

## Articles

# Effect of Herbivory on the Nutritional Value of Six Hardwood Species for White-Tailed Deer in the Allegheny Forest

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## Abstract

Herbivores alter plant quantity and quality through direct tissue consumption and indirectly via the structural and chemical allocational strategies plants deploy in response to herbivory. Herein, we examine how browsing by white-tailed deer *Odocoileus virginianus* alters nutritional quality of six regenerating hardwood species: red maple *Acer rubrum*, black cherry *Prunus serotina*, birch *Betula* spp., pin cherry *Prunus pensylvanica*, white ash *Fraxinus americana*, and American beech *Fagus grandifolia*. Using an established, large-scale experiment that manipulated deer access to fenced plots, we tested whether browsing altered the nutritional quality and biomass as well as nutritional capacity to support deer of six hardwood species in an early successional hardwood forest of Pennsylvania, USA. Pin cherry was the most nutritious of the six species, with greater dry matter digestibility and digestible protein and lesser neutral detergent fiber. Areas exposed to browsing had less browse biomass of stems and leaves yet greater digestible protein, an effect driven by digestible protein of pin cherry. We found no effect of browsing on neutral detergent fiber or dry matter digestibility. Although deer browsing reduced biomass of the six hardwood species, it did not alter the nutritional capacity to support lactating females in the summer. Our results confirm that browsing limits tree regeneration and available browse and provides conservative conclusions on how deer can alter their diet quality.

Keywords: digestible protein; exclosures; hardwoods; nutritional carrying capacity; regeneration; white-tailed deer

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## Introduction

In temperate forests, plant tissues and structural components vary seasonally with changes in temperature, light, and moisture. In general, plants emerge from winter dormancy producing protein-rich leaves and stems early in the growing season, shifting to more fibrous structural components (e.g., cellulose and hemicellulose) later in the growing season (Schultz et al. 1982; Moen 1985; Gaucher et al. 2005; Carbone et al. 2013). Foraging herbivores, such as deer (Cervidae), similarly shift diet selection and intake rates in response to plant phenological changes and their own life history nutritional demands (Shipley and Spalinger 1992; Dumont et al. 2005; Wagoner et al. 2013; Ulappa et al. 2020). Deer follow the phenological changes of the plants. In the middle latitudes of the United States, selection shifts from abundant, highly digestible, protein-rich new-growth found in early spring and summer to less digestible fiber (structural carbohydrates) from late summer through late autumn (Schultz et al. 1982; Moen 1985; Carbone et al. 2013). Timing and availability of protein-rich new-growth forage in the spring are essential to meet the high energetic demands of parturition and lactation, whereas timing and availability of carbohydrate-rich growth in late summer and early autumn influence growth rates, reproductive recruitment, and overwinter survival (Cook et al. 2004; Johnstone-Yellin et al. 2009; Rodriguez-Hidalgo et al. 2010; Tollefson et al. 2010, 2011).

The interrelatedness of deer and their forage resources is furthered because browsing can directly or indirectly alter plant quantity and quality through differential structural and chemical plant allocational strategies. Inherent interspecific differences in the nutritive (e.g., protein), less nutritive (e.g., fiber) properties, and chemical defenses (Gershenson 1993; Kimball and Provenza 2003; Jones et al. 2010; Felton et al. 2018; Dykes et al. 2020; Brozdowski et al. 2021) influence deer selection of forage over space and time. Plants may increase or decrease the nutritional quality in response to herbivory, suggesting that deer can influence their own resources (Schmitz 2008). Deer preference for high-quality forage can alter the plant community composition toward less preferred, low-quality forage (Bradshaw and Waller 2016), or it can increase plant allocation in defense strategies in preferred species (McNaughton 1983; Kimball and Provenza 2003), leading to depauperate and less nutritive foraging conditions. Alternatively, browsing may cause plants to allocate resources toward more new, protein-rich growth rather than fortifying established growth with increased fiber and indigestible lignin (McNaughton 1983). Moreover, browsing can activate dormant meristems that stimulate growth of lateral leaves (McNaughton 1983) and thereby increase both the nutritional quality and relative abundance of plant biomass. In this case, herbivory could maintain or improve forage quality.

Herein, we examine whether browsing by white-tailed deer *Odocoileus virginianus* (hereafter deer) alters nutritional content and the nutritional capacity (based on an index for nutritional carrying capacity) of six hardwood species to meet summer requirements. Using established deer exclosures across 6,500 km<sup>2</sup> in the Allegheny hardwood forests of northwestern Pennsylvania, USA, we tested how plant

abundance and nutritional quality of six dominant hardwood species varied 5 y after overstory harvests. We designed the overstory harvests to create abundant and forage-rich early successional vegetation. We focused on six dominant hardwood species (i.e., ~80% of all stems; see Table S1, *Supplemental Material*, for all available species) because prior work at these sites demonstrated that they are the most abundant species after a disturbance (Horsley et al. 2003): red maple *Acer rubrum*, black cherry *Prunus serotina*, birch *Betula* spp., pin cherry *Prunus pensylvanica*, white ash *Fraxinus americana*, and American beech *Fagus grandifolia* (nomenclature follows NRCS [2010]). We hypothesized that 1) the six species would vary in their nutritional value to deer; 2) browsing would reduce biomass but improve nutritional quality because allocation toward new growth after browsing bouts would reduce fiber and increase protein; and 3) greater nutritional quality would outweigh the biomass losses, resulting in equivalent, or potentially greater, nutritional value relative to areas protected from browsing. By focusing on nutritional content of browse and nutritional requirements of deer rather than just overall changes in abundance, we aimed to investigate the impact of browsing on nutritional value of forage available to deer.

