

The canary in the coal mine: Sprouts as a rapid indicator of browse impact in managed forests



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ABSTRACT

Forest managers are frequently confronted with sustaining vegetation diversity and structure in landscapes experiencing high ungulate browsing pressure. Often, managers monitor browse damage and risk to plant communities using vegetation as indicators (i.e., phytoindicators). Although useful, the efficacy of traditional phytoindicators is sometimes hampered by limited distribution and abundance, variable browse susceptibility, and lagged responses. In contrast, sprouts possess traits which make them readily available and attractive to browsers, yet fairly resilient to tissue loss. Here, we experimentally evaluate whether hardwood tree stump sprouts are effective and sensitive phytoindicators of deer browse pressure. We measured sprout abundance and height in fenced and unfenced plots at 17 shelterwood harvested sites scattered across a 6500 km² region where deer densities varied by nearly an order of magnitude. We found browsing did not alter the proportion of stumps sprouting and sprout density; however, browse pressure varied among the four most abundant species. *Acer rubrum* and *Acer saccharum* were heavily browsed, although browse pressure on *A. saccharum* decreased in areas with greater canopy openness. *Fagus grandifolia* and *Prunus serotina* were less preferred. Differences in palatability altered size hierarchies. Averaged across all species, browsing reduced sprout height by 39%, relative to protected sprouts. Under ambient browsing, *P. serotina* was 60–100% taller than other species and significantly taller than *A. saccharum* and *F. grandifolia*. However, within fences *A. saccharum* and *A. rubrum* doubled in size, relative to browsed individuals, and were as tall as *P. serotina*. Deer impact on sprout height within unfenced forest stands was negatively correlated with estimated deer densities ($R^2 = 0.46$). Thus, we suggest sprout surveys can provide a measure of impact across much larger areas. Our results demonstrate that sprouts, particularly those of *Acer* species, offer an abundant, easily measured, and reliable indicator of browse pressure. Moreover, browse impacts on sprouts emerged before impacts were detected on seedling abundance, height, or biomass. We argue sprouts can warn of imminent browse risk to seedlings (and perhaps non-woody vegetation) and thereby allow managers to take actions to mitigate or avert losses to the regenerating seedling cohort.

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1. Introduction

Abundant empirical documentation indicates that overabundant populations of white-tailed deer (*Odocoileus virginianus*) and other ungulates can undermine multiple ecosystem services provided by forests including biodiversity and sustainable wood and fiber production (reviewed by Côté et al., 2004; Fuller and Gill, 2001; Gill, 1992; Hobbs, 1996; Rooney and Waller, 2003; Russell et al., 2001). As selective browsers, deer alter the growth, survival,

and fecundity of plants through tissue consumption (Krueger et al., 2009; Long et al., 2007) resulting in widespread changes in patterns of species composition, reductions in diversity, alterations to successional pathways, and inhibited forest regeneration (Côté et al., 2014, 2004; Rooney and Waller, 2003; Russell et al., 2001; Waller and Alverson, 1997).

In spite of the well-known effects of ungulates on forest ecosystems, land managers are confronted with the challenge of sustaining vegetation diversity, structure, and function within forests impacted by intense browsing. Thus, many forest management agencies monitor either deer populations (e.g., fecal pellet surveys; Acevedo et al., 2010; deCalesta, 2013) or browse impacts on plant communities (Kirschbaum and Anacker, 2005; Morellet

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et al., 2001). Vegetation-based indices (i.e., phytoindicators) of browsing are typically preferred as they allow a rapid and cost-effective assessment of browse impacts on forest communities (Iijima and Nagaike, 2015). Vegetation indicators include browse surveys (Oak browsing index; Chevri er et al., 2012; Sugar maple browse index; Frelich and Lorimer, 1985), measurements of morphological characteristics of browse-sensitive species (e.g., height or impact to reproductive structures; reviewed by Kirschbaum and Anacker, 2005), demographic characteristics of plant populations (Knight, 2003; McGraw and Furedi, 2005), and even integrated indices that consider responses at the plant community-level (Filazzola et al., 2014; Frerker et al., 2013) or across taxonomic groups (e.g., plants and insects; Bachand et al., 2014). Ultimately, monitoring browse indicators provides managers critical data to sustainably manage their resources. For example, McGraw and Furedi (2005) incorporated browsing pressure to model the population viability of *Panax quinquefolius*, a valuable non-timber forest product species. Moreover, land managers are currently using phytoindicator surveys to adaptively manage deer hunting pressure on public and private lands (Pennsylvania DCNR, 2013; Stout et al., 2013).

