A new rapid and efficient method to estimate browse impacts from twig age

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ABSTRACT

High densities of white-tailed deer restrict the regeneration of tree species, reduce understory cover and diversity, enhance invasions of exotic species, and facilitate the spread of human and deer diseases. Deer managers often base management decisions on estimated deer densities and carrying capacities, generating controversy. It may be simpler, cheaper, and more appropriate to manage deer populations in relation to their effects on local habitat conditions. Here, we describe a method based on the mean ages of woody twigs on saplings exposed to browsing. Growth can be traced back at least five years on deciduous species using terminal bud scale scars, generating estimates for the minimum interval between browsing events. We applied this method to three species of maple (*Acer*) growing in canopy gaps in- and outside a 5–7 year-old fenced deer exclosure in a mature forest in upper Michigan. Maples are palatable to deer but resprout readily after browsing. The method was simple and efficient to implement in the field with negligible among-observer variation. Mean twig age responded sensitively to differences in deer impacts among species, across the fence, and over time (all p < 0.002). *Acer rubrum* and *pensylvanicum* had lower mean twig ages than *A. saccharum* reflecting higher rates of browsing. Twig age showed a larger deer effect size and r^2 values than the sapling height or browse indicators (Cohen's d = 34.85 vs. 1.39 and 9.55 for height and browse; r^2 = 0.556 vs. 0.154 and 0.331). Twig ages declined with height outside the fence while rising inside, providing a second independent indicator of deer impacts. Twig ages provide a direct indicator of deer browse on regenerating trees with lower sampling variance and higher independence from local environmental conditions than height or browse incidence. We should next test the twig age method in other contexts and species to confirm that it is an efficient, sensitive, and reliable indicator of deer impacts and habitat conditions.

1. Introduction

Deer and elk selectively browse a variety of woody shrubs and trees and graze many herbaceous species. At higher densities, they eat more species and increasing fractions of the food available, indirectly favoring species that tolerate or avoid herbivory. At this point, ungulates act as a keystone herbivore to alter community structure and the distribution and abundance of many species (McShea and Rappole, 1992; Waller and Alverson, 1997; Augustine and DeCalesta, 2003; Côté et al., 2004; Goetsch et al., 2011). Cascading effects of ungulate browsing include the suppression of tree growth (Lucas et al., 2013), altered populations of small mammals (deCalesta, 1994) and birds (DeCalestra, 1994; Allombert et al., 2005; Cardinal et al., 2012), faster soil nutrient cycling (Gass and Binkley, 2011), and accelerated invasions of exotic earthworms and weedy plants (Williams and Ward, 2006; Eschtruth and Battles, 2009; Knight et al., 2009; Davalos et al., 2015; Dobson and Blossey, 2015). In eastern North America, high white-tailed deer

populations have limited rates of sapling recruitment enough to alter forest type and composition across broad regions (Bradshaw and Waller, 2016). High deer densities have also facilitated increases in disease load by facilitating the spread of Chronic Wasting Disease (Storm et al., 2013) and boosting populations of the ticks that spread Lyme and other tick-borne human diseases (Wilson et al., 1985; Deblinger et al., 1993; Kilpatrick et al., 2014).

Despite the number, severity, and significance of ungulate (deer henceforth) effects, few programs exist to monitor these in a systematic and continuing way (Morellet et al., 2007). This prevents most deer managers from basing their decisions on the magnitude of these effects. Instead, deer populations are usually managed to favor hunting and viewing opportunities using estimated deer densities to steer management relative to perceived biological and/or social carrying capacities. The uncertainties inherent in these estimates have added to the controversies surrounding deer management. Estimating deer densities is technically demanding, requiring extensive field sampling (e.g., scat-

group count data) or elaborate population models. Models like the Sex-Age-Kill model used in several states depend on accurate records of hunter kills plus measures or assumptions for several key variables (Millspaugh et al., 2009). In practice, estimating deer densities has proved to be costly, imprecise, and most reliable at large spatial scales. However, even if estimating deer densities were cheap and accurate, these densities would not necessarily tell us whether the deer herd could be supported by current habitat conditions or the trajectory of habitat conditions at each site.

Assessing habitat conditions is usually simpler, cheaper, and more accurate than first estimating deer density and then using that estimate to manage the deer herd. This means that having standard methods to monitor habitat conditions could give forest and wildlife managers a valuable tool for assessing the capacity of the land to sustain local deer populations. Having local data on habitat conditions would also match trends in many states to manage deer at more local levels. These data will also gain value once methods are standardized and applied across broader regions and successive years. These broad spatial and temporal data, in turn, would facilitate more comprehensive studies of regional differences and trends.

Here, we introduce a streamlined method for estimating deer impacts and habitat conditions by estimating the number of years that twigs can grow unmolested before being browsed (an inverse measure of the browsing rate). We first present the rationale for this measure and its basic design. We then describe how it is applied in the field and how the data it generates can be analyzed to infer browsing impacts. We test the method's sensitivity by comparing results from saplings in- and outside a fenced exclosure and among three species of maple (*Acer*). We also compare the power of twig age measures relative to two alternative measures – sapling height and the incidence of fresh browsing. We also explore relationships between twig ages and sapling height to test the hypothesis that taller saplings experience greater rates of browsing in the presence of deer. We conclude that this method has considerable promise and deserves to be tested in other species and locales. If its promise is borne out, the twig age method could be used to construct a network to efficiently monitor deer habitat conditions.

