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NOTE

Partitioning and predicting forage biomass from total aboveground biomass of regenerating tree species using dimensional analyses

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Abstract: Foresters and wildlife biologists use biomass estimates as proxies of habitat structure, productivity, and carrying capacity. Determining biomass, however, is challenging without destructive harvests. We provide a dimensional analysis approach to partition browse biomass (BB) from total aboveground biomass (AGB) of six regenerating hardwoods in the Allegheny forests of Pennsylvania, USA. First, we determined the average diameter of browsed twigs for each species. Then, we created a subset of potential browsable twig and foliage biomass from total AGB in 439 individuals harvested within paired exclosure (fenced) and control (unfenced) plots at 15 sites. We fit species-specific allometric equations to estimate BB and AGB using basal diameter and height as predictors and tested the effects of fencing. Although overall stem height and BB were greater within exclosures, fencing did not significantly affect relationships between either predictor and BB or AGB, thereby enabling general and robust ($R^2 \geq 0.80$) equations for most species. Our work provides biomass equations for regionally dominant species and size classes that are underrepresented in the literature, yet critical to forest renewal and wildlife. Moreover, by sampling variable sites and levels of browse pressure, reported equations lessen site-specific biases. Finally, our methodology provides a template to generate forage biomass prediction equations for other plant and ungulate species.

Key words: Odocoileus virginianus, herbivory, allometry, regression, Allegheny hardwoods.

Résumé : Les forestiers et les biologistes de la faune utilisent les estimations de la biomasse comme éléments substitutifs de la structure de l'habitat, de la productivité et de la capacité de charge. Cependant, sans récoltes destructives la détermination de la biomasse constitue un défi. Nous présentons une approche d'analyse dimensionnelle pour séparer la biomasse de brout (BB) de la biomasse aérienne totale (BAT) chez six essences feuillues qui se régénèrent dans les forêts alléghéniennes de la Pennsylvanie, aux États-Unis. Nous avons d'abord déterminé le diamètre moyen des rameaux broutés de chaque essence. Ensuite, nous avons établi des sous-ensembles constitués de la biomasse des rameaux et de celle du feuillage pouvant être broutés à partir de la BAT de 439 individus récoltés dans des parcelles jumelées, situées à l'intérieur (parcelles clôturées) et à l'extérieur (parcelles témoins non clôturées) d'exclos à 15 endroits. Nous avons ajusté des équations allométriques spécifiques à chaque essence pour estimer la BB et la BAT en utilisant le diamètre basal et la hauteur comme prédicteurs et nous avons testé les effets dus à l'installation de clôtures. Même si dans l'ensemble la hauteur des tiges et la BB étaient plus élevées à l'intérieur des exclos, la présence de clôtures n'a pas significativement influencé les relations entre l'un ou l'autre des prédicteurs et la BB ou la BAT, rendant possible la production d'équations générales et robustes ($R^2 \geq 0{,}80$) pour la plupart des essences. Notre travail fournit des équations de biomasse pour des essences dominantes régionalement et des classes de taille sous-représentées dans la littérature et pourtant essentielles pour la régénération de la forêt et la faune. De plus, en échantillonnant différents niveaux de pression de broutage et de variables de site, les équations présentées réduisent les biais spécifiques au site. Finalement, notre méthodologie fournit un schéma pour générer des équations de prédiction de la biomasse du fourrage pour d'autres espèces de plantes et d'ongulés. [Traduit par la Rédaction]

Mots-clés : Odocoileus virginianus, broutage, allométrie, régression, feuillus alléghéniens.

Introduction

Tree and stand biomass estimates are extensively used to monitor productivity, assess timber or fuel volumes, and understand carbon budgets in forests worldwide (Cairns et al. 2003; Feldpausch et al. 2012; Parresol 1999). These estimates can also be used to assess responses to forest management treatments, competition, and herbivory (De Jager et al. 2017). In wildlife ecology, plant biomass estimates have been used as proxies of habitat structure and correlated to both insect and bird diversity (Bergen et al. 2007; e.g., Halaj et al. 2000). Perhaps more commonly, wildlife ecologists use biomass estimates to quantify forage availability or to estimate nutritional carrying capacities for herbivores, including ungulate browsers (Hobbs and Swift 1985; McCall et al. 1997; Potvin and Huot 1983).