Vegetation-based indices have many merits; however, they also suffer from shortcomings that may limit their broad application. For example, indicators based on browse impacts to focal plant species are inadequate if the chosen species are rare or absent within sampled stands, or entirely consumed (Frerker et al., 2013). Effective browse indicators should also be consistently browsed; hence, many phytoindicators are focused on highly palatable species (Kirschbaum and Anacker, 2005). However, even among palatable species, browse susceptibility can vary depending on plant size or relative abundance (e.g., Faure-Lacroix et al., 2013). For example, small seedlings are disproportionately less susceptible to browsing than larger seedlings within a deer's 'molar zone' (0.2–1.8 m; Frerker et al., 2013; Waller and Alverson, 1997) resulting in lagged responses to current browse pressure as seedlings develop and grow into larger, vulnerable size classes. Finally, palatability and susceptibility to browsing can vary across resource gradients (e.g., nitrogen, light; Tripler et al., 2002). Therefore, ideal indicators should be widely distributed, abundant, susceptible to browsers, palatable across various resource gradients, and browse tolerant.

Resprouting woody species (e.g., stump sprouts) circumvent many of the limitations on availability, browse-susceptibility, and tolerance that often limit the utility of other phytoindicators. Many hardwood species sprout prolifically after being top-killed (reviewed by Tredici, 2001; Vesik and Westoby, 2004) and are found consistently and abundantly in windthrown and harvested forest communities (Clarke et al., 2013; Dietze and Clark, 2008; Forrester et al., 2014; Poorter et al., 2010; Ristau and Horsley, 1999). Additionally, although deer preferentially browse on sprouts growing in disturbed areas versus seed origin stems (Harlow et al., 1997; Moore and Johnson, 1967), these sprouts are tolerant to browsing due to abundant carbohydrate reserves in rootstocks (Bond and Midgley, 2001; Faison et al., 2014; Poorter et al., 2010). Sprout growth rates also are 3–4 times greater than seedlings (0.5–1.0 m/yr; Dietze and Clark, 2008; Ristau and Horsley, 1999; Tredici, 2001) and thus enter quickly into larger size classes that are more vulnerable to deer browsing. By possessing traits which make them rapidly available and attractive to browsers, yet fairly resilient to tissue loss stump sprouts should serve as reliable and useful indicators of browse impact.

Here, we experimentally evaluate whether hardwood tree stump sprouts are effective and sensitive phytoindicators of deer browse pressure. If so, we predict stump sprout size and abundance will be more adversely affected than seedling size or abundance or overall woody biomass. We further predict browse impact on sprouts will intensify with increasing deer densities. Our

experimental approach collected data on sprout and seed origin stems within paired fenced and unfenced plots across multiple sites distributed over a large spatial scale and where deer densities varied by nearly an order of magnitude. Thus, we are able to test phytoindicator sensitivity and reliability across a broad range of deer densities.

2. Materials and methods

2.1. Study area

We conducted our study in 17 northern hardwood forest sites distributed across a 6500 km² area of northern Pennsylvania, USA (Appendix A). Major tree species are red maple (*Acer rubrum*), sugar maple (*Acer saccharum*), black cherry (*Prunus serotina*), and American beech (*Fagus grandifolia*), with lesser abundances of hemlock (*Tsuga canadensis*), birches (*Betula alleghaniensis*, *Betula lenta*), and white ash (*Fraxinus americana*) (Marquis, 1975). Understory vegetation is dominated by unpalatable striped maple (*Acer pensylvanicum*), beech (mostly root sprouts) in the shrub layer, and ferns (e.g., *Dennstaedtia punctilobula* and *Thelypteris noveboracensis*) in the herb layer (Royo et al., 2010).