2. Motivation and rationale

The impacts that herbivores have on tree seedlings and saplings (henceforth saplings) reflect a race between growth and herbivory. Both are measured as rates or, inversely, as time intervals. When deer are dense, tree saplings have shorter intervals in which to grow before experiencing another bout of browsing that acts to limit growth. When deer are sparse, these intervals are long, allowing sapling growth to balance losses from other sources (insect herbivory, diseases, and attrition due to falling debris). This balance implies that faster growing saplings can tolerate higher rates of browsing while saplings growing slowly (due to either shade or a conservative growth strategy) may suffer more from herbivory. Thus, saplings growing under sunnier conditions generally tolerate more browsing. Conversely, slow-growing seedlings and saplings of shade-tolerant conifers like *Tsuga canadensis* and *Thuja occidentalis* that can spend decades in the "molar zone" are highly susceptible to even intermittent browsing. For deer-palatable species that already occur sparsely under shady conditions, browsing can further reduce their densities to such low levels that recruitment is effectively curtailed (Bradshaw and Waller, 2016).

Several methods exist to assess deer impacts on forest vegetation. None has yet emerged as a standard despite the value of having measures that could be compared over time and among sites. The species used to assess browsing should be widespread and of intermediate palatability because species that are highly palatable disappear quickly once deer populations increase while species avoided by deer provide no signal of deer effects (except perhaps by increasing in relative abundance). Herbaceous species that have been used to indicate deer impacts include *Trillium* (Rooney and Gross, 2003; Jenkins et al., 2007),

Clintonia (Balgooyen and Waller, 1995), *Chelone* (Williams et al., 2000), and other species (Webster et al., 2001). Such species may disappear, however, with more herbivory. In addition, their abundance or condition can reflect plant as well as deer density (Augustine et al., 1998) or may vary among communities (Frerker et al., 2013). This makes it difficult to use herbaceous plant species as standard indicators.

Woody species provide advantages as indicators of deer impact. First, they retain a woody structure that can be observed and measured even as they are browsed to the point of death. Second, woody seedlings and saplings often persist across a range of sizes, tolerating some deer herbivory while retaining evidence of these impacts. Third, canopy trees provide long-lived seed sources that provide a continuous rain of seeds even if seedlings continue to disappear due to browsing. To estimate rates of deer browsing, Frelich and Lorimer (1985) introduced a method based on enumerating the freshly browsed fraction of terminal twigs in sugar maple (*Acer saccharum*) located in the browsing zone. Several studies in the upper Midwest have used this method, but we have found it suffers from high sampling variance (reflecting the patchiness of deer browsing) and estimates often vary among observers. It therefore seems best suited for assessing large differences among sites. Morellet et al. (2001, 2003, 2007) introduced a simpler method that relies on surveying any and all woody seedlings and saplings already present, scoring these simply as having browsable twigs present at points along a transect and which of those show any sign of browsing. Such simple scoring avoids having to identify species or estimate browsing rates within stems affording statistical advantages provided sample sizes are large enough to dampen sampling variance reflecting patchy consumption. Rawinski (2016) proposed another method that also uses extant plants by measuring the height of the ten tallest saplings of particular tree species found within a plot. Blossey et al. (2017) proposed propagating and planting hundreds of red oak seedlings as sentinels to assess deer impacts. Their approach has advantages including using a standardized food source and being able to assess deer effects even at locations where deer have eliminated natural seedlings. However, it also requires advance efforts to locate sites and propagate and plant seedlings that must then be relocated and tracked in successive years. All these methods have merit and deserve to be directly compared to evaluate which are most reliable and informative.

Most efforts to estimate browse impacts on woody species measure one of three things: a) vegetative condition of the sapling or shrub (cover, height, density, etc.), b) reproductive condition (the number or frequency of flowers and fruits), or the incidence or fraction of browsed twigs. An interesting exception to these are methods that use plant architecture to infer browsing in western rangelands (Keigley and Frisina, 1998; Keigley et al., 2003). Because their method is mostly qualitative, we do not discuss it further. Woody plant cover, height, and density, however, all vary greatly in response to local differences in seed rain, seed bed conditions, soil nutrients, and light levels which also greatly affect flowering and fruiting. Estimating the current incidence of browsing avoids these problems, but patchy deer browsing and variation among observers inflate sampling variance. The twig age method reduces these sources of environmental variation by instead estimating the intervals between episodes of deer herbivory. As noted above, measuring the rate instead of the amount of herbivory addresses the key process of interest: the race between growth and consumption. Twig growth may be fast or slow, depending on both the species being observed and its local environment, but what matters is whether twigs are growing faster than they are being removed. Mean twig longevity also averages over 2–3 stems and up to 5 years of growth, further reducing sampling variance.

It would be difficult and time-consuming to quantify rates of twig growth by marking individual plants and measuring annual extension growth on their many twigs. It would be similarly laborious to measure intervals between deer consumption directly (e.g., by regularly revisiting marked twigs to record intermittent events of herbivory). Such measures are unnecessary, however, if the key variable of interest is

Fig. 1. Terminal twig tears reflecting deer browse.
Source: http://wdfw.wa.gov/living/deer.html.

how long a twig can grow before its growth is curtailed by herbivory. We particularly sought a method that did not require marking and re-visiting particular individuals but instead just sampled woody plants present at a site.

In most deciduous woody species, it is straightforward to age twigs back at least five years to a parent twig that has ended its own growth using successive terminal bud-scale scars (TBSS's – see photos in Supplemental Material 1 – Protocol). This generates an integer – the number of years the twig has grown without being browsed. In species and locations where browsing recurs regularly, it will often be browsing that has killed the parent twig. This is often obvious in parent twigs that were browsed recently as deer browse leaves characteristic ragged tears (Fig. 1). In other cases, however, it will be difficult or impossible to positively identify past browsing as mechanical abrasion, falling bran-ches, and other events also abort twig growth. Fortunately, the method does not require us to determine what killed the parent twig. Instead, we simply accept that twig ages underestimate the actual mean time between browsing events. Nevertheless, regular browsing will generate lower twig ages in areas where browsing frequently kills twigs. Using twig ages instead of trying to estimate the frequency of browsing sim-plifies the method, allowing a single brief visit and survey to generate plentiful data. These data are also internally averaged over recent (up to five) years and multiple (here two) twigs within each sapling. We therefore hypothesized that mean twig ages can provide efficient and sensitive estimates of deer impacts that could be used to reliably compare how deer impacts vary over species, treatments (e.g., ex-closures), regions, and times.