## Study Site

We conducted our study at 16 northern hardwood forest sites distributed throughout a 6,500-km<sup>2</sup> area of northern Pennsylvania. Beside the six dominant hardwood species listed above, the understory included striped maple *Acer pensylvanicum* and root sprouts of beech *Betula* spp. (see Table S1), *Rubus* spp. in the shrub layer, and ferns (e.g., eastern hayscented fern *Dennstaedtia punctilobula* and New York fern *Thelypteris noveboracensis*) in the herb layer. The climate is humid temperate (mean annual precipitation, 114 cm [range: 89–148 cm], with mean precipitation of 12.5 cm [range: 7.1–16.9 cm] during our study period (May–August 2017). Estimated deer densities at these sites in the 3 y before sampling were  $7.1 \pm 0.5$  deer/km<sup>2</sup> (mean  $\pm$  SE, range: 5–11.4), which was moderate given historic trends in the region (Redding 1995). Other wildlife present include wild turkey *Meleagris gallopavo*, *Peromyscus* spp., various squirrels *Sciuridae*, ruffed grouse *Bonasa umbellus*, black bear *Ursus americanus*, Canidae (gray fox *Urocyon cinereoargenteus*, red fox *Vulpes*, coyote *Canis latrans*), and passerine birds and raptors typical of temperate forests. We chose the 16 sites from an established study design throughout this region. From 2012 to 2013, Royo et al. (2016) established two 0.42-ha (60 m  $\times$  70 m) plots at 25 sites and randomly selected one plot to prevent deer browsing by using fencing (hereafter fenced plots) and the other to allow deer browsing (hereafter control plots). U.S. Forest Service managers reduced stand density with a combination of harvest and broadcast herbicides to reduce understory as part of a larger long-term study on forest regeneration (Royo et al. 2016). Fence construction occurred in summer 2013 by using 2.4-m-tall plastic fencing (Deerbusters, Inc.). We selected the 16 sites in this study from the larger set (see Royo et al. 2016, 2017) to maximize site productivity differences (determined by integrated moisture index, canopy openness, soil pH, soil nutrients, elevation,



slope, and aspect) and thus broaden the generality of findings. Selected sites had an elevation of  $598 \pm 10.5$  (mean  $\pm$  SE) and their mean integrated moisture index (Iverson et al. 1997), a composite measure of productivity, ranged from 29.4 (xeric) to 55.6 (mesic). For additional details on site ranking according to productivity, see appendix A in Morgan et al. (2019).

## Methods

### Vegetation sampling and browse biomass estimates

Within each  $60\text{ m} \times 70\text{ m}$  plot, we established a  $40\text{ m} \times 50\text{ m}$  sampling grid with  $10\text{ m} \times 10\text{ m}$  spacing (plus a 10-m buffer around the perimeter), which created 30 sampling nodes. To estimate browse biomass of the six species in each plot, we surveyed  $1\text{-m}^2$  circular quadrats at every other node, resulting in 15 nodes sampled per plot. Surveys of that year's growth consisted of counts separated by height classes: less than 30 cm, 30–150 cm, and greater than 150 cm. We obtained basal diameter measurements for individual trees of the six species within the two largest height classes ( $\geq 30\text{ cm}$ ) and up to 180 cm because deer typically do not browse biomass less than 30 cm, nor can they reach beyond 180 cm (Bernes et al. 2018). Using the basal diameter of up to five stems per size class for each species, we estimated browse biomass by using regression equations developed from samples collected from June to August 2016 for the six species in this study area (Morgan et al. 2019). We scaled our allometric biomass equations for trees taller than 180 cm to account for only the fraction of the plant material available to deer (Morgan et al. 2019).

From June to August 2017, we collected leaf and stem tissue from our six target species if encountered along every other transect created by the sampling grid (three transects per plot, 20 m apart). To account for individual variability, we collected leaf and stem tissue from individuals of a given species encountered along each transect as evenly as possible. In each plot, we composited browse biomass (accessible to deer 30–180 cm) of each species encountered by transect. We then separated leaves and stems for nutritional analyses because they differ in nutritional quality (Ulappa et al. 2020; Hanley et al. 2012). To ensure we only assayed the browsable parts of the stems, we trimmed each stem to the average browsing diameter for each species as determined by our previous work (Morgan et al. 2019). We froze all samples at  $-18^\circ\text{C}$  to preserve nutritional content until we could proceed with laboratory analysis.

### Nutritional analysis

We freeze dried all frozen samples by using a VirTis BenchTop Pro freeze dryer (SP Scientific, Warminster, PA, USA) according to protocols for vegetation and ground samples to pass a 1-mm screen by using a Wiley mini mill (Thomas Scientific, Swedesboro, NJ, USA). Once dried and ground, the browse stems composited by transect resulted in less than the approximately 4 g of dried, ground material required for all nutritional assays precluding analysis at the transect scale; therefore, we composited and analyzed freeze-dried browse stems at the plot scale. Using sequential