2.2. Experimental design

All experimental sites are forests where managers initiated a regeneration sequence via a shelterwood system. The initial establishment harvest reduced average basal area across all sites from an average of 26.1 m²/ha to 16.2 m²/ha (see Table 1 for specific changes by site). Additionally, 16 of the 17 sites also received broadcast herbicide treatments (typically sulphometron methyl with or without glyphosate; Marquis et al., 1984) to control dense layers of plants species (e.g., ferns) interfering with tree regeneration. The combination of herbicide and shelterwood harvests is a common silvicultural system used in the northeastern U.S. and elsewhere that stimulates diverse seedling recruitment and growth several years prior to a final removal harvest (Hannah, 1988; Horsley, 1994; Nyland, 2002).

Within each site, we established paired 4200 m² (60 m × 70 m) plots and randomly assigned one plot as a deer exclusion (fence) treatment and the other an unfenced control in 2013. Centered within each plot, we established a 2000 m² (40 m × 50 m) sampling area, divided into a 10 m × 10 m grid, so as to leave a ~10 m wide buffer between the perimeter of the plots and the sampling area. Exclusion construction was completed by September 2013 except for one site (Rush) in which harvest occurred during winter of 2013/14. At this site, the exclusion was constructed in early spring 2014.

We surveyed vegetation in summer 2014. We censused tree regeneration in 1 m² circular subplots located at the nodes of the 10 m × 10 m grid (30 subplots per plot). We counted all seed origin or seedling sprout stems by species and height class (0.05–0.3, 0.3–0.9, 0.9–1.5, and >1.5 m) and recorded heights of the tallest individual of each species. We surveyed all stumps contained within the 2000 m² area delineated by the grid. If possible, stumps were identified to species. For each stump we measured diameter along the widest axis, the number of sprouts per stump (sprout density), the height of the tallest sprout, and browse pressure (i.e., proportion of sprouts that were browsed). We conducted biomass harvests in 1 m² circular subplots placed 5 m north of 9 randomly selected nodes in both the exclusion and control plots. In each subplot we clipped all vegetation to 1 cm height by functional group (subshrub, woody, annual grass, perennial grass, annual forb, or perennial forb). Following clipping, vegetation was dried for 3–5

Table 1

Summary of 17 sites used in the study. Data includes year of herbicide and shelterwood harvest treatments, pre and post-harvest basal areas (m²/ha), and estimated overwinter deer densities in 2014 (deer/km²).

Name	Herbicide year	Harvest date	Pre-harvest basal area	Post-harvest basal area	Deer density
Balaton Timber	2009	2012	N/A	19.51	9.9
Bradford 40	2012	2011	23.18	8.03	8.7
Bump Run #3	2012	2013	22.95	16.07	4.2
BWAC9	2011	2012	32.13	6.31	2.7
Cash Crop	2009	2013	24.10	14.92	4.6
Close Call	2010	2013	19.71	14.92	2.9
Compressor	2012	2012	24.97	21.23	5.7
McKean 37	2012	2010	N/A	14.92	6.4
Potter 11/Kickoff	2012	2013	N/A	20.66	4.6
Potter6	2012	2012	N/A	19.51	9.0
Rush	2010	2014	27.31	14.34	6.1
Screaming Eagle	2009	2012	25.25	16.07	3.5
Second Look	2012	2013	23.45	16.64	9.0
Shake-N-Bake	2009	2012	27.77	18.36	5.9
Shakespeare	N/A	2013	29.84	17.21	8.6
Sorry About That	2010	2012	32.59	17.21	7.8
Treed Bear	2009	2012	26.16	20.08	3.4

days and dried samples were weighed and mean biomass per plot calculated for each functional group.

For each site, we estimated deer densities using fecal pellet surveys conducted throughout the 2.6 km² (1.609 km × 1.609 km) area surrounding each study site in spring (April–early May). Estimates derived from pellet group counts represent the average number of deer over winter and therefore, the number of adult deer surviving into the spring and summer (deCalesta, 2013).