3. Materials and methods

3.1. Field site, fenced exclosure, and sampled populations

To explore the efficiency and sensitivity of using twig ages to esti-mate and compare deer impacts, we developed a practical and efficient field protocol for measuring twig ages in tree saplings (Supplemental Material 1) plus an associated data sheet (Supplemental Material 2). Instead of marking and revisiting particular plants, this method pro-vides a 'snapshot' measure of recent deer browsing based on twig longevity. For field workers unfamiliar with the tree species being studied or how to use terminal bud scale scars to age twigs, some training is necessary. In practice, we found this training takes only 20 min.

We applied this method to three species of maple (*Acer saccharum*, *A. rubrum*, and *A. pennsylvanicum*) growing in a mature hemlock (*Tsuga canadensis*) – hardwood forest north of Marquette, Michigan in the Huron Mountain Club. Maples are well-suited for assessing deer impacts in that they are simple to identify, have easily visible twig architecture and TBSS's, are moderately to very abundant in many habitats, wide-spread in their distribution, of intermediate palatability, and consumed

often by deer but able to tolerate moderate browsing and rebound in growth (cf Frelich and Lorimer, 1985). We used the data generated from this protocol to compare sapling heights, twig ages, and the twig age by height relationship among the three species and between field plots located within and outside a fenced 2 ha deer exclosure con-structed in 2010. This exclosure allowed us to compare twig ages in sapling populations exposed to more and less deer herbivory in plots matched for forest soil and light conditions. The sampled populations all grew within light gaps caused by treefalls of the kind that regularly occur within old-growth forests. These gaps greatly increased the density and potential growth rates of these saplings, allowing rapid and efficient sampling. Such aggregations of saplings attract frequent deer visits and regular browsing as confirmed by fresh deer scat and images on a movement-triggered field camera (Reconyx 500). By applying the protocol in similar locations in 2015, 2016, and 2017, we were able to assess the repeatability of the method and how differences in browse impacts changed between 2015 and 2017.

The exclosure fence was constructed in June 2010 using black polypropylene 'invisible fence' (e.g., https://www.deerbusters.com/deer-fence-rolls/) and steel and nylon reinforcing wires. We found breeches in the fence due to tree falls and animal damage in May or early June of 2012, 2013, 2014, and 2017. These breeches were all repaired immediately and checked again in mid- to late-Summer and Fall to ensure that they remained primarily intact through the growing season. Tufts of hair along rips in the fence, newly browsed stems, and photos of deer inside the fence on the field camera confirmed that some deer browsing occurred inside the exclosure. Thus, any difference in estimated deer effects in- vs. outside the exclosure underestimates the actual effects of deer at this site.

3.2. Sampling saplings

Details of the method and a step-by-step protocol are described in Supplemental Material 1. Briefly, observers identify a suitable popula-tion of saplings and progress along a strip transect, randomly sampling individuals spaced 1 + m apart. Observers measure their height and age two terminal twigs on each sapling by counting successive terminal bud scale scars back to a parent twig that was browsed or otherwise killed. In 2017, we also recorded the incidence of fresh leaf or twig herbivory on all saplings. If the sample twig is itself browsed, we score its age as 0. We find we can take and record these observations and measurements at a rate of about one per minute, allowing field workers to obtain a good sample size for a species within an hour. We in-tentionally did not record data on light levels, soil conditions, or other environmental factors as the goal was to focus on twig ages rather than absolute growth rates or responses to conditions other than deer browsing. Nevertheless, local conditions apart from deer likely affect the distribution of twig ages. Future research may identify whether and how such effects affect these twig age results.
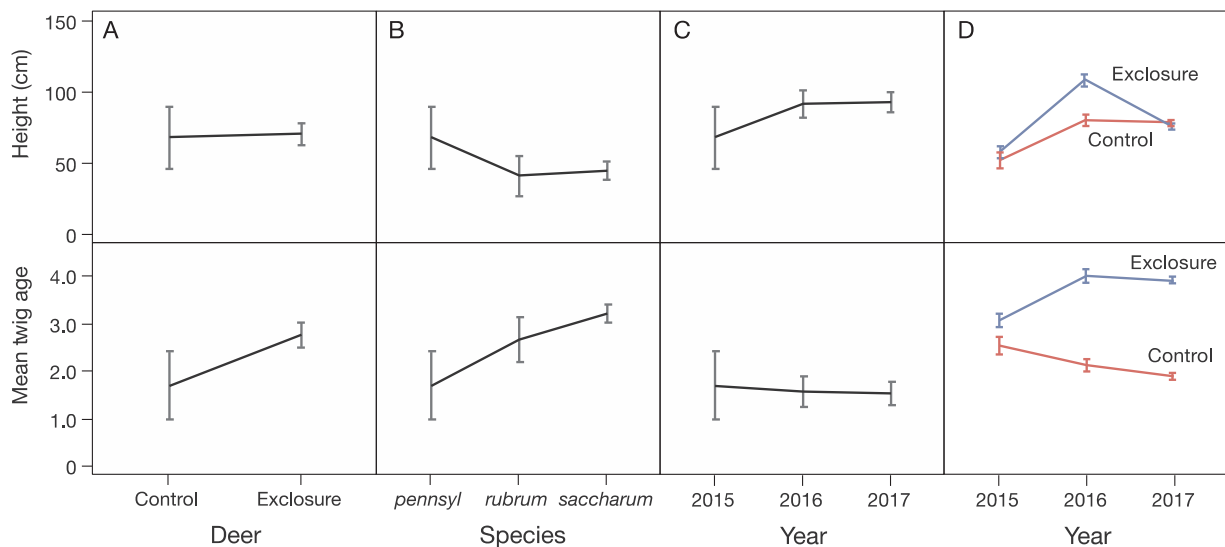
Fig. 2. Responses of sapling height and mean twig age (in years) to the three main predictor variables: deer exclosure (A), species (B), year (C), and the deer x year interaction (D). Values shown are least-squared means adjusted for other predictors in a general linear model that included all 2-way interactions. Error bars show standard errors of the estimates. The mean twig age model shows greater sensitivity to the exclosure effect and species and less sensitivity to year than the height model. It also had a larger overall F-value and coefficient of determination (F = 47.2 and adjusted r^2 = 0.50 vs. 21.0 and 0.30).