Field-based methods of estimating biomass via dimensional analyses (sensu Whittaker and Woodwell 1968) often rely on de-

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structive harvesting of the aboveground plant material followed by the development of allometric regression equations that predict biomass using readily measured attributes such as diameter or height (Baskerville 1972; Jenkins et al. 2004). Once developed, subsequent studies can then use published equations to nondestructively sample biomass. Although allometric equations exist for many tree species, published equations cannot be used to assess forage availability or nutritional carrying capacity reliably in regenerating forests. Firstly, published equations are heavily skewed toward larger trees and rely on diameter at breast height (DBH; 140 cm) as a measure of size (Ter-Mikaelian and Korzukhin 1997). In contrast, in early-successional habitats where ungulates concentrate their browsing, the bulk of the woody browsing occurs on seedlings and small saplings, some of which may not even attain the required size to measure DBH (Greenberg et al. 2011; Johnson et al. 1995). Secondly, biomass estimations focused on plant productivity typically predict total aboveground biomass (AGB) or biomass by specific components (e.g., wood vs foliage; Cairns et al. 2003; Feldpausch et al. 2012; Peichl and Arain 2007). In contrast, studies with a foraging emphasis require biomass estimates of the plant structures relevant to the herbivore, usually browsable twigs and foliage (Shafer 1963; Telfer 1969*b*). Moreover, significant amounts of the AGB of taller seedlings and saplings may exist beyond the reach of browsers (Waller and Alverson 1997). Hence, available equations that predict total AGB may overestimate available forage biomass.

Here, we provide allometric biomass prediction equations for the six most common regenerating species in the Allegheny hardwood forest type: red maple (*Acer rubrum* L.), black cherry (*Prunus serotina* Ehrh.), birch (*Betula* spp.), pin cherry (*Prunus pensylvanica* L. f.), white ash (*Fraxinus americana* L.), and American beech (*Fagus grandifolia* Ehrh.). Although allometric biomass equations exist for these species (e.g., Tritton and Hornbeck 1982), these are generally derived from larger size classes (e.g., mature trees) in other regions and in such a manner that does not allow the partitioning of the biomass relevant to browsers. Our goal was to derive a set of seedling and sapling equations for use by either wildlife biologists or foresters to nondestructively quantify the fraction of biomass for their needs. Specifically, our approach fractions out biomass of plant structural components considered browsable, focusing on the vegetation stratum accessible to white-tailed deer (*Odocoileus virginianus* (Zimmermann, 1780), 0.2–1.8 m; Waller and Alverson 1997) from the total AGB. Hence, wildlife managers could use one set of equations to estimate browse biomass (BB) and calculate forage availability, for example, whereas forest managers could use the total AGB equations to estimate productivity. Moreover, to reduce uncertainties from site-to-site variation known to affect allometric relationships (for critique, see Ter-Mikaelian and Korzukhin 1997), our estimates are derived from several widely scattered northern hardwood forest sites with intermediate to low mesic moisture gradients and variable browsing intensities to provide generalizable allometric equations.

Materials and methods

Study area

We conducted our study (30 June – 17 August 2016) at 15 northern hardwood forest sites distributed throughout a 6500 km^2 area of northern Pennsylvania, USA. The 15 sites used in this study were selected from a larger set of 25 sites (see Royo et al. 2016, 2017) to maximize site productivity differences within the range that existed at all sites and thus broaden the generality of our predictive equations (Appendix A). To do this, we calculated the integrated moisture index (IMI; Iverson et al. 1997) for all sites and ran a cluster analysis to guide selection of sites with wide-ranging IMI values (PROC CLUSTER; SAS Institute, Inc. 2013). The IMI combines GIS-derived topographic and soil features of the landscape into a single index that can be statistically related to a number of ecological processes, including moisture availability, productivity, soil nitrogen, and species composition (Iverson et al. 1997).