We quantified canopy openness using hemispherical canopy photographs taken directly above each vegetation sampling node in summer 2013. Percent canopy openness was calculated from each photograph using HemiView version 2.1 (Rich et al., 1999). Canopy openness measures above each node were treated as subsamples and were averaged to obtain a canopy openness value for each plot.

2.3. Statistical analyses

We examined the effect of deer browsing on proportion of stumps producing ≥1 sprout, sprout density, sprout height, and browsed pressure using analyses of covariance on a randomized complete block design. We tested overall (all species) responses to treatment and further explored variation among species by restricting the dataset to the four most abundant species (red maple, sugar maple, American beech, and black cherry). We modeled treatment (fence/control) and species as fixed effects, and site and treatment(site) as random model effects. Because canopy openness can influence stump sprout abundance, growth, and vigor (Keyser and Zarnoch, 2014), we included canopy openness as a covariate in the model. This approach first required testing the homogeneity of slopes assumption. If the full model found no significant fixed effect × canopy openness interaction, the interaction was removed and the analyses proceeded using an equal slopes model testing only the covariate. However, in cases where the fixed effect × canopy openness interaction was significant we used an unequal slopes model and treatment differences were tested for three levels of the canopy openness covariate (Littell et al., 2006). The three levels were low (10th percentile, 13% canopy openness), average (mean, 21% canopy openness), and high (90th percentile, 26% canopy openness).

Analyses were conducted using generalized linear mixed models and we utilized least-squared means to test pair-wise differences between treatments or among species (Proc Glimmix; SAS Institute Inc., 2011). Species were not evenly represented between treatments or across sites and therefore we report Type III Sums of Squares. We examined homoscedasticity and normality of the residuals within each treatment or among species using boxplots

and Levene's test. Models were run using the Kenward–Rogers denominator degrees of freedom method. Proportional data (proportion sprouting, browse pressure) was modeled using a binomial distribution (Bolker, 2008) and sprout density and average height were modeled using a normal distribution. We excluded sprouts found within slash piles (branches removed from harvested logs) from our analyses because this woody debris can hinder access by deer, hence confounding our design (Bergquist et al., 1999; Grisez, 1960). Indeed, sprouts within slash piles were tallest, regardless of whether they were in the enclosures or controls (141.9 ± 25.3 cm and 117.9 ± 20.1 cm, respectively).

We explored the relationship between deer density and deer impact on vegetation using linear regression analyses (Proc Reg; SAS Institute Inc., 2011). We identified and, if necessary, removed outliers exhibiting large residuals and leverage using the Cook's D metric (Cook, 1977). Observations were considered outliers if they had a Cook's D value >4/n, where n represents the number of observations (Bollen and Jackman, 1990). Our four vegetation indices were mean sprout height, seedling height, seedling density, and woody biomass. We define deer impact (*I*) as the log response ratio between the mean response in the unfenced, \bar{x}_C , and fenced, \bar{x}_F , plots (Osenberg et al., 1997; Rooney, 2009): $I = \ln(\bar{x}_C/\bar{x}_F)$. Negative values of *I* indicate a detrimental deer impact while positive values indicate a beneficial deer impact.

3. Results

3.1. Browse impacts on sprouts

We surveyed 1099 stumps with a total of 2599 sprouts representing 11 species and 10 genera (Table 2). Several individuals could only be identified to genus level, due to a lack of sprouts, leaves, or short stump heights and decay. Maples were the most abundant species representing nearly half of the stumps and sprouts surveyed (Table 2). Across species, approximately 47% of the stumps surveyed produced sprouts and deer browsing limited this metric (43.2 ± 4.3% versus 50.0 ± 4.3% in control versus fence, respectively; $F_{1,14} = 4.69, P = 0.048$). The proportion of stumps with sprouts varied among species with red maple most likely to produce at least one sprout and black cherry least likely to sprout; deer browsing did not affect this metric (Table 3). Sprout density (all species) was unaffected by browsing ($F_{1,14} = 0.01, P = 0.93$), even when analyses were restricted to the four common species (Table 3). Greater canopy openness increased the proportion of stumps which sprouted when examined across all species ($F_{1,14} = 6.5, P = 0.02$) and when restricted to the four most common ($F_{1,68} = 10.43, P = 0.002$).