fiber analysis with sodium sulfite (Goering and Van Soest 1970; Ankom 200 fiber analyzer, Ankom Technology, Fairport, NY, USA), we measured fiber content of approximately 0.5 g of each sample (see Cook et al. [2022]) by determining the percent neutral detergent fiber (NDF), acid detergent fiber, acid detergent lignin, and acid insoluble ash. We corrected NDF, acid detergent lignin, and acid insoluble ash for potential laboratory analysis bias by using correction equations by Cook et al. (2022). We calculated percent crude protein as 6.25 times the percent nitrogen content (Robbins 1993), which we determined by using a carbon-nitrogen TruSpec analyzer (LECO, St. Joseph, MI, USA; Dairy One, Ithaca, NY, USA). For plots that lacked sufficient leaf material for nutritional assays, we assigned the mean nutritional values of the plot with the most similar productivity characteristics (appendix A in Morgan et al. [2019]), which occurred for fewer than 9% of the composited plant samples. We determined presence of protein-binding capacity of tannins, which decreases digestibility (Robbins et al. 1987a, 1987b; but see Jones et al. [2010]), by using the Martin and Martin (1982) bovine serum albumen precipitation assay (Wildlife Habitat Lab, Washington State University, Pullman, USA) in a subset of samples of each species and fencing treatment. We assigned average tannin content to all samples of the same species and fencing treatment. We estimated percent dry matter digestibility (DMD; percentage of food intake assimilated; fiber  $\times$  bovine serum albumen) and percent digestible protein (DP; percentage of protein assimilated; crude protein  $\times$  bovine serum albumen) by using summative equations by Robbins et al. (1987a, 1987b), which incorporated any reduction in digestibility caused by tannins.

### Nutritional requirements

Using the estimated browse biomass (Morgan et al. 2019), DMD, and DP values for each of the six species, we used the Forage Resource Evaluation System for Habitat for Deer (FRESH) model (Hanley et al. 2012) modified to run in R Statistical v3.6.3 software (R Core Team 2021) to assess nutritional quality and quantity of the six species in each plot. This model uses biomass and nutrition data to predict the number of days a given plot can support a female deer with one fawn (deer days [dd/ha]), also called nutritional carrying capacity. We acknowledge that we cannot use the output to predict the number of deer that a site can support because we tested only six species of all available forage. Instead, our goal was to use the FRESH model-derived nutritional capacity as a relative index that integrates quantity and quality of the six species with deer requirements, for a more robust analysis than provided with nutritional values alone. We used the nutritional requirements of a lactating deer with one fawn (daily metabolic energy requirement = 69,086 kJ, digestible energy = 11.5 kJ/g, DP = 8 g of DP/100 g of forage, dry mater intake = 1,751 g/kg body mass; Hanley et al. 2012) for a conservative estimate of spring and summer nutritional needs for deer.

### Statistical analysis

We analyzed all data with SAS v9.4 software (SAS Institute, Inc. 2013) using an  $\alpha$  of 0.05. We used an analysis of covariance with fencing treatment and species considered the



fixed variables. We included the date of sampling (Julian date) as a continuous covariate to account for changes in phenology that occur during the growing season and our sampling period (June–August) between sites. We sampled paired plots within a site within 1 d of each other. The overall experimental design is a randomized complete block with the fencing treatment (i.e., fenced plots vs. control plots) randomly applied to the pair of plots within a site. We estimated output from the FRESH model at the fencing treatment level so we included site as a random factor to account for differences among pairs. By contrast, we estimated average DMD, NDF, DP, and browse biomass values at the species level within each fencing treatment. For these analyses, models include the fixed effects of the fencing treatment and species and both a site and a species  $\times$  fencing treatment interaction nested within site as random effects. We modified sites with 0.00 dd/ha to 0.01 dd/ha to allow statistical analysis.

We analyzed DMD, NDF, and DP with a Gaussian distribution due to their normal distribution; however, nutritional capacity and browse biomass were right skewed and overdispersed and thus modeled with a lognormal distribution. We backtransformed means and standard errors (SEs) for nutritional capacity and browse biomass to the original scale by using the delta method (SAS v9.4), and we used the Kenward–Rogers denominator degrees of freedom adjustment for each model. We further explored pairwise comparisons for any significant fencing treatment, species, or fencing treatment  $\times$  species effect by using the LSMEANS statement (SAS v9.4).

## Results

Averaged across fencing treatments, availability of browse biomass varied among species with birch as the most abundant (43.9%) and black cherry the least abundant (3.45%; see Table S1). Between fencing treatments, the browse biomass of the six species in control plots exposed to browsing was nearly 60% less than within fenced plots ( $F_{1,15} = 6.26$ ;  $P = 0.024$ ), with pin cherry 95% less in control plots ( $F_{1,15} = 49.95$ ;  $P < 0.0001$ ; Table 1; Figure S1, *Supplemental Material*) than in fenced plots. Deer browsing did not affect the browse biomasses of all other species. Nutritional quality (NDF, DMD, and DP) for both the leaf and stem portions of their browse biomass varied significantly among the six species regardless of fencing treatment (Table 2). For leaf tissue, pin cherry was consistently divergent from other species, possessing significantly less NDF and significantly greater DMD and DP (Table 3) than any other species. Similarly, for stem tissue, pin cherry had significantly less NDF than other species, the greatest DMD along with white ash and maple, and greatest DP along with birch and beech. Despite exhibiting relatively greater amount of DP, beech also ranked highest or among the highest in stem and leaf NDF and among the lowest in stem and leaf DMD (Table 3). Red maple had the lowest leaf DP, and maple and ash had the lowest stem DP (Table 3). We found no other species consistently differentiated itself from others. Even when comparing relative rankings between leaf and stem tissue for a given nutritional measure, a species could be among the lowest ranked for leaf

**Table 1.** Browse biomass and deer days per hectare (dd/ha) in fenced plots and control plots averaged across 16 sites from Forage Resource Evaluation System for Habitat for Deer (FRESH) analysis for six species of hardwoods (red maple *Acer rubrum*, black cherry *Prunus serotina*, birch *Betula* spp., pin cherry *Prunus pensylvanica*, white ash *Fraxinus americana*, and American beech *Fagus grandifolia*) and for pin cherry only in the Pennsylvania Allegheny Forest, USA, June–August 2017. Means  $\pm$  SE are backtransformed using the delta method, and ranges are nontransformed data. Different letters denote statistical difference between treatments ( $\alpha = 0.05$ ).