Site preparation and surveys

In 14 of the 15 sites, managers conducted the initial cut of a shelterwood sequence to reduce stand relative density (i.e., <75% relative density) and applied broadcast herbicides (tank mix of glyphosate and sulphometuron methyl; Marquis et al. 1992) to control interfering plant species 3–8 years prior to sampling (Appendix A). At a 15th site, managers ultimately chose not to proceed with a harvest but did apply herbicide in 2012. Within each site, we established paired 0.42 ha (60 × 70 m) plots and randomly assigned one plot a deer exclosure (fence) treatment while the other served as an unfenced control. Exclosure construction occurred in May–September 2013. Vegetation surveys at these sites in 2015 determined that six species formed the bulk (~94%) of the stems in the regenerating tree community: red maple (55.7%), black cherry (14.6%), birch (9.8%), pin cherry (8.1%), white ash (4.4%), and American beech (1.4%). Thus, we focus biomass estimation on these species given their importance in hardwood forest regeneration regionally (USDA Forest Service 2018) and because they form part of the summer browse of white-tailed deer (Horsley et al. 2003).

Browsing diameter and biomass harvest

To quantify potential browse available to white-tailed deer accurately, we conducted an initial sampling to quantify the average portion of a twig that deer consumed. We conducted this sampling at three experimental sites (First Hunt, Irvine Run, and Cash Crop) where inventory data indicated that we could find all species. In total, we harvested 100 browsed twigs for each species with the exception of pin cherry, where only 30 twigs were harvested due to the paucity of stems in the control plots. Following Shafer (1963), we calculated mean browse diameter by species by measuring and averaging the diameter of the twig proximal to where it was clipped by deer.

Following this initial quantification, at each of 15 sites, we harvested up to six individuals for each species, three from inside the exclosure and three in the unfenced control plot, to estimate biomass. Harvested individuals were selected arbitrarily from the pool of seedlings and saplings (≥20 cm in height, <5.1 cm DBH) present throughout each 0.42 ha treatment plot. Our goal was not to obtain a random sample, but rather to harvest regenerating seedlings and saplings throughout the known size gradient for that species at that site to adequately model the size–biomass relationship. Sampled individuals were not of sprout origin with the exception of American beech, which regenerates extensively through root suckers in the region (Jones and Raynal 1987). For each individual, we measured basal diameter (1 cm above soil surface; mm) and height (cm). Because of variability in species composition and abundance, not every species was present at all sites nor was it always possible to harvest six total stems from a site.

To quantify both total AGB and biomass available to deer (BB), plant material, by individual, was broken down into three components: (1) browsable foliage (i.e., all foliage in the 20–180 cm stratum), (2) browsable twigs (all twigs ≤ browse diameter for each species in the 20–180 cm stratum), and (3) other (all remaining nonbrowsable plant material). Individuals taller than 180 cm were processed as follows: plant material within the 20–180 cm stratum (i.e., within browse height) was processed into the three components described above, and plant material taller than 180 cm (i.e., above browse height) was bulked along with the other nonbrowsable portion. Using our browse diameter estimates, a single twig often contained multiple secondary branches and buds, and in these cases, all secondary material was sampled. Smaller plant material was placed in paper bags and oven-dried at 70 °C for 3 days before being weighed. Larger plant material was sectioned,

Table 1. Analysis of variance results on basal diameter (mm), stem height (cm), total aboveground biomass (AGB; grams) and browse biomass (BB; grams): (*a*) overall test results followed by (*b*) sampling effort (*N*) and mean values (±1SE) of each size and biomass metric for each of the six species, as well as the overall average across species for each metric.

(*a*) Overall test results

	Basal diameter (mm)		Height (cm)		BB (g)		AGB (g)	
Effect	*F* value (df)	*P* value	*F* value (df)	*P* value	*F* value (df)	*P* value	*F* value (df)	*P* value
Treatment	0.34 (1, 118)	0.562	10.49 (1, 118)	0.002	4.72 (1, 118)	0.032	3.41 (1, 118)	0.067
Species	14.96 (5, 118)	<0.0001	16.62 (5, 118)	<0.0001	19.17 (5, 117)	<0.0001	11.67 (5, 118)	<0.0001
Treatment × species	2.23 (5, 117)	0.056	2.14 (5, 116)	0.066	2.06 (5, 116)	0.076	1.99 (5, 116)	0.085