Table 2
Total number and relative abundance of stumps, by species, surveyed across all 17 sites in northwestern Pennsylvania.

Species	Total stumps	Relative abundance
<i>Fagus grandifolia</i>	353	32.12%
<i>Acer</i> spp.	208	18.93%
<i>Acer rubrum</i>	192	17.47%
<i>Acer saccharum</i>	113	10.28%
<i>Prunus serotina</i>	109	9.92%
Unknown	31	2.82%
<i>Fraxinus americana</i>	30	2.73%
<i>Betula</i> spp.	21	1.91%
<i>Ostrya virginiana</i>	18	1.64%
<i>Liriodendron tulipifera</i>	6	0.55%
<i>Acer pensylvanicum</i>	5	0.45%
<i>Betula allegheniensis</i>	5	0.45%
<i>Tilia americana</i>	4	0.36%
<i>Carya cordiformis</i>	2	0.18%
<i>Quercus</i> spp.	2	0.18%
Total	1099	100.00%

Deer browsing limited stump sprout height development. Across all species, sprouts within exclosures were twice as tall as those in controls (81.9 ± 7.6 cm and 50.0 ± 7.6 cm, respectively; $F_{1,14} = 17.38$, $P = 0.0008$). Browsing impacts on height development also differed among species (significant treatment \times species interaction; Table 3). Under ambient browsing, black cherry sprouts were 60–100% taller than other species and were significantly taller than both sugar maple and beech sprouts. Protection from browsing increased red maple and sugar maple sprout height by 80% and 130%, respectively. Within fences, the average sprout height of the maples was equivalent to that of black cherry (Table 3). Canopy openness did not affect sprout height (All species: $F_{1,14} = 0.02$, $P = 0.89$).

Deer exhibited distinct browse preferences among the four common species, although preference varied depending on the level of canopy openness (significant species \times canopy openness interaction; Table 4). Red maple was heavily browsed (72–87% of available stumps browsed) across the canopy openness gradient. In contrast, browse pressure on sugar maple and beech declined as canopy openness increased, although browsing on sugar maple was 2–5 times greater than on beech throughout the canopy openness gradient. Browsing on black cherry averaged 32%; however, we could not obtain reliable estimates of browsing at the tail ends of the canopy openness gradient due to limited sample size.

Table 3
Results of analyses of covariance on proportion of stumps producing ≥ 1 sprout, mean sprout density, and mean sprout height for the four most abundant species combined. The four species varied in sprouting probability; hence, we present the mean proportion of stumps producing sprouts, by species. Height differed among species and between treatments; hence, we present mean height (cm), by species, in both the fenced and control areas. Superscripts denote pairwise differences among species (proportion sprouting) or among species and treatments (height). CO: canopy openness; Trt: treatment.

	Proportion sprouting		Sprout density		Height no refugia	
Treatment	$F_{1,68} = 0.84$; $P = 0.3632$		$F_{1,49} = 0.02$; $P = 0.8866$		$F_{1,49} = 13.27$; $P = 0.0007$	
Species	$F_{3,68} = 13.99$; $P < 0.0001$		$F_{3,49} = 2.29$; $P = 0.0899$		$F_{3,49} = 7.92$; $P = 0.0002$	
Trt \times species	$F_{3,68} = 0.94$; $P = 0.4250$		$F_{3,49} = 0.69$; $P = 0.5597$		$F_{3,49} = 4.31$; $P = 0.0090$	
Canopy openness	$F_{1,68} = 10.43$; $P = 0.0019$		$F_{1,49} = 0.07$; $P = 0.7985$		$F_{1,49} = 0.00$; $P = 0.9850$	
Trt \times CO	–		–		–	
Species \times CO	–		–		–	
	Proportion sprouting			Heights		
				Control	Fence	
<i>A. rubrum</i>	0.76 ± 0.05^a			<i>P. serotina</i>	88.10 ± 16.40^{ab}	81.43 ± 12.02^{ab}
<i>A. saccharum</i>	0.71 ± 0.06^a			<i>A. rubrum</i>	55.55 ± 8.70^{bc}	104.25 ± 8.96^a
<i>F. grandifolia</i>	0.50 ± 0.05^b			<i>A. saccharum</i>	44.53 ± 11.30^c	93.14 ± 10.08^a
<i>P. serotina</i>	0.40 ± 0.07^b			<i>F. grandifolia</i>	42.64 ± 9.29^c	50.94 ± 8.98^c