In this study, we sampled saplings of *Acer saccharum*, *rubrum*, and *pennsylvanicum* in- and outside the fenced exclosure in treefall gaps in the summers of 2015–2017. On July 2, 2015, DMW measured heights (cm) and twig ages (years) on 204 saplings in < 4 h using up to three twigs on each sapling. Counts of saplings in 12 replicate 3.14 m^2 round quadrats yielded an average sapling density of 5.41/m^2. Densities did not differ in- vs. outside the exclosure. In 2016, DMW measured heights and ages on 2–3 twigs on each of 87 saplings in < 2 h. In 2017, two newly trained workers measured heights, twig ages, and scored fresh browse in 303 saplings in about 5 person-hours. The binary (0/1) browse variable noted any direct evidence of deer browse in the current year. It only added seconds to the time needed to sample each sapling. It provides a way to confirm that smaller twig ages are associated with browsing and allowed us to compare the twig age method to methods based on the presence of fresh browsing on saplings (e.g., Morellet et al., 2003).

3.3. Data and analyses

The method generates real number data on sapling height, the mean age of terminal twigs within each sapling, and (in 2017) binary data on whether saplings were freshly browsed or not. We applied several simple linear models to these data. All models were well-behaved and no data transformations were necessary to achieve uniform, well-distributed residuals. We constructed parallel models of sapling height and mean twig age in order to compare the relative power and sensitivity of these variables to higher and lower densities of deer (the exclosure effect). These models included the effects of year, exclosure, species, and all 2-way interactions. We then focused on twig age, analyzing how this variable responded to deer among the three species and the three years. These analyses included seedling height as a covariate and the height x deer interaction, allowing us to test whether twig age responds differently to height in vs. outside the exclosure. We began with combined analyses incorporating data from all years and species. These models, however, differed and often had complex interactions, making clear that species respond individualistically to the predictor variables. To simplify these analyses and their interpretation, we computed individual models for each species, allowing us to explore their responses in detail. As before, we began with fully factorial models including interactions then progressively eliminated non-significant terms to arrive at a final reduced model.

For the 2017 data that included browse incidence and two different new observers, we analyzed the relationship of these to the other variables. We detected no observer effects, leading us to conclude that inter-observer variation is low. We therefore ignore observer in subsequent models. We then compared the relative sensitively of twig age and browse incidence to the deer (exclosure) treatment using a nominal logistic model for the binary browse response. We also compared how mean twig age differed between browsed and unbrowsed stems, how height differed between these groups within each species, and effect sizes (Cohen's d) for all three indicators.

4. Results

4.1. Efficiency of the method

We confirmed that measuring sapling heights and aging twigs in these maple species is simple, straightforward, and efficient. In our setting, field workers processed saplings at rates of 40–50 + saplings per hour. Adding the binary browse scoring increased processing time only slightly. Entering the data was similarly simple and quick with the 2017 data set taking under an hour. These times could be reduced further if workers used voice-activated recorders and automated data input (Toczlydowski, 2017).

4.2. Relative responses of sapling height and twig age

Both height and twig age were approximately normally distributed with small and evenly distributed residual errors (Fig. 2). We calculated the ratios of the standard errors of the estimates to their adjusted least-square means in six cells reflecting each of the species by year and deer by year combinations. These coefficient of variation ratios were small for both sapling height and twig age, but always smaller for twig age (0.08 vs. 0.048 and 0.045 vs. 0.039). Thus, sampling variance is smaller for twig age.

Both sapling height and mean twig age respond to deer (exclosure effect), species, and year but do so in quite different ways (Table 1, Fig. 2). Sapling height was most sensitive to year (F = 57.8) with deer effects only entering the model significantly in the year x deer interaction (F = 11.0, both p < 0.001). While sapling height varied mostly by year with no significant species x deer interaction (F = 1.37, NS), there was no main effect of year for twig age (F = 0.43, Fig. 2A) but a

Table 1
Results of combined linear model of sapling height and mean twig age over all three maple species and all three years. N = 592. Adjusted r^2 values are 0.34 for sapling height and 0.50 for twig age. For corresponding profile plots, see Fig. 2.

