density post-disturbance can be directly related to shrub resprout vigor (Bellingham and Sparrow, 2000; Bond and Midgley, 2001; McCarron and Knapp, 2003). Resprout biomass may be influenced by disturbance characteristics, such as frequency and timing, as well as the availability of resources, such as light (Keeley, 2006). Our initial hypotheses
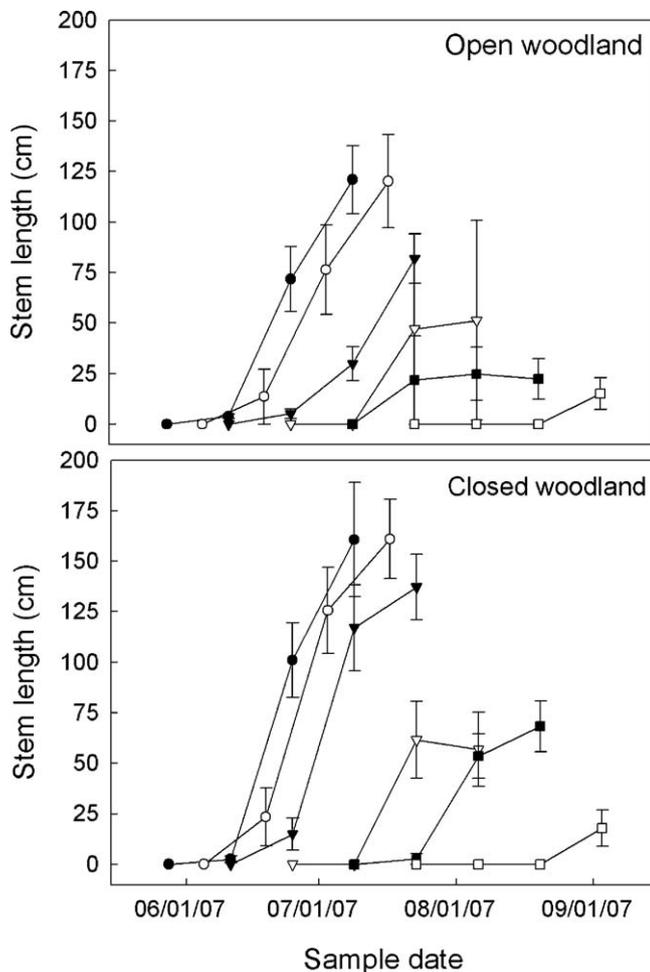

Fig. 3. Seasonal effects on mean biomass (g ± SE) resprouted by *Corylus americana* following clipping in open and closed-canopy oak woodlands at Cedar Creek Ecosystem Science Reserve in east central Minnesota, USA. Standing shrub biomass was clipped on the date indicated on the x-axis and resprout biomass was harvested 6 weeks later. Open savannas were maintained by prescribed fire approximately once every four years during the 40 years leading up the experiment, in closed-canopy forests fire was excluded.

Fig. 4. Seasonal effects of clipping on mean length (cm ± SE) of stems resprouted by *Corylus americana* in open and closed-canopy oak woodlands at Cedar Creek Ecosystem Science Reserve in east central Minnesota, USA. Open and closed symbols are alternated to provide visual clarity. Standing shrub biomass was clipped on the date indicated on the *x*-axis and resprouted stem lengths measured every two weeks for six weeks. Open savannas were maintained by prescribed fire approximately once every four years during the 40 years leading up the experiment, in closed-canopy forests fire was excluded.

4.1. Characteristics of shrubs in disturbance-prone habitats

Several specific traits allow shrubs to persist under the stress of repeated top-kill. First, rapid replacement of biomass (i.e. high resprout vigor) and re-colonization through rhizomatous growth or seed dispersal after disturbance can allow shrubs in disturbance-prone ecosystems to capitalize on increased nutrient and light availability immediately following disturbance (Heisler et al., 2003; Huffman et al., 1994; McCarron and Knapp, 2003; Royo and Carson, 2006). For *C. americana* growing in Midwestern oak savanna and woodlands, resprouting was strongly influenced by light availability and timing of top-kill. Single early season disturbances (such as wildfires or prescribed fires) may have little effect on the standing biomass later in the season. Second, many shrubs can tolerate a broad range of habitat conditions, including limited light availability (Tappeiner et al., 2001). In our study, *C. americana* was a dominant understory species in both open savanna and closed-canopy forest. Although open- and closed-grown shrubs differ in total biomass resprouted, stem length recovered rapidly and to a similar extent in both habitats (Fig. 4). Our data thus support the hypothesis that tolerance to environmental stressors like low light may allow shrubs to per-

sist in refugia with reduced habitat quality (Bond and Midgley, 2001).

We also found *C. americana* had reduced resprout vigor after multiple clippings, representing high intensity browse or targeted management or other intra-seasonal disturbance. It is possible that this constitutes an anti-herbivory adaptation (i.e., browse avoidance) (Del-Val and Crawley, 2005) but given limited subsequent recovery this seems unlikely. The reduced resprout vigor with multiple clippings more likely reflects depleted carbohydrate stores (Chapin et al., 1990). *C. americana*'s tolerance for the stresses of disturbance-prone ecosystems seems to fit within the general life history traits of other woody plants, where resprouting after top-kill is essential to long-term abundance and survival (Bond and Midgley, 2001; Keeley, 2006; Kruger and Reich, 1997c).