Table 4
Results of analyses of covariance on browse pressure (proportion of sprouts browsed). Browse pressure was modeled using unequal slopes ANCOVA (significant species \times canopy openness); therefore, species differences in browsing pressure (Least Square Means ± 1 SE) were tested at three levels of the canopy openness covariate. Due to limited numbers of *P. serotina* the tail ends of the canopy openness gradient, we could not reliably estimate browse pressure (non-est). Superscripts denote significant pairwise differences among species within a given canopy openness level.

	Browse pressure		
Species	$F_{3,12} = 3.27$; $P = 0.0588$		
Canopy openness	$F_{1,12} = 0.12$; $P = 0.7300$		
Species \times CO	$F_{3,12} = 11.59$; $P = 0.0007$		
	Canopy openness		
Year	Low (13%)	Mean (21%)	High (26%)
<i>A. rubrum</i>	0.72 ± 0.13^a	0.82 ± 0.05^a	0.87 ± 0.05^a
<i>A. saccharum</i>	0.91 ± 0.07^a	0.81 ± 0.06^a	0.72 ± 0.12^b
<i>P. serotina</i>	non-est	0.32 ± 0.14^b	non-est
<i>F. grandifolia</i>	0.49 ± 0.16^a	0.17 ± 0.05^b	0.08 ± 0.04^c

3.2. Deer impact on vegetation indices

Over-winter deer densities, as estimated from fecal surveys, ranged from 2.7 to 9.9 deer/km² (Table 1). Deer impact (i.e., log-response ratio) on sprout height tended to decline as deer densities increased ($I_{\text{Sprt Height}} = -0.08 \times \text{DeerDensity} - 0.09$; $F_{1,16} = 3.51$; $P = 0.08$, $R^2 = 0.19$). Outlier analyses indicated one site (Bump Run) was a clear outlier with a squared residual value an order of magnitude greater than the average of all other sites (Cook's $D = 0.43$). This site exhibited very low sprout heights relative to controls despite having low deer densities (4.2 deer/km²). Further examination revealed species in fences were faster-growing and palatable maples, while estimates in the control were driven by slow-growing and unpalatable beech. When this outlier was removed from the analysis, deer impact on stump sprout height was strongly predicted by ambient deer densities ($I_{\text{Sprt Height}} = -0.11 \times \text{DeerDensity} + 0.13$; $F_{1,15} = 11.73$; $P = 0.004$, $R^2 = 0.46$; Fig. 1). In contrast, ambient deer densities were not related to seedling height ($I_{\text{Sdl Height}} = 0.06 \times \text{DeerDensity} - 0.64$; $F_{1,16} = 3.38$; $P = 0.09$, $R^2 = 0.18$), seedling abundance ($I_{\text{Sdl Abun}} = 0.07 \times \text{DeerDensity} - 0.48$; $F_{1,16} = 3.90$; $P = 0.07$, $R^2 = 0.21$), or woody biomass ($I_{\text{Biomass}} = 0.04 \times \text{DeerDensity} - 0.55$; $F_{1,16} = 0.07$; $P = 0.79$, $R^2 = 0.005$).