(*b*) Sampling effort and mean values of each size and biomass metric

Treat	*N*	Basal diameter, mean ± SE (mm)	Stem height, mean ± SE (cm)	BB, mean ± SE (g)	AGB, mean ± SE (g)
Birch					
Control	43	13.3±1.4 } AB	128.9±12.4 } A	28.5±7.4 } A	102.2±34.6 } AB
Fence	43	14.3±1.4 }	151.1±12.2 }	37.2±7.0 }	122.5±25.9 }
Pin cherry					
Control	39	8.1±1.2 } C	97.5±12.9 } AB	11.8±5.0 } B	77.4±31.9 } BC
Fence	45	13.9±1.3 }	171.1±13.0 }	20.4±3.6 }	170.2±41.7 }
American beech					
Control	29	15.5±1.8 } A	94.6±8.6 } BC	31.5±9.7 } A	154.1±78.6 } A
Fence	27	14.6±1.5 }	105.2±9.3 }	33.8±10.6 }	140.6±55.6 }
Red maple					
Control	46	8.6±0.8 } CD	76.3±8.4 } CD	14.4±3.5 } B	42.6±13.3 } C
Fence	44	9.3±0.9 }	94.3±9.2 }	11.6±2.0 }	46.8±20.2 }
White ash					
Control	19	12.2±3.4 } BCD	67.4±8.4 } CD	4.8±1.2 } BC	17.1±4.8 } CD
Fence	22	10.0±0.8 }	82.7±10.8 }	7.9±1.6 }	33.5±15.1 }
Black cherry					
Control	38	5.6±0.4 } D	57.1±4.3 } D	2.2±0.4 } C	7.6±1.7 } D
Fence	44	6.5±0.6 }	69.9±6.0 }	5.8±1.8 }	15.6±4.6 }
Overall					
Control	214	10.2±0.6	89.0±4.5a	16.1±2.4a	67.1±14.5
Fence	225	11.3±0.5	115.9±5.0b	19.3±2.2b	89.3±12.9

Note: Uppercase letters following braces denote significant Tukey-adjusted pairwise differences among species; lowercase letters denote significant overall treatment effects averaged across species.

placed in a greenhouse for several weeks to initially dry, and then oven-dried and weighed in the same manner in which the smaller components had been processed.

We first examined whether height, basal diameter, total aboveground biomass (AGB = sum of all components, regardless of size class), or browse biomass (BB = twigs + foliage within browsable stratum) estimates of harvested individuals varied among species and between treatment (i.e., fence vs control) using analysis of variance (ANOVA), with site modelled as a random effect and species and treatment modelled as fixed effects (PROC REG; SAS Institute, Inc. 2013). For each species, we averaged the values of all harvested stems within a treatment plot to avoid pseudoreplication.

We used linear regression (PROC REG; SAS Institute, Inc. 2013) to fit species-specific regression equations using linearized power functions of the form $\ln(y) = a + b \cdot \ln(x)$, where y represents either AGB or BB (expressed in grams) and x represents either basal diameter squared (D^2; in mm) or basal diameter squared times height (D^2H; H is measured in cm) (see Crow and Schlaegel 1988). For each species, we first tested whether the relationship between biomass estimates (AGB or BB) and predictor metrics (D^2 or D^2H) differed between fencing treatments by testing the homogeneity of slopes assumption (Milliken and Johnson 2002) in an analysis of covariance (ANCOVA) context (PROC GLM; SAS Institute, Inc. 2013). Namely, an insignificant treatment × predictor interaction indicates that fencing did not alter the slope of the relationship between biomass estimates and predictors, in which case, we pooled the data for both treatments to develop a general regression equation model for the species. In contrast, if a treatment × predictor interaction was detected, we developed separate regression equations for the species both inside and outside exclosures to account for impacts of herbivory. Finally, we calculated a correction factor defined as $\exp(SEE^2/2)$, where SEE refers to the standard error of the estimate, to adjust for bias caused by logarithmic transformation (Baskerville 1972). For all analyses, we considered p values ≤0.05 as significant.

Results

Determination of browse diameters was based on 530 individuals (30 for pin cherry and 100 for each of the other species). Average browse diameters and their ranges were, respectively, 1.1 mm and 0.6–1.6 mm for pin cherry, 1.3 mm and 0.2–2.5 mm for birches, 1.4 mm and 0.2–2.7 mm for black cherry, 1.8 mm and 0.6–4.8 mm for white ash, 2.2 mm and 1.0–4.3 mm for American beech, and 2.7 mm and 0.9–5.4 mm for red maple. Biomass estimates come from 439 harvested and processed individuals (214 in control plots, 225 within exclosures) across 15 sites (Appendix A, Table A1). Among the individuals harvested for this study, average height was 102.5 cm (range: 19.5–406 cm) and basal diameters averaged 10.8 mm (range: 1.8–73 mm). Basal diameter, stem heights, AGB, and BB differed among species (Table 1). Averaged across treatments, pin cherry and birch (primarily *B. lenta* and *B. allegheniensis*) were tallest, American beech was intermediate in height, and red maple, white ash, and black cherry were the shortest (Table 1B). Basal diameter was greatest in American beech, followed by birch,