Source	df	Height		Twig age	
		F ratio	P value	F ratio	P value
Deer	1	0.43	0.512	3.39	0.066
Species	2	6.55	0.002	6.97	0.001
Year	2	57.81	< 0.001	2.16	0.116
Deer × year	2	11.01	< 0.001	11.62	< 0.001
Species × year	4	2.45	0.045	6.77	< 0.001
Species × deer	2	1.37	0.256	14.86	< 0.001

large species x deer interaction (F = 14.9, p < 0.001). Additional deer effects on twig age are evident in the deer x year interaction (F = 11.6, p < 0.001, Fig. 2D) and an almost significant deer main effect (F = 3.39, p = 0.066, Fig. 2A). Twig age thus responds sensitively to deer in a species- and year-specific manner. We therefore analyzed species individually as well (see below). Twig age also provided greater power than sapling height in the overall model with F = 47.3 (vs. 23.9) and an adjusted r^2 of 0.50 (vs. 0.34). Note, too, that sapling height increased over time while mean twig age remained steady (Fig. 2C). This suggests that these indicators are not inter-changeable and that twig age may reflect browse pressure better than sapling height.

4.3. Species specific responses

Acer pennsylvanicum saplings tended to be 'leggy' and grew taller than its congeners (Fig. 2B). Twig ages in this species also showed the highest sensitivity to deer browse and the lowest sensitivity to other predictor variables (Table 2). Most of the high variance accounted for in this model (63%) results from the direct effect of deer. Saplings growing inside the exclosure had a mean age of 2.67 years (adjusted least square mean) while those growing outside lived only a tenth as long (0.25 yrs). Twig ages increased from a mean of 1.51 yrs in 2015 to 2.80 yrs in 2016 and 2.81 yrs in 2017. Twig ages in *Acer rubrum* respond to all three predictor variables (Table 2; Fig. 3A) as well as the deer x year interaction (Fig. 3C). As with *A. pennslyvanicum*, this model had a high coefficient of determination (r^2 = 0.62). Twigs in sugar maple were generally older than the other two species (Fig. 2B) and less sensitive to the deer effect across the fence (e.g., 2.74 vs. 3.68 yrs in *A. saccharum* in 2017 compared to 1.66 vs. 4.03 yrs in *A. pennsylvanicum* and 1.56 vs. 3.41 yrs in *A. rubrum*). Twig ages in *A. saccharum* responded only to the deer (exclosure) effect and the deer x height interaction (Table 2) with a lower overall r^2 (0.25). Its twigs also declined less in age than *A. rubrum* between 2016 and 2017 (Fig. 3B vs. 3A) and more steeply in response

Table 2
Separate linear models for each of the three maple species. Each model emerged from a backward elimination procedure that began with three predictor variables (year, deer, and height) and their 2-way interactions. These reduced models show only variables that significantly affected twig age within each species. Note that deer (the exclosure effect), alone or in combination with height provide the most power for predicting twig age in all species.

Species	Predictor	df	Sum of squares	F	p	Overall r^2
pennsylvanicum	Deer	1	211	304	< 0.001	0.63
	Year	2	44.3	32.0	< 0.001	
rubrum	Deer	1	5.6	10.8	0.001	0.62
	Year	2	10.9	10.5	< 0.001	
	Height	1	7.3	14.0	0.002	
	Year × deer	2	17.5	16.8	< 0.001	
saccharum	Deer	1	43.7	42.3	< 0.001	0.25
	Height	1	0.00	0.00	0.985	
	Deer × height	1	6.5	6.32	0.013	

to height outside the exclosure than in other species (Fig. 3D). Thus, in sugar maple in particular, the decline in twig age with height reflects deer effects.

4.4. Observations of fresh browse

Scoring fresh browse reflects the direct effect of deer providing a check for the indirect inferences made from twig age. As expected, browse incidence responded strongly to the deer effect with saplings far more likely to be browsed outside than inside the fence (73% vs. 12.6%, chi-square = 92.0, p < 0.0001). Taller saplings were also more likely to be browsed (Fig. 4a). Saplings with fresh browse had younger twigs than those lacking fresh browse (1.94 vs. 3.58 years averaging across species, F = 129, p < 0.001, r^2 = 0.3; Fig. 4B). This confirms that differences in twig age at this site largely reflect differences in deer browse rather than other causes of twig mortality. Unlike twig age, species only slightly affected the incidence of fresh browse at our site (chi-square 4.75, p = 0.093). Adding browse incidence to the twig age model raised r^2 values from 0.50 to 0.56 (Table 3a) reflecting a gain in power and supporting our inference that browsing often drives declines in twig age. This confirmation provides a useful internal check for surveys lacking experimental exclosures. The model for browse incidence (Table 3b) has substantially less power than the model for twig age (r^2 = 0.30 vs. 0.50 or 0.56). Thus, browse incidence indicates deer browsing less effectively than twig age. Finally, we calculated effect sizes in the 2017 results. Twig age showed a larger deer effect size and r^2 value than either sapling height or browse (Cohen's d = 34.85 vs. 1.39 and 9.55 for height and browse; r2 = 0.556 vs. 0.154 and 0.331).

5. Discussion

5.1. Utility of the method

Collecting data on habitat conditions is both less expensive and more reliable than relying on imprecise estimates of deer density to guide deer management. This is especially true once such indicators are standardized, allowing data to accumulate over time and space. Such approaches, however, can only work if the methods we use to monitor deer impacts and habitat conditions are efficient, reliable, and informative. We sought a method to monitor deer impacts on woody plants in forest understories that could be applied with minimal training and rapidly yield results of high accuracy and reliability. The twig age method meets these criteria while generating less sampling variance than the sapling height and fresh browse indicators.