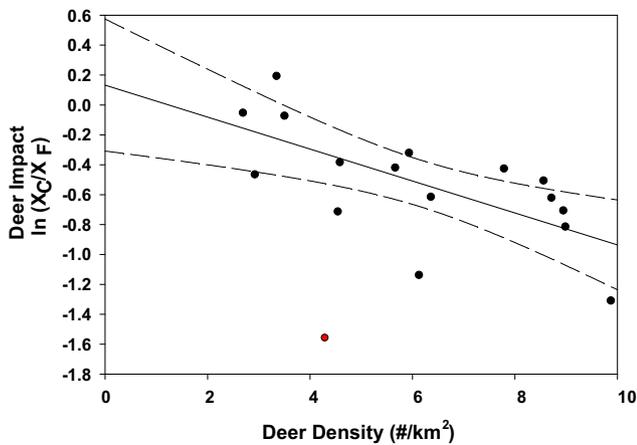


Fig. 1. Relationship between deer density and deer impact on stump sprout height across 17 sites in northwestern Pennsylvania. Deer impact is the log-response ratio of average stump sprout heights exposed to ambient browsing (X_c) and no browsing (X_f), where negative numbers indicate smaller sprouts under ambient browsing relative to protected sprouts. Regression results ($I_{\text{Sprt Height}} = -1.1 \times \text{DeerDensity} + 1.33$; $F_{1,15} = 11.73$; $P = 0.004$, $R^2 = 0.46$) exclude outlier located at bottom, left of the graph. Dashed lines represent 95% confidence interval.

4. Discussion

4.1. Sprouts as an effective indicator of deer browsing impacts

Effective indicators should be easily measured, demonstrate a rapid and predictable response to stress, anticipate changes to a system, and be broadly applicable (Dale and Beyeler, 2001). Valuable indicators, should warn of imminent risk to management objectives such as canaries warned miners of the accumulation of toxic gases in coal mines. Our results, representing a wide distribution of sites with variable deer densities and canopy openness, identify maple stump sprouts, and those of red maple in particular, as an abundant, easy to census phytoindicator. Moreover, these sprouts have the added advantage that they are rapidly growing, preferentially browsed yet surprisingly resilient to browsing, and can predict large-scale variation in deer abundance. Hence, we argue that sprouts represent a highly reliable and responsive indicator of potential browse impacts following forest harvests.

In North America, red and sugar maple rank among the most broadly distributed and most abundant species in temperate hardwood forests (Murphy et al., 2006). For these species, as well as a majority of hardwood species worldwide, sprouting is a common response to stress (Keyser and Loftis, 2015; Tredici, 2001; Vesk and Westoby, 2004). Furthermore, browsing on maples, particularly on red maple, was intense regardless of canopy conditions, and yet these individuals, although reduced in height, were still readily available under ambient browsing. Thus, we suggest maples represent an ideal species to examine browse impact across a broad geographic region and under a range of canopy disturbance conditions. Several other hardwood tree species with broad geographic distributions, including some *Populus* spp. or *Quercus* spp. exhibit prolific sprouting and are highly palatable to browsers (Kochenderfer and Ford, 2008; USDA-FEIS, 2015). Sprouting from some woody shrubs is also highly palatable, yet resilient to browsing (Faison et al., 2014). Hence, the utility of sprouts of tree and shrub species have applicability as browse phytoindicators in a variety of hardwood forest types.

Browse susceptibility is affected by palatability and relative abundance (Tripler et al., 2002). For the maples, we cannot discount either mechanism given that these species are palatable (Gray and Servello, 1995; Crawford, 1982) and also were abundant at our sites. In contrast, American beech suffered low to moderate browse

pressure, depending on canopy openness, despite being abundant at our sites. This species is a non-preferred browse for white-tailed deer, often receiving limited browse pressure when compared to other woody species (Miller et al., 2009; Horsley et al., 2003). Black cherry stumps were infrequent (10% of all stumps) and produced the lowest number of stump sprouts. The limited availability of black cherry sprouts at our sites may have influenced the low browse pressure on this species. However, this species is known to be unpalatable to deer due to high levels of cyanogenic glycosides (Burns and Honkala, 1990).

The utility of sprouts as browse indicators is likely constrained to forests where trees have been stressed or top-killed by harvesting. Thus, we do not suggest sprouts become a replacement phytoindicator for browsing, but rather a complementary source of information to assist the decision making process. Dale and Beyeler (2001) and others have argued that combinations of complementary indicators can improve our ability to effectively monitor impacts to natural communities (see also Bachand et al., 2014; Frerker et al., 2013). Nonetheless, we demonstrated that deer impact on sprout height (i.e., log-response ratio between ambient browsing no browsing) in relatively small areas (<1 ha) robustly predicted estimated deer densities at larger spatial scales (i.e., 259 ha). Thus, sprouts may be a much more sensitive and reliable predictors of browse impact in areas where they occur and could potentially provide a measure of impact across much larger areas.