pin cherry, red maple, white ash, and black cherry. Biomass hierarchies were similar for both AGB and BB, with American beech having the most biomass per individual, followed by birch, pin cherry, red maple, white ash, and black cherry. Averaged across all species, individuals sampled within exclosures were taller and had greater BB (Table 1).

Species-specific biomass allometric models based on either D^2 or D^2H did not differ between treatments for any species (i.e., equal slopes, nonsignificant treatment × predictor interaction) except white ash. Examination of the white ash data revealed that one outlier data point was exerting significant leverage as determined by a Cook's D metric > 1 (Cook 1977). Following the removal of the outlier, treatment slopes were equal (see Appendix B, Fig. B1). Thus, species-specific models predicting AGB and BB used the pooled data from both treatment plots. Species-specific allometric models based solely on basal diameter (D^2) explained between 63% and 91% of the variance in available BB (Table 2A) and 83%–95% of the variance in total AGB (Table 2B). The addition of height to the equation (D^2H) improved prediction ability by 4%–5%, on average, when compared with just D^2. Prediction efficiency (i.e., R^2) ranged from to 70% to 91% in BB and from 90% and 96% in AGB. Variance explained by the models was lowest for black cherry and greatest for pin cherry.

Discussion

Within the range of sizes sampled in our study, the equations offered here provide a nondestructive method to estimate both total browse biomass (BB) and aboveground biomass (AGB) of six common hardwood species found in regenerating hardwood stands during peak summer browsing periods. The addition of height to the equations added little to the models' performance, which is supported by other studies (reviewed by Jenkins et al. 2004), thereby allowing for less labor-intensive measurements. Averaged across species, models predicting total AGB explained more of the variance than those predicting BB. Indeed, even within species, in all cases except one (i.e., American beech, D^2 models), AGB models had higher explanatory power. This result is consistent with other work documenting that foliage and branch biomass components exhibit more variability, presumably because of canopy position, light availability, and tissue loss from herbivory (Bond-Lamberty et al. 2002; Fatemi et al. 2011). Moreover, our calculation of BB is restricted to plant material within the browsable height strata and thus is increasingly undersampled in taller individuals where much of the twigs and foliage escape browsing.

Averaged across all species, the R^2 values for AGB reported in this paper are lower (average R^2 using D^2 predictor = 0.89) than values reported for seedlings and saplings of these species in other work (average $R^2 \approx 0.95$; Elliott and Clinton 1993; Telfer 1969*a*, 1969*b*; Williams and McClenahen 1984). The increased variability in our data may be a product of our broad sampling scheme throughout 15 dissimilar sites, whereas many published equations are often generated from harvests occurring in far fewer sites. Additionally, the variation observed in our sampling may arise from a morphologically plastic response to light variability exhibited by young trees (e.g., Fatemi et al. 2011) given that overstory harvests occurred 3–8 years prior to sampling and mean canopy openness ranged from 13.8% to 29.3% across our sites. Thus, while our equations may slightly underperform other published seedling and sapling biomass equations in terms of variance explained, we argue that our equations are more broadly applicable as they come from seedlings and saplings experiencing a wide range of stand age, light, and site-quality conditions.

Our data suggest that exposure to browsing (i.e., no fencing) reduces stem heights and BB, particularly for pin cherry, a highly palatable tree species (Horsley et al. 2003). Although our sampling technique precludes a definitive hypothesis test, these findings of diminished stem heights and plant abundance mirror results from randomized vegetation surveys at these sites (Royo et al. 2016, 2017). Interestingly, the relationship between predictor size metrics and AGB or BB did not vary as a result of treatment (i.e., equal slopes) for any species. These results demonstrate that biomass production for individuals of a given size is equivalent regardless of whether or not stems are exposed to browsing. At least three possible explanations may explain this result. Firstly, hardwood seedlings, including several species in this study, are capable of recovering from low to moderate tissue loss with regrowth (Gill 1992; Stout 1986), thereby nullifying any negative browsing effect. Alternatively, the failure to observe this difference may represent a cumulative browsing effect wherein prior chronic losses in leaf tissue result in a concomitant suppression in both stem growth and biomass production (e.g., Brookshire et al. 2002). Finally, the relatively short time span (2.5 growing seasons) be-

Table 2. Biomass prediction equations, $\ln(y) = a + b \cdot \ln(x)$, where y is either (*a*) browse biomass (foliage + browsable twigs) or (*b*) total aboveground biomass of six dominant species in the regeneration layer of shelterwood harvest sites in northwestern Pennsylvania, USA.