	Browse biomass		(dd/ha)	
	Mean $\pm$ SE	Range	Mean $\pm$ SE	Range
<b>All species</b>				
Control	10.36 $\pm$ 4.14a	0.10–122.05	3.95 $\pm$ 1.93a	0.00–30.09
Fenced	24.95 $\pm$ 9.98b	1.18–100.05	8.14 $\pm$ 3.04a	0.00–41.56
<b>Pin cherry only</b>				
Control	0.076 $\pm$ 0.051a	0.00–52.12	1.88 $\pm$ 1.80a	0.00–28.55
Fenced	2.14 $\pm$ 1.44b	0.00–63.77	5.47 $\pm$ 2.62b	0.00–36.42

tissue and among the highest ranked for stem tissue (e.g., white ash DMD).

There was no overall fencing treatment effect for NDF of leaves or stems nor DMD of leaves or stems (Table 2). DP, on the other hand, was 6.1% greater for leaf tissue ( $10.7 \pm 0.4\%$  [mean  $\pm$  SE] vs.  $10.0 \pm 0.4\%$ ; Figure 1) in control plots and 40.3% greater for stem tissue ( $1.6 \pm 0.2\%$  vs.  $1.1 \pm 0.2\%$ ; Figure 2) than fenced plots (Table 2). Post hoc tests following the fencing treatment  $\times$  species effect revealed that the significant difference in DP (Table 2) was driven entirely by greater DP in pin cherry leaves (Figure 1) and stems (Figure 2) in control plots. The average number of dd/ha did not differ by treatment for all six species ( $F_{1,15} = 1.85$ ;  $P = 0.19$ ; Table 1). When we tested whether the greater DP of the pin cherry affected the nutritional capacity, we found that browse biomass of pin cherry alone within fenced plots supported deer nearly three times longer than control plots exposed to browsing ( $F_{1,15} = 4.52$ ;  $P = 0.051$ ; Table 1).

## Discussion

Our indirect measurements of browsing impact by using exclosures, coupled with direct measures of nutritional quality, allowed us to provide conservative conclusions about the browsing impacts on diet quality and quantity of six broadleaf species for deer without directly observing deer foraging behavior. Data support our hypothesis that the six species would vary in nutritional value to deer and fencing treatment would affect browse quantity and nutritional quality. However, pin cherry largely drove any fencing treatment effects observed. Similarly, the FRESH model output, which integrated both forage quantity (browse biomass) and quality (DP and DMD) with deer requirements, was unaffected by browsing unless we restricted analyses to pin cherry.

We found browsing reduced the total biomass of browsable leaf and stem tissue of six species available to deer by 60%. Our results bolster the corpus of evidence



**Table 2.** Effects of exclosures on the nutritional value for white-tailed deer *Odocoileus virginianus* of six species of hardwoods (red maple *Acer rubrum*, black cherry *Prunus serotina*, birch *Betula* spp., pin cherry *Prunus pennsylvanica*, white ash *Fraxinus americana*, and American beech *Fagus grandifolia*) in the Pennsylvania Allegheny Forest, USA. We analyzed composite samples from 16 paired plots with a fencing treatment (fenced plots and control plots) for neutral detergent fiber (NDF), dry matter digestibility (DMD), and digestible protein (DP) in June–August 2017. We used a generalized linear mixed model ( $\alpha = 0.05$ ), and *df* represents degrees of freedom/density degrees of freedom.

Explanatory Variable	NDF			DMD			DP		
	df	F	p	df	F	p	df	F	p
<b>Leaf</b>									
Treatment	1/15.3	1.98	0.1796	1/15.6	2.48	0.1351	1/126.5	6.79	0.0102
Species	58/115.5	52.66	<0.0001	5/117.0	29.33	<0.0001	5/126.8	70.73	<0.0001
Treatment × Species	5/117.2	0.96	0.4464	5/118.1	0.82	0.5406	5/126.2	2.70	0.0236
Julian Date	1/14.0	3.79	0.0717	1/14.0	5.01	0.0419	1/14.6	6.46	0.0229
<b>Stem</b>									
Treatment	1/16.8	1.88	0.1881	1/17.1	0.17	0.6861	1/116.3	4.90	0.0288
Species	5/109.0	34.81	<0.0001	5/106.6	16.63	<0.0001	5/118.2	6.90	<0.0001
Treatment × Species	5/110.5	0.84	0.5208	5/107.1	2.18	0.0616	5/115.9	2.48	0.0356
Julian Date	1/14.8	6.00	0.0273	1/14.5	10.27	0.0061	1/13.5	0.43	0.5244