Wildlife biologists traditionally manage deer relative to their estimates of animal density and perceived carrying capacity, with both commonly averaged over large regions. However, deer impacts can be low or high at the same deer density, depending on browse availability which can vary greatly at a local level. Thus estimates of deer density do not provide an accurate predictor of likely deer impacts nor can they predict the sustainability of managing deer at any set density. Basing management decisions on observed browsing rates or twig age instead, as proposed here, is intrinsically simpler and more direct. Such measures depend on the ratio of deer to available browse rather than absolute deer density or averaged measures of habitat conditions. Managing deer directly with reference to the impacts they have on habitat conditions avoids having to work indirectly by first estimating deer density and then judging the sustainability of that density relative to estimated habitat conditions. Managing deer from indicators of deer impacts also avoids the time, effort, costs, and (often) contention associated with estimating deer numbers. Such estimates tend to have large sampling variance, compounding the potential for disagreements between wildlife managers and hunters.

Ultimately, the ability of any forest plant to thrive depends on how quickly or persistently they can grow relative to the rates at which their twigs are being removed by herbivory and other forces. The twig age
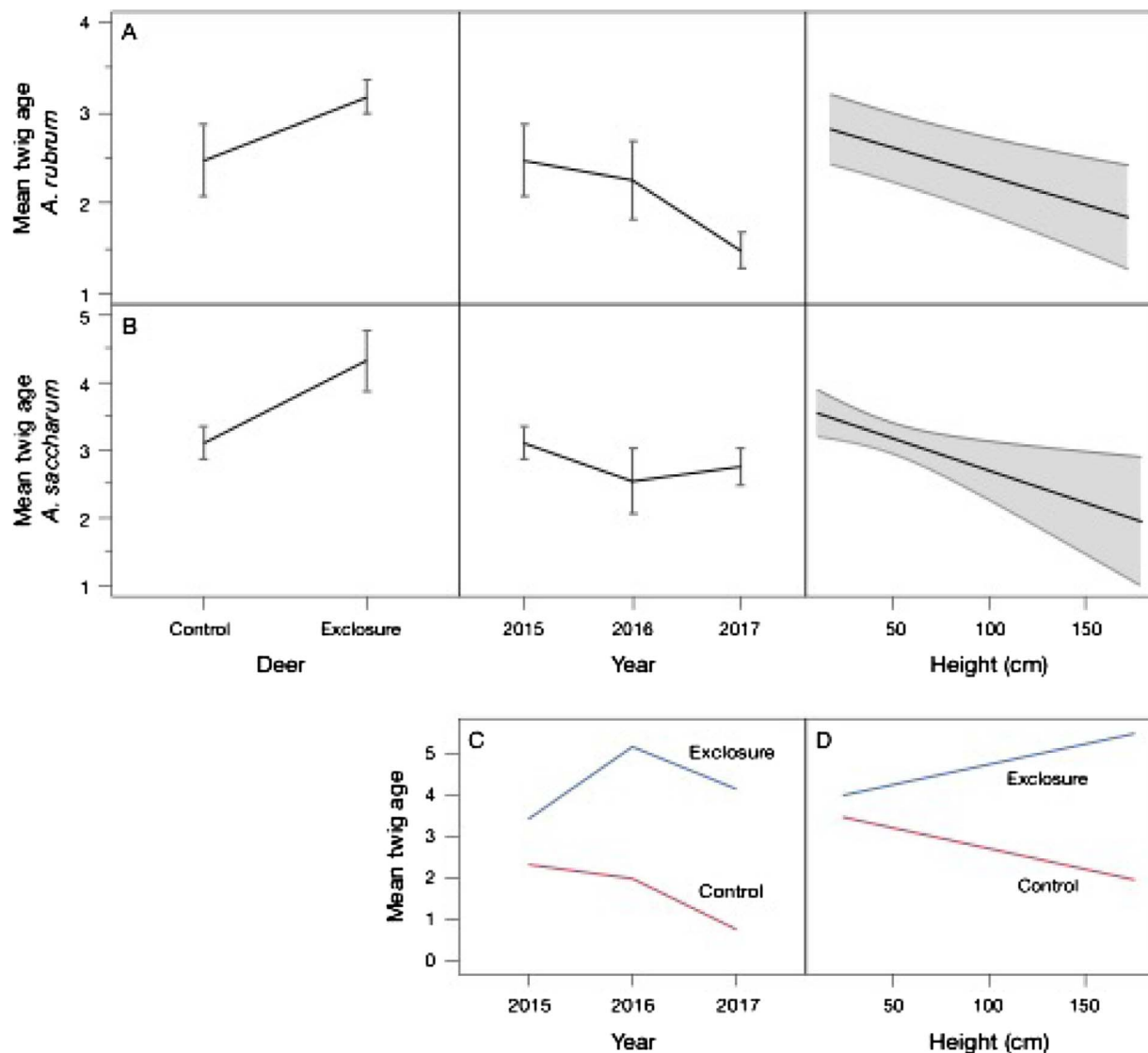
Fig. 3. Results from the linear models analyzing mean twig age in *Acer rubrum* and *A. saccharum*. Twig ages decline in taller saplings and outside the exclosure. A) The sensitivity of twig age to the main effects of year, deer, and sapling height in *A. rubrum* (see Table 2). The main effects were highly significant with exclosure effects after 2015 (C). B) In *A. saccharum*, only deer, alone and in combination with height (D), affected mean twig age.

method provides an (under)estimate of this key variable – the interval between browsing events. Twig age would not provide a good indicator of deer browse if the many other external and internal forces that kill twigs occurred more commonly than browsing. In the situation we studied, however (aging twigs in the browsing zone in a forest with moderate deer density), deer herbivory appears to cause most twig mortality. By tracing twig age back up to five years, we gain a measure that integrates browse impacts over recent years. The twig age method presented here also generates information on each sapling's height and browse condition. We thus gain three useful indicators, strengthening the value of all. We may also learn how to cross-calibrate these methods or derive a more powerful combined indicator.