(*a*) Browse biomass (BB)

	a	*b*	SEE	Model R^2	CF
American beech					
D^2	−2.21	0.98	0.39	0.87	1.08
D^2H	−4.10	0.72	0.34	0.91	1.06
Birch					
D^2	−2.90	1.11	0.60	0.87	1.20
D^2H	−5.01	0.78	0.55	0.89	1.16
Black cherry					
D^2	−3.02	1.04	0.80	0.63	1.38
D^2H	−5.09	0.75	0.72	0.70	1.29
Pin cherry					
D^2	−3.48	1.15	0.56	0.91	1.17
D^2H	−5.56	0.78	0.56	0.91	1.17
Red maple					
D^2	−2.73	1.09	0.60	0.77	1.20
D^2H	−4.14	0.70	0.55	0.81	1.16
White ash					
D^2	−3.55	1.13	0.55	0.75	1.16
D^2H	−4.80	0.72	0.48	0.80	1.12

(*b*) Total aboveground biomass (AGB)

	a	*b*	SEE	Model R^2	CF
American beech					
D^2	−2.72	1.27	0.54	0.86	1.16
D^2H	−5.30	0.95	0.40	0.92	1.09
Birch					
D^2	−2.88	1.31	0.63	0.90	1.22
D^2H	−5.35	0.92	0.57	0.92	1.18
Black cherry					
D^2	−2.91	1.30	0.58	0.83	1.18
D^2H	−5.34	0.92	0.45	0.90	1.11
Pin cherry					
D^2	−3.23	1.45	0.52	0.95	1.14
D^2H	−6.06	1.00	0.44	0.96	1.10
Red maple					
D^2	−3.20	1.39	0.50	0.88	1.13
D^2H	−5.03	0.91	0.37	0.93	1.07
White ash					
D^2	−4.84	1.67	0.45	0.88	1.11
D^2H	−6.07	1.00	0.29	0.95	1.04

Note: Equations are based on basal diameter ($x = D^2$) or basal diameter squared × height ($x = D^2H$). To adjust for bias from logarithmic transformation, we present the standard error of the estimate (SEE), a model goodness-of-fit (R^2), and a correction factor (CF) based on Baskerville (1972).

tween fence construction and sampling, coupled with a sampling approach designed to derive allometric relationships rather than population-level responses, inherently limits our ability to test and detect deer browsing impacts.

Notably, black cherry BB exhibited poor goodness-of-fit (R^2 = 0.63 and 0.70 for D^2 and D^2H, respectively) relative to other sampled species in this study. We suggest that tissue loss from cherry leaf spot (*Blumeriella jaapii*) accounts for high variability in biomass for this species. Known as a significant agent of tissue loss and mortality (Stanosz 1992), this pathogen was prevalent on black cherry seedlings in summer 2016, causing a high incidence of necrotic and senesced leaves (A.A. Royo, personal observation). Also notable, AGB predictions for this species were more robust (0.83–0.90) and closer to reported values in the literature (Williams and McClenahen 1984).