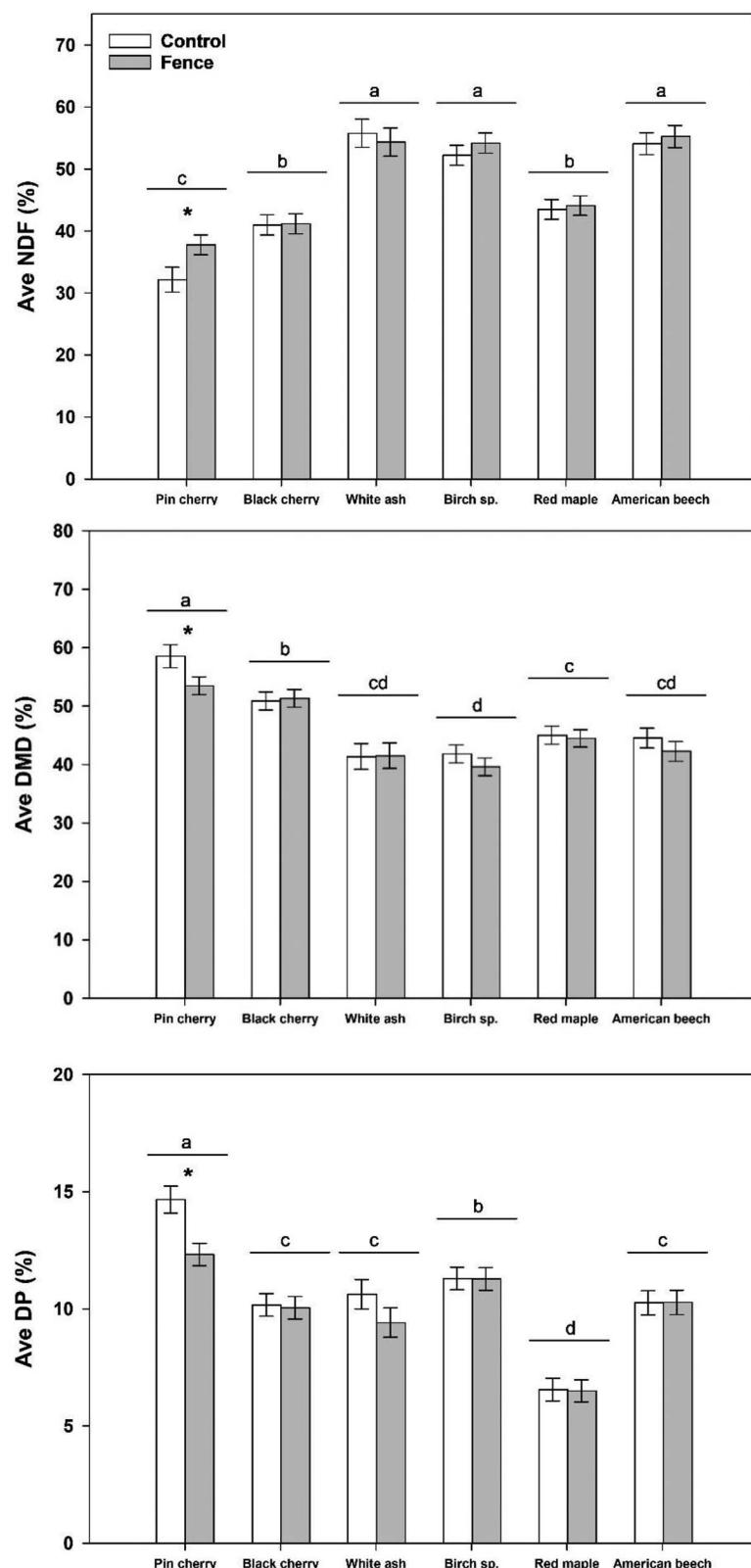
demonstrating unequivocally that browsing limits regeneration abundance (Habeck and Schultz 2015; Royo et al. 2016, 2017; Bernes et al. 2018; Redick and Jacobs 2020; Champagne et al. 2021; Jones et al. 2023). And yet, our focus on browse availability for deer rather than forest regeneration likely represents a conservative estimate of biomass reduction and constraints on tree regeneration. Results from previous research at this study site found browsing reduced overall plant cover by approximately 70% (Royo et al. 2017) and stem heights by 20–30% (Morgan et al. 2019; Royo et al. 2017). We see a stronger effect of browsing on browse biomass when focusing on pin cherry, a species highly favored by deer in the spring and summer (Horsley et al. 2003), which was reduced by an order of magnitude. We also note that the sites are dominated (approximately >60%) by American beech and birch, which are more preferred by deer during winter and autumn, respectively (Horsley et al. 2003). If we continued our study through all seasons, we may have seen a treatment effect in these species as well. Still, browse biomass of these species in the study site represents only 21–24% of the total aboveground biomass, which is a portion that diminishes over time as trees grow larger (Morgan et al. 2019) beyond the height accessible to deer. Further research could determine whether

deer choose the less preferred of the six species once trees grow beyond the browsable stratum or if they move to new sites altogether.