To date, most indicators of deer impacts have relied on measuring plant height, density, cover, browse incidence, or reproductive condition (but see Keigley and Frisina 1988 for a method based on architecture). These indicators tend to have high sampling variance as they respond sensitively to variable environmental conditions (e.g., ambient light). In contrast, the twig age indicator estimates the minimum time interval between browsing events and is insensitive to differences in plant growth and abundance. Plants growing in light gaps, for example, often experience higher rates of twig extension and place more leaves

along new twigs. This variation does not affect measures of twig age, however, reducing its sampling variance. Likewise, saplings growing faster in canopy gaps tend to attract more deer browsing, as do certain species and twigs on the top of saplings short enough to browse. Twig ages can capture signatures of this variation as we saw in the differences detected among *Acer* species. Here, we may see a mix of strategies as exemplified by *Acer pennsylvanicum* (fast-growing, but heavily browsed) and *A. saccharum* (slower growing but less browsed – Fig. 2B).

An initial criterion for a method to monitor deer impacts is that it be simple and efficient, facilitating widespread use. Twig age meets these criteria in requiring only a single 'snapshot' visit to each site and no special tools, equipment, or lab procedures beyond a tape measure, smart phone (for a picture and location information), and data sheet or voice recorder to record the data. While site locations can be marked for re-location and resurveying, we see no particular advantage to this. The method also requires no technical knowledge or elaborate training beyond being able to reliably identify the species being surveyed and how to recognize and count terminal bud-scale scars. Such training can be accomplished within 30 min by reading the protocol and demonstrating the technique. This simplicity suggests that the twig age method could readily be taught to citizen scientists widening its use. It
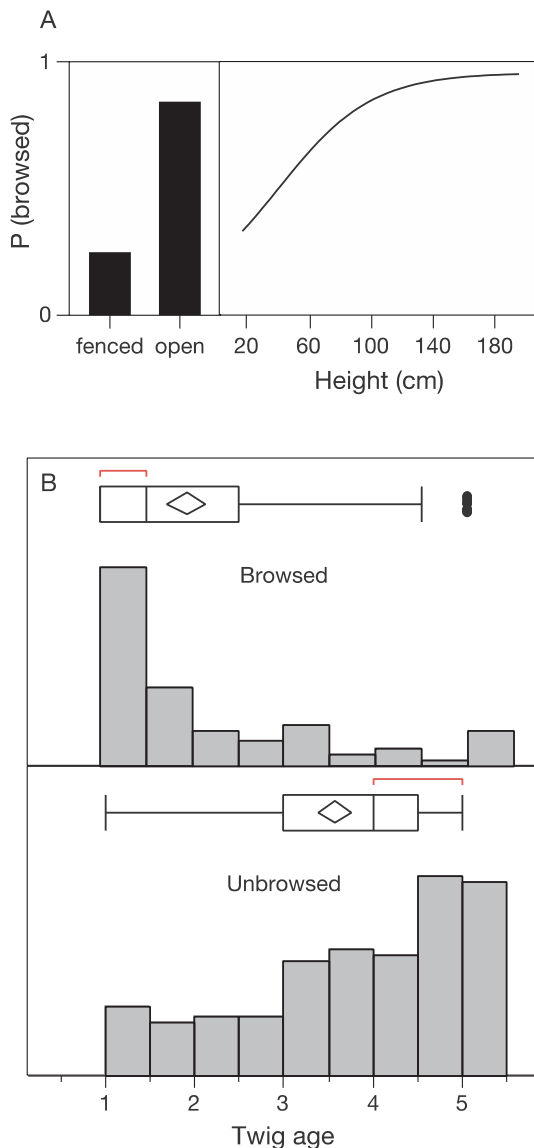
Fig. 4. Results from 2017 using the binary "fresh browse" variable. a) The probability that fresh deer browse increases in saplings outside the exclosure (left) and in taller saplings located outside (right). b) Distributions of twig age in saplings of all three species of maples that show signs of fresh deer browse or not.

Table 3
Responses of the twig age and browse indicators in 2017. a) Response of mean twig age to predictor variables including the presence of fresh browse. Overall $r^2 = 0.56$. b) Response of the browse indicator to deer, height, and the deer x height interaction in the nominal logistic model. No species effects were significant. Overall $r^2 = 0.35$.

a)

Source	DF	Sum of squares	F ratio	Prob > F
Exclosure	1	139	147	< 0.001
Browse	1	8.66	9.15	0.003
Species	2	24.1	12.8	< 0.001
Height	1	4.04	4.27	0.040
Exclosure × species	2	26.3	13.9	< 0.001

b)

Source	DF	L-R ChiSquare	Prob > ChiSq
Exclosure?	1	128	< 0.001
Height	1	14.7	0.001
Exclosure × height	1	6.37	0.012

from twig age and other indicators (Fig. 2B). These responses suggest that sapling height could be an inconsistent and potentially misleading indicator of browse impacts. Among these three, twig age emerges as the most reliable, informative, consistent, and powerful indicator of deer impacts.

Measures of twig age have several desirable statistical properties. Duplicate checks of field workers and the lack of any observer effect suggests that the method is replicable. It also appears statistically efficient. Although we recommend sampling 50 saplings per species per site, the method generated consistent results in 2016 for these maples with even smaller sample sizes (25, 26, and 36). This efficiency may result from averaging over 2–3 twigs within each sapling and integrating browse impacts over several recent years of growth. This internal averaging may reduce sampling variance. Twig age also showed statistical power in being able to discriminate not only between areas that differ greatly in levels of browsing (the fence effect) but also among the three species and three years covered in this study. The statistical models of twig age describe a remarkably high fraction (> 50%) of its total variation with consistently low residual errors. Twig ages also provide sensitive indicators for shifts in deer effects over time (Figs. 2D and 3C) and how browsing tends to increase in taller saplings (Fig. 3D).