4.2. Potential controls on shrub resprouting

Resprout biomass declined as clip frequency increased (Fig. 1). It is likely that repeated clipping reduced individual plant resprout vigor during the summer in the 3× and 6× treatments in part because stored carbohydrate reserves were increasingly depleted with each clip treatment. Resprouted stems initially are a sink for energy and carbon since they must produce photosynthetic structures before assimilating any new photosynthate. As stems and leaves develop they begin to contribute new carbon to plant reserves (Keel et al., 2007). However, if resprouted stems are repeatedly removed before reserves can be replenished, then every subsequent clip treatment may further deplete resources available for resprout. We hypothesize that shrubs clipped more frequently likely replaced a smaller fraction of initial biomass because of depleted carbohydrate reserves. In contrast, once-clipped shrubs in high light regained over 80% of initial biomass in twelve weeks. We hypothesize that after the single clip treatment shrubs allocated stored carbohydrate reserves to new stems and leaves. Since the clip occurred early in the growing season (although after first leaf flush) new stems and leaves had time to develop and contribute photosynthate to growth and maintenance as well as resupply pools of stored sugar and starch.

The potential importance of carbon availability in determining resprout vigor is further supported by the influence of light condition on resprout vigor. Shrubs in closed-canopy forest produced an order of magnitude less biomass in any given clip treatment whether biomass was measured as the total resprouted stem biomass or mean individual stem biomass. Low light conditions may have resulted in lower realized photosynthetic rates and thus less carbon assimilation to fuel the cost of new shoot production as well as to replenish stored reserves. Alternatively, differences in initial morphology and size (Table 1) may have played a role. Specifically, the higher numbers of stems in the open savanna shrubs may have provided more buds from which to resprout, increasing resprout vigor. In addition, if clones were larger than our treatment area then carbohydrates from unclipped stems connected to clipped stems via rhizomes may have contributed to resprout vigor. However, we do not think this was a mechanism since such resource sharing would have dampened the effect of repeated clipping.

Timing of disturbance within the growing season markedly affected resprout vigor; shrubs clipped later in the season had shorter stems and lower biomass production (Figs. 3 and 4). It is possible that our clip frequency results reflect timing more strongly that frequency. Lower production later in the growing season could result if conditions for new photosynthate production are poorer due to drought and reduced soil water, increased canopy shading, reduced soil nutrient resources, or if plants shift in carbon allocation strategies with time, or some combination thereof. The 2006 growing season was dry, receiving approximately 275 mm of rain-

fall (compared to an average of ~500). However, rainfall during each of the six week regrowth periods was not related to differences in resprout biomass (data not shown). In fact, there was more rainfall in July and August than in June. Seasonal changes in canopy cover were likely not a factor, as the canopy of both open and closed sites was in full leaf by the time the experiment began (late May). Although photosynthetic efficiency of resprouted stems may decline as daylength or light intensity diminish during the growing season, it is difficult to envision photosynthesis declining so rapidly during mid-summer, given ample evidence that photosynthesis of woody species in oak woodlands, including sprouts, remains nearly at a plateau through most of the growing season (Reich et al., 1991). Finally, it is possible that shifts in allocation underlie seasonal patterns. Allocation to new biomass growth might depend on cues unrelated to resource availability but associated with other seasonal changes such as photoperiod (Sloan et al., 2007; Volaire and Norton, 2006). It may be that sufficient reserves exist but rather than producing replacement tissue late in the growing season when the investment in new tissue may not be 'paid back', plants delay resprouting until the following growing season. We note that peak solar radiation occurs in late June. Further experimentation is needed to fully understand mechanisms that underlie the strong seasonality of resprout growth in *C. americana*.

4.3. Implications for shrub management

Shrub expansion has become problematic for certain management goals in some disturbance dependent ecosystems where natural resource values, habitat quality, plant diversity, abundance of economically desired species, and/or ecosystem function have been altered by increases in shrub abundance (Briggs et al., 2005; Cibilis et al., 1999; Finsinger et al., 2006). The vigorous regrowth of biomass in shrubs clipped once early in the year may help explain shrub expansion in some systems managed with spring fires (McCarron and Knapp, 2003). If peak biomass production in *C. americana* generally occurs in June and early July (as following the June 5 clipping in Experiment 2), then a typical prescribed burn in late spring may have little inhibitory effect on resprout vigor since few, if any, belowground reserves have been invested at this point (Kruger and Reich, 1993). This corroborates previous research showing greater treatment effect of a summer fire on *Corylus cornuta* resprout biomass compared to one in spring (Buckman, 1964).

Our results suggest that monthly clip treatments or a single late July clip could reduce standing *C. americana* biomass to less than 10% of initial biomass under high light conditions (Figs. 1 and 3). However, evaluation of the long-term impacts of our treatments is necessary to confirm their efficacy as a management tool. The limited resprouting of *C. americana* clipped late in the year or frequently could be of value to oak savanna restoration, as many degraded sites identified for restoration require both thinning of the tree canopy layer and understory management. Whether responses of other shrubs to variation in quantity and timing of stem removal is similar is not known, but if so, might be relevant to shrub management in other systems.

5. Conclusions

Resprout growth of woody shrubs is important to our understanding of the ecology and management of many ecosystems particularly in fire-prone areas where trees and herbaceous vegetation also constitute important components of the community structure. In our study, *C. americana* resprout biomass was related to light availability and the frequency and timing of clip treatments. The most vigorous resprouting occurred when shrubs were clipped once early in the growing season. Differences in resprout vigor among habitats and clip treatments were likely related to the demand for stored carbohydrates by resprouted stems and the capacity for plants to replenish carbon stores and provide new carbon and energy to emerging stems.

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