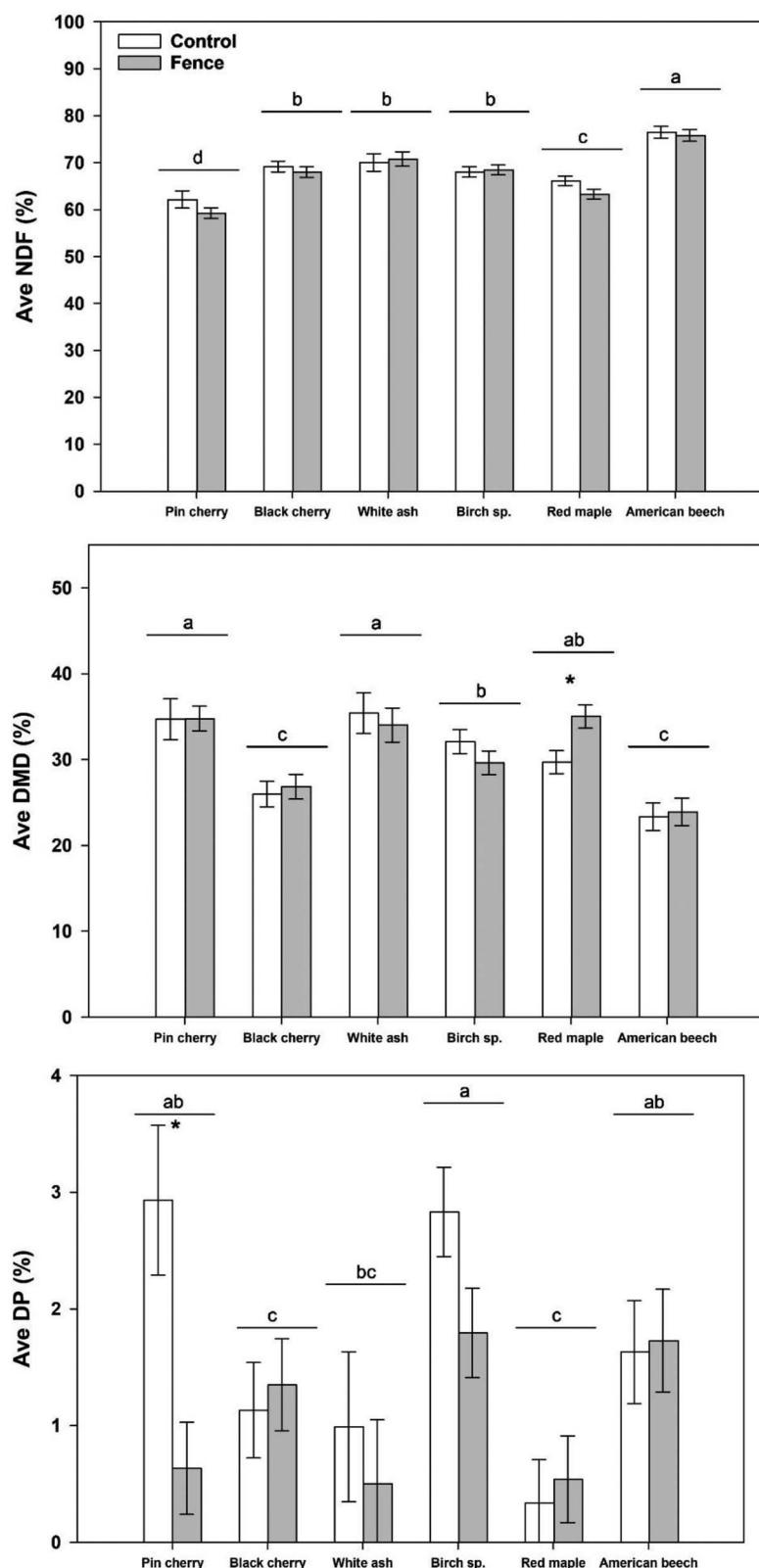
As expected, the six species varied in nutritional content regardless of fencing treatment (Table 1). In general, white ash, the birches, and American beech were the least nutritious. The ranking of nutritional quality detected partially supports the resource availability hypothesis (Coley et al. 1985; Coley 1987) prediction that investment in defensive compounds is inversely related to growth rate. Fast-growing pin cherry was the most nutritious forage available to deer with both leaves and stems having less NDF and greater DMD and DP (Table 2) than the other species. Because NDF is incorporated in the DMD calculation (Robbins et al. 1987a, 1987b), we expected the inverse relationship between NDF and DMD. The slow-growing, highly shade-tolerant American beech was consistently among the least nutritive species with the greatest NDF, suggesting heavy investment in structural carbohydrates. The nutritional hierarchies of the other four species, in contrast, were less consistent and depended both on the tissue examined and the nutritional value assessed. Inconsistent nutritional results among red maple, black cherry, the birches, and white ash may simply reflect that these species are relatively similar in their growth and survival strategies, particularly when contrasted with

**Table 3.** Average  $\pm$  SE nutritional quality regardless of fencing treatment of six species of hardwoods (red maple *Acer rubrum*, black cherry *Prunus serotina*, birch *Betula* spp., pin cherry *Prunus pennsylvanica*, white ash *Fraxinus americana*, and American beech *Fagus grandifolia*) in the Pennsylvania Allegheny Forest, USA, collected June–August 2017. We determined neutral detergent fiber (NDF), digestible protein (DP), and dry matter digestibility (DMD) for browsable leaves and browsable stems. Different letters denote statistical difference between species ( $\alpha = 0.05$ ).

Species	Leaf			Stem		
	NDF%	DMD%	DP%	NDF%	DMD%	DP%
Pin cherry	35.0 $\pm$ 1.4c	56.0 $\pm$ 1.3a	13.4 $\pm$ 0.4a	60.7 $\pm$ 1.1d	34.7 $\pm$ 1.4a	1.8 $\pm$ 0.4ab
Black cherry	41.1 $\pm$ 1.3b	51.1 $\pm$ 1.2b	10.1 $\pm$ 0.4c	68.6 $\pm$ 0.8b	26.4 $\pm$ 1.0c	1.2 $\pm$ 0.3c
White ash	55.1 $\pm$ 1.7a	41.4 $\pm$ 1.6cd	10.0 $\pm$ 0.5c	70.4 $\pm$ 1.2b	34.7 $\pm$ 1.6a	0.7 $\pm$ 0.4bc
Birch spp.	53.2 $\pm$ 1.3a	40.7 $\pm$ 1.2d	11.3 $\pm$ 0.4b	68.3 $\pm$ 0.8b	30.9 $\pm$ 1.0b	2.3 $\pm$ 0.3a
Red maple	43.8 $\pm$ 1.3b	44.7 $\pm$ 1.1c	6.5 $\pm$ 0.4d	64.7 $\pm$ 0.7c	32.4 $\pm$ 0.9ab	0.4 $\pm$ 0.3c
American beech	54.7. $\pm$ 1.4a	43.4 $\pm$ 1.3cd	10.3 $\pm$ 0.4c	76.1 $\pm$ 0.9a	23.6 $\pm$ 1.1c	1.7 $\pm$ 0.3ab



**Figure 1.** Differences between nutritional quality of leaves of six species of hardwoods (red maple *Acer rubrum*, black cherry *Prunus serotina*, birch *Betula* spp., pin cherry *Prunus pensylvanica*, white ash *Fraxinus americana*, and American beech *Fagus grandifolia*) in plots that exclude deer (fenced plots) and plots that allow for deer browsing (control plots). We determined neutral detergent fiber (NDF), dry matter digestibility (DMD), and digestible protein (DP) for browsable leaves in the Pennsylvania Allegheny Forest, USA, collected June–August 2017. Error bars represent SE. Different letters denote statistical difference between species, and asterisks denote statistical difference between fencing treatments ( $\alpha = 0.05$ ).