Many methods exist to measure effects of deer herbivory on plant species (see Motivation and Methods). Several of these are simple, repeatable, or accurately indicate deer effects – but rarely all three. Approaches based on plant density, understory composition, and plant height/reproductive condition reflect responses not only to deer but also to local soil/seedbed conditions, recent disturbances, and light conditions. This sensitivity to environmental conditions generates high variance, requiring us to either control for confounding variables in complex analyses or greatly expand sampling. Similarly, when we measure the current incidence or extent of browsing, we obtain data that directly reflect the impacts we are interested in, but the patchy, intermittent nature of browse events increases sampling variance, necessitating high replication. Other methods tend to provide information that lags when such impacts occurred. Demographic profiles of tree species, for example, provide remarkable evidence of substantial deer impacts that act cumulatively over multiple decades to curtail tree regeneration in many species (Bradshaw and Waller, 2016). However, such indicators seriously lag the impacts they document, limiting their utility for real-time monitoring and management. Although the twig age method is not immune to environmental variance and some lag, our results suggest that it provides reliable contemporary information with less replication than most other methods.

To test our hypothesis that the twig age method is efficient and

is also efficient in generating useful data on three different variables in a short period of time (~1 min per sapling).

More fundamentally, any useful method for monitoring deer impacts must reliably indicate differences in habitat conditions and the local intensity of browsing. The twig age method succeeds here, too, by responding strongly to conditions in- and outside the fenced exclosure (Fig. 2A), differentially between saplings with and without current browse damage (Fig. 4B), and strongly to height outside but not inside the fence (Fig. 3D). It also generated smaller residual error variances and higher r^2 values, effect sizes, and levels of significance than current browse and sapling height. Current browse did respond strongly to the fence (and via a fence by height interaction) but with considerably less power ($r^2 = 0.3$) and showed no species-specific effects (Table 3B). Twig age also responded more sensitively to the deer effect, both alone and in the deer x species interaction, than sapling height. Height, in contrast, showed no significant difference across the fence (Fig. 2A), considerable variation among years (interacting inconsistently with the deer effect), and a ranking among species (*Acer pennsylvanicum* > *rubrum* > *saccharum*) inverse to the browsing susceptibility inferred

effective, we should explore how well it works in other species and regions. As we showed, one can combine twig age data across species to gain statistical power. However, the many species-by-deer interactions led us to analyze the data separately by species to reveal specific responses. Comparing mean twig ages among species studied at several locales might allow us to cross-calibrate the method by showing how twig ages in one species match up with twig ages in other species at similar levels of browsing. This would enhance the value of the method by allowing comparisons among different community types and regions that support different dominant species. It might also prove possible to derive synthetic indexes of deer impacts with even greater reliability and power.

The twig age method should also be tested side-by-side against other simple methods to compare their cost, simplicity, and the statistical power and value of the data generated. These include: a) the Morellet et al. (2003) method that scores browse on all saplings, ignoring species; b) Rawinski's (2016) "ten tallest" method based on sapling heights in selected species; and c) Blossey et al.'s (2017) "sentinel oak" method based on planting propagated oak seedlings. Once further testing demonstrates which one (or combination of) these methods serve best, we would be equipped to build the regionally extensive, long-term monitoring programs we need.

5.2. Management implications

Research (see Introduction) suggests that the number and severity of deer impacts have increased considerably in recent decades. Deer have thrived in today's temperate forests for many reasons (McShea et al., 1997; Warren, 1997; Côté et al., 2004). These include more intensive forest management, the ability of deer to consume a broad range of species, hunter preferences for shooting bucks, and the desire of state game management agencies to favor large deer herds to increase license revenues. Deer also have the capacity for rapid population growth – in contrast to many of the slow-growing, shade adapted forest plant species they eat. This discrepancy means that short-term carrying capacity (K) for deer populations may often exceed their long-term K. This realization led Aldo Leopold and others since to argue for limiting deer populations before they exceed K and damage their forage base (Leopold, 1943; Leopold et al., 1947). It also motivates the search for reliable indicators to monitor overbrowsing and habitat impacts.

The twig age method is designed to equip forest and wildlife managers with a simple and efficient indicator of how deer currently affect tree regeneration and habitat conditions. Managers must make controversial decisions about target deer densities relying often on rough estimates of deer densities at large spatial scales (McShea et al., 1997; Frye, 2008). Aside from being expensive to estimate accurately, deer densities provide no information on current habitat conditions, their trends, and how browsing is modifying those (Morellet et al., 2007; Blossey et al., 2017). Managers, often under pressure to maintain high deer densities, would benefit if they had reliable real-time field data on deer impacts and their trends. Such information is both directly relevant to management by providing a solid scientific footing for decision-making and easily interpretable, allowing managers to explain and justify their management decisions. Such considerations led Pennsylvania to reorient deer management from emphasizing deer densities to monitoring habitat conditions instead (Latham et al., 2009). Efficient and effective methods to monitor habitat conditions, once tested and standardized, should further this reorientation.

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Comments from L. Allen-Waller, J. Courteau, B. Blossey, and T. Rawinski improved the manuscript.

Author contributions statement

DMW conceived the idea, designed the basic method, conducted field work to test it in 2015 and 2016. He also analyzed the data, and wrote the initial draft and revised the manuscript. SJ and JW helped develop the method, construct / maintain the exclosure, and field test the method in 2017. All authors contributed critically to the drafts and gave final approval for publication.

Data accessibility

All data used here provided as .csv files associated with this article.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2017.09.001.

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