4.2. Management implications

White-tailed deer browsing can impede habitat conservation (McGraw and Furedi, 2005; Pellerin et al., 2006), habitat restoration (Gonzales and Arcese, 2008; Opperman and Merenlender, 2000), and sustainable forest management (Horsley et al., 2003; Tremblay et al., 2007). The successful establishment of a diverse and abundant sapling cohort following a harvest often hinges on browsing impacts experienced during early establishment (Horsley et al., 2003; Nuttle et al., 2014; Nuttle et al., 2013). Therefore, managers need metrics that rapidly assess browse impact before large-scale changes to vegetation occur (Dale and Beyeler, 2001).

In forest areas managed for regeneration we suggest browsing intensity on sprouts provides a quick and reliable assessment of browse pressure prior to the seedling cohort entering the larger size classes (e.g., >20 cm) where they become vulnerable to deer browsing (Frerker et al., 2013; Kittredge and Ashton, 1995; Waller and Alverson, 1997). This information allows managers to avert losses to the regenerating cohort through actions such as deer herd reduction (Miller et al., 2010; Royo et al., 2010; Tanentzap et al., 2011) or protecting harvested areas by fencing (Marquis et al., 1992; Vercauteren et al., 2006).

The use of sprouts as browse impact indicators should include monitoring sprout height development under ambient browsing as well as in protected areas. Sprout development can be compared in protected exclosures versus exposed areas or on individually fenced stumps (e.g., “sentinel seedlings”; Boulanger et al., 2014). Chemical deer repellants may also be used to protect sprouts (Kochenderfer and Ford, 2008). Managers could also simply estimate browse impact by comparing sprout development within and outside slash piles, if these are available.

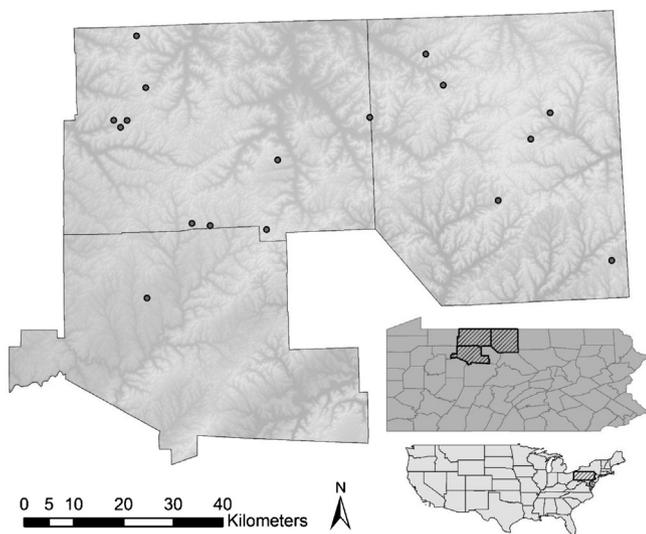
The SILVAH silvicultural prescription guidelines suggest that even moderate deer impacts levels can limit the contribution of sprouts to the regeneration stocking by 50% and completely eliminate it at higher impact levels (Brose et al., 2008). Furthermore, Kochenderfer and Ford (2008) found browsing diminished the probability of *Quercus rubra* and *Quercus montana* sprouts reaching 1.5 m in height by approximately 60% and limited overall sprout height of *Q. montana* sprouts by 45%, relative to fenced sprouts. Finally, Horsley and colleagues (2003) experimentally concluded

negative browse impacts on vegetation can begin at approximately 8 deer/km². Our regression results suggest that browsing will reduce sprout height by 48.5% ($e^{-0.722}$) at that deer density, relative to fenced plots. Therefore, we suggest managers utilize a 50% reduction in height in exposed sprouts, relative to protected sprouts within the first year post-harvest, as an indicator of excessive deer impact on vegetation. Managers should consider monitoring sprouts, particularly those of palatable woody species, as an essential addition to their toolkit of browse indicators.

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Appendix A. Map showing the 17 sites scattered throughout a 3 county region in northwest Pennsylvania, USA.



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