The equations presented here were derived from sampling multiple forest sites distributed across a large spatial scale that encompassed a broad range of growing conditions and white-tailed deer browsing intensities to provide broadly generalizable allometric equations. Our study complements the rich literature on tree allometric equations (Jenkins et al. 2004; Ter-Mikaelian and Korzukhin 1997) by deriving equations for regenerating seedlings and saplings, size classes that are woefully underrepresented in existing data (but see Elliott and Clinton (1993) and Williams and McClenahen (1984)). The six chosen taxa represent the overwhelming majority (86%–93%) of the regeneration in early-successional forests regionally (Ristau and Horsley 1999) and comprise roughly one-third of the seedlings in forestland throughout the northeastern United States (USDA Forest Service 2018). Moreover, our approach serves as a model for researchers interested in calculating woody BB of other plant species. By first calculating average browse diameter and determining the browsable stratum, researchers can generalize our approach for any herbivore and desired woody forage (e.g., 7 mm browse diameter, 0–2.5 m browse stratum for *Cervus elaphus*; Frair et al. 2005). This method offers a significant time savings over either the traditional harvest techniques or methods that rely on a separate survey focused on mean mass of browse and twig counts (Rutherford 1979; Shafer 1963; Telfer 1969*b*), allowing researchers and managers to estimate AGB or BB more efficiently. Finally, although we recognize deer browse on other vascular and nonvascular vegetation (e.g., forbs and grasses), these growth forms are more easily quantified using plot clipping techniques. Allometric regression estimation approaches for tree regeneration such as the one detailed here can complement the more tractable biomass harvests of herbaceous growth forms.

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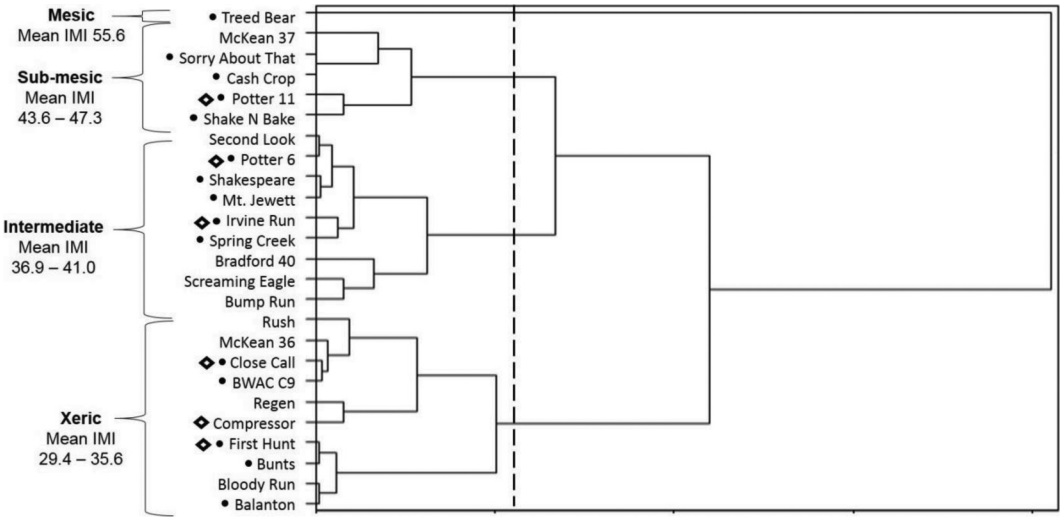
Appendix A

Site selection

An integrated moisture index (IMI) representing the long-term potential soil moisture on a scale of 0 to 100 is derived from topographic hillshading, flow accumulation of water downslope, curvature, and soil water-holding capacity (Iverson et al. 1997). Curvature, flow accumulation, and hillshade were derived from a 1 m digital elevation model. Flow accumulation was processed using an infinite directional algorithm developed by Tarboton (1997). Available water-holding capacity to a depth of 150 cm was derived from soil data within the Natural Resources Conservation Service Soil Survey Geographic (SSURGO) database. Each component was standardized on a scale of 0 to 100, then cumulated to the same scale according to IMI = (curvature × 0.1 + flow accumulation × 0.3 + hillshade × 0.4 + AWC × 0.2). For each site, IMI values were averaged within a 200 m radius centered on the centroid of the enclosures (Fig. A1).

Fig. A1. Cluster dendrogram for site selection using mean integrated moisture index (IMI). The analysis suggested that the sites be segregated into four or five clusters. We chose four clusters, indicated by the dashed vertical line, each representing a different moisture regime (mesic, sub-mesic, intermediate, and xeric). Solid circles (●) indicate sites selected for this study. Within a defined IMI cluster, both northern hardwood sites and oak sites (◇), if available, were chosen to increase diversity of site types.