**Figure 2.** Differences between nutritional quality of stems of six species of hardwoods (red maple *Acer rubrum*, black cherry *Prunus serotina*, birch *Betula* spp., pin cherry *Prunus pensylvanica*, white ash *Fraxinus americana*, and American beech *Fagus grandifolia*) in plots that exclude deer (fenced plots) and plots that allow for deer browsing (control plots). We determined neutral detergent fiber (NDF), dry matter digestibility (DMD), and digestible protein (DP) for browsable stems in the Pennsylvania Allegheny Forest, USA, collected June–August 2017. Error bars represent SE. Different letters denote statistical difference between species, and asterisks denote statistical difference between fencing treatments ( $\alpha = 0.05$ ).

American beech and pin cherry, two species at the extremes of the shade tolerance spectrum (Pacala et al. 1996; Niinemets and Valladares 2006; Humbert et al. 2007).

For all six species across all sites, fenced plots that eliminated browsing did not increase fiber content of browse biomass (as indicated by NDF and DMD; Table 1) as we had expected. We hypothesized that browsing of plants in the control plots would limit development of structural defenses in the form of fiber and instead allocate energy toward new growth high in protein. We did find that red maple stems in fenced plots had greater DMD than controls (Figure 2), but this was not enough to drive a fencing effect overall (Table 2). Isolating the leaves and stems of pin cherry, alternatively, showed browse biomass had greater DP in the control plots than in the fenced plots that are protected from browsing (Figures 1 and 2; Table 2). We found the fast-growing, highly shade-intolerant pin cherry presented less structural defenses in the form of carbohydrates (as indicated by NDF) and more in new growth (as indicated by DP). Shabel and Pearn (1994) found pin cherry at low density, like our control plots, had greater compensatory growth after browsing than plots with high pin cherry density. Continual herbivory of pin cherry may result in an increase in lateral stem growth and this new, younger growth has greater protein than other macromolecules, suggesting DP itself is sensitive to foraging in a fast-growing species. None of the five other taxa exhibited consistent browsing-induced differences in nutritive components. We suggest the failure to find browsing effects in these species is a direct result of weak to nonexistent browsing pressure on these species via both defensive allocations and a lack of apprenancy (see Table S1). Apart from pin cherry, all the species studied rate as moderate-to-low preference for deer, particularly in summer (Horsley et al. 2003; Latham et al. 2005; Rossell et al. 2005), making it difficult to detect a browsing-induced effect. Although these six species form the bulk of the regenerating tree community (Table S1), they differ considerably in their frequency of occurrence among sites, their overall relative abundance, and stem height, thus diminishing not only their apprenancy to deer, but likely also weakening our ability to detect a statistical difference. For example, white ash, often considered highly preferred (Sample et al. 2023), was only found in 7 of 16 sites and represented only approximately 6% of the available browse (Table S1). Our analysis also reports that white ash and black cherry, both considered moderately shade-intolerant, present contrasting foliar nutritional profiles, with ash containing greater structural carbohydrate allocation and lesser digestibility (i.e., DMD) relative to black cherry. Inconsistencies among species in nutritive value in our analysis may arise from variations in phytochemical, rather than structural, defensive allocations. In some species (e.g., American beech), defense strategies focus on high allocation to structural components (high NDF). Others, including birch and black cherry, allocation toward phytochemical defenses may help deter browsing (Palo 1984; Burns and Honkala 1990; Bryant et al. 1994; Champagne et al. 2021), whereas white ash invests relatively little in these compounds (Cipollini et al. 2011).

The results of the FRESH model (Hanley et al. 2012) do not support our hypothesis that compensatory growth

of browsed plants (quality) in control plots would compensate for reductions in overall browse biomass (quantity). However, we also did not find the opposite to be true either: the greater browse biomass within fenced plots did not significantly increase the number of days the six species could support. When analyzing pin cherry alone, fenced plots could support a lactating female with one fawn nearly three times as long as controls, which was statistically significant despite lower DP of pin cherry in fenced plots. The lack of fencing effect overall on the six species together along with the significant fencing effect of pin cherry alone suggests that difference in quality is not enough to alter the nutritional capacity in dense plots. We acknowledge that deer eat more than the six hardwood species assessed. Although these six species dominated the regenerating tree community within the plots, other preferred taxa, including forbs and shrubs (e.g., *Rubus* spp.) were abundant (Royo et al. 2017). Our focus on nutrition available from only six hardwoods precludes definitive conclusions about how many deer the landscape can support; however, the goal of our study was to determine the effects of herbivory on these six species, not the carrying capacity of sites. Our hypotheses made predictions on how the energetic needs of deer, and their browsing impacts, could be structured by both forage quantity and quality, which is why we used the FRESH model-derived nutritional carrying capacity as a relative index that integrates quantity and quality of the six species alone. Deer will alter their selection based on both quality and quantity (Robbins 1993), and foraging theory predicts the increase in browse biomass would result in longer patch residence times even if quality is low (Hobbs and Swift 1985; Shipley and Spalinger 1995). The lack of significance between the plots may suggest that quality can temper quantity, but further research testing foraging decisions in plots with uniform species occurrence, including forbs, is needed.