We used Proc Cluster (SAS 9.2, SAS Institute, Inc., Cary, North Carolina, USA) in a hierarchical cluster analysis to define core clusters consisting of similarly classified sites based on their mean IMI values. The average linkage method was used to compute distance among the clusters (Sokal and Michener (1958). Pseudo F and pseudo T^2 values suggested that four or five clusters segregated the sites most accurately. Mean IMI was used in the cluster analysis to segregate study sites as it is related to an array of site characteristics, including moisture availability, productivity, soil nitrogen, and species composition (Table A1; Iverson et al. 1997). We used two metrics to select 15 of the 25 sites: (*i*) placement within clusters, with sites chosen from four clusters to ensure good variation in IMI and associated site characteristics, across the study sites, and (*ii*) forest type, with at least one oak–hickory dominated site per cluster chosen to maximize species diversity across the sites.

Table A1. Site characteristics of 15 experimental sites.

			Soil nutrients (mg·kg^{-1})												
Site	Canopy open	Soil pH	NO_3	NH_4	Ca	K	Mg	P	Plant available H_2O	IMI	Elevation (m)	Slope (°)	Aspect	Harvest year	Herbicide year
Balanton	0.2	3.9	0.9	31.9	61.6	36.4	20.2	2.0	12.7	29.4	640.9	5.2	S	2012	2009
BuntsRun	0.2	3.7	11.4	36.0	55.5	41.5	20.7	1.3	20.2	29.9	544.6	2.8	S	2008	2012
BWAC – C9	0.1	3.8	1.8	33.8	51.6	45.1	16.4	3.4	13.6	34.6	700.2	3.3	W	2012	2011
Cash Crop	0.2	4.0	2.6	19.3	81.3	37.7	13.4	1.1	14.3	45.6	640.2	6.7	NE	2013	2009
Close Call	0.2	4.1	18.8	13.9	134.7	46.7	22.0	5.3	15.2	34.7	610.5	3.4	S	2016	2010
First Hunt	0.2	4.3	0.8	8.4	44.0	49.5	13.5	1.5	17.5	30.0	513.7	2.9	SE	2011	2012
Irvine Run	0.3	4.2	4.1	19.0	146.2	59.5	31.7	3.4	19.4	40.1	513.9	1.6	E	2010	2012
Mt. Jewett	0.1	4.4	1.3	17.5	50.0	41.7	16.1	1.1	14.7	40.4	680.0	4.7	E	N/A	2012
Potter11	0.2	4.5	7.7	14.1	96.3	53.7	20.1	4.0	14.4	44.3	641.0	2.2	N	2013	2012
Potter6	0.2	4.3	9.1	10.6	112.6	51.9	23.3	2.8	14.3	40.8	687.8	4.8	NE	2012	2012
Shake-n-Bake	0.2	4.1	14.4	15.8	86.9	58.9	22.6	1.5	15.6	43.6	564.1	25.9	SE	2012	2009
Shakespeare	0.2	4.2	3.9	20.9	60.8	60.8	17.1	1.0	18.3	40.6	650.9	18.1	E	2013	N/A
Sorry About That	0.3	3.7	4.0	5.9	27.5	17.6	10.1	0.6	10.5	45.7	608.3	26.5	NW	2012	2010
Spring Creek	0.2	4.4	3.3	21.3	42.6	50.1	15.0	0.9	17.0	39.5	544.4	3.6	SE	2011	2012
Treed Bear	0.2	4.0	18.4	46.8	80.2	75.6	25.8	1.7	19.2	55.6	531.6	14.2	N	2012	2009
Mean	0.2	4.1	6.8	21.0	75.5	48.4	19.2	2.1	15.8	39.6	604.8	8.4			
Minimum	0.1	3.7	0.8	5.9	27.5	17.6	10.1	0.6	10.5	29.4	513.7	1.6			
Maximum	0.3	4.5	18.8	46.8	146.2	75.6	31.7	5.3	20.2	55.6	700.2	26.5			

Note: Proportion canopy openness was determined by hemispheric photography. We calculated site moisture availability and productivity using the integrated moisture index (IMI) based on GIS-derived metric (see Appendix B; Iverson et al. 1997).

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Appendix B

Appendix Figure B1 appears on the following page.

Fig. B1. Seedling and sampling browse biomass (BB) measurements (ln[grams]) versus basal diameter measurements (ln[millimeters]) for six hardwood species. Plotted relationships represent the data from individuals sampled within exclosures (—●—) and control (—○—) and dotted lines represent 95% confidence intervals. Relationships for each treatment are for demonstrative purposes only as lines did not significantly differ from one another. Equations presented in Table 2 represent relationships based on pooled data.