Our equivocal results could also reflect landscape level variation in biomass. For example, 7 of the 16 fenced plots and 10 of the 16 control plots could support a lactating female with one fawn for less than 1 dd/ha. Yet the maximum support for fenced and control plots is 41.5 and 30.1 dd/ha, respectively (Table 1). The lack of statistical difference in the number of days each site could support may result from landscape variation rather than fencing effects. However, we chose our 16 sites specifically to maximize site productivity differences and broaden the generality of findings. The effects of landscape heterogeneity may only be confirmed with careful manipulation and control of available browse in field sites or use of tractable deer in captive environments that restrict browsing. Finally, deer will alter diet selection based on seasonal nutritional needs (Robbins 1993) and biomass availability (Ford et al. 1993; Morrison et al. 2002; Lashley et al. 2011). Because deer select more protein in the summer to support growth and lactation compared with fiber and fat in the autumn (Dostaler et al. 2011), we expected the continued selection of the high protein new growth. Furthermore, plants allocate resources toward the production of more structural carbohydrates later in the growing season at the same time deer select for digestibility over protein. If we continued our study into the fall, we may have seen more distinct, overall fencing effects on NDF and DMD.



Browsing significantly decreased the available biomass of leaves and stems for the six species by 60%, while also enhancing the nutritional quality of browse accessible to deer. Our data highlight pin cherry as the most nutritious among the six taxa and suggest a sensitivity to herbivory that drove the observed treatment differences. Exposure to herbivory in pin cherry likely induced a shift in energy allocation from structural defenses to new growth rich in protein, making it a valuable resource during crucial months for parturition and lactation, specifically spring and summer. Despite the increased nutritional value of pin cherry under herbivory, our results did not support the hypothesis that compensatory growth in control plots would counterbalance reductions in browse biomass for all six taxa, including pin cherry alone. Our study underscores the significance of considering both quantity and quality of forage in comprehending the effects of deer herbivory, yet further investigation into all vegetation accessible to deer beyond the six species is warranted. A more comprehensive analysis, incorporating available shrubs and forbs, along with accounting for seasonal diet variations, could offer a more robust understanding of the impact of exclosures on nutritional quality in future research.

## Supplemental Material

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**Table S1.** Frequency ( $N$  sites found out of 16), stem density ( $N$  stem/ $m^2$ ), and relative abundance (%) of all woody individuals (trees and arborescent shrubs) surveyed in the 16 paired plots (fenced plots and control plots) in the Allegheny Hardwood forests of northwestern Pennsylvania, USA, from June to August of 2017. Species represented in this study are in bold.

Available: <https://doi.org/10.3996/JFWM-23-031.S1> (19 KB DOC).

**Figure S1.** Available browse biomass (reachable by white-tailed deer, *Odocoileus virginianus*, at 180 cm high) of six hardwood species (red maple *Acer rubrum*, black cherry *Prunus serotina*, birch *Betula* spp., pin cherry *Prunus pensylvanica*, white ash *Fraxinus americana*, and American beech *Fagus grandifolia*) estimated using previously derived allometric equations at the same sites (Morgan et al. 2019) in 16 paired plots (fenced plots and control plots) in the Allegheny Hardwood forests of northwestern Pennsylvania, USA (surveyed from June to August of 2017). Error bars represent standard error. Different letters denote statistical difference between species, and asterisks denote statistical fencing treatment  $\times$  species effects.

Available: <https://doi.org/10.3996/JFWM-23-031.S2> (131 KB PDF).

**Reference S1.** Morgan Q, Johnstone-Yellin TL, Pinchot CC, Peters M, Royo AA. 2019. Partitioning and predicting forage biomass from total aboveground biomass of

regenerating tree species using dimensional analyses. Canadian Journal of Forest Research 49:309–316.

## Archived Material

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**Data A1.** Total browse biomass and estimated nutritional carrying capacity (i.e., deer days per hectare) for white-tailed deer, *Odocoileus virginianus*, based on six dominant regenerating hardwood species (red maple *Acer rubrum*, black cherry *Prunus serotina*, birch *Betula* spp., pin cherry *Prunus pensylvanica*, white ash *Fraxinus americana*, and American beech *Fagus grandifolia*) for 16 regenerating Allegheny hardwood forest sites in northwestern Pennsylvania, USA (surveyed from June to August of 2017). Data are provided as averages by treatment (fenced plots and control plots; Glover et al. 2023).

Available: <https://doi.org/10.2737/RDS-2023-0058> (2 KB XLSX).

**Data A2.** Browse biomass for both stem and leaf tissue as well as average nutritional quality data (neutral detergent fiber [NDF], dry matter digestibility [DMD], and digestible protein [DP]) for 16 regenerating Allegheny hardwood forest sites in northwestern Pennsylvania, USA (surveyed from June to August of 2017). Data are provided by treatment (fenced plots and control plots) and species, for six dominant regenerating hardwood species (red maple *Acer rubrum*, black cherry *Prunus serotina*, birch *Betula* spp., pin cherry *Prunus pensylvanica*, white ash *Fraxinus americana*, and American beech *Fagus grandifolia*; Glover et al. 2023).

Available: <https://doi.org/10.2737/RDS-2023-0058> (16 KB XLSX).

**Reference A1.** Glover LM, Volponi SN, Royo AA, Johnstone-Yellin TL. 2023. Biomass and nutritional qualities of six regenerating hardwood species in the Allegheny hardwood forest type. Fort Collins, Colorado: Forest Service Research Data Archive.

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