TWIG PRODUCTION PATTERNS AMONG MOOSE FORAGE SPECIES AND IMPLICATIONS FOR FOREST MANAGEMENT

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ABSTRACT: A declining moose (*Alces alces*) population in northeastern Minnesota is a serious concern of the Gichi Onigaming Anishinaabeg (Grand Portage Band of Lake Superior Chippewa). A better understanding of the variation in moose forage production at the plant level among tree and shrub species and over time may be important to moose recovery in areas where nutrition may be limiting, while managers need practical methods to monitor forage density. Using data from an extensive 2019 moose browse survey at Gichi Onigaming (Grand Portage Indian Reservation, MN) and Minong (Isle Royale, MI), we fit models of twig production (number of twigs per plant) within moose reach as a function of species, canopy cover, and stem height. We validated the best fit model against an independent data set and used the model to simulate stand-level forage density over time for 3 tree species preferred by moose. Twig production varied non-linearly with stem height. An increasing then decreasing unimodal curve with height fit better than allometric models or species means. Peak twig production, height at peak production, and rate of production decline with height varied among species. Paper birch (*Betula papyrifera*) and balsam fir (*Abies balsamea*) generally had the greatest peak twig production, greatest heights at peak production, and lowest rates of decline with height. Among trees, quaking aspen (*Populus tremuloides*) generally had lower peak twig production, lower height at peak production, and greater rates of decline with height than most other trees and some tall shrubs. Peak twig production was greater under open canopy than under closed canopy for seven species. Model validation indicated that predictions were well correlated with observations and outperformed alternative models but had consistent over-prediction bias. Simulations of regenerating aspen, paper birch, and red maple (*Acer rubrum*) forests indicated that whereas aspen produced ~ 1.4-2.2 times more peak forage biomass than paper birch or red maple, paper birch and red maple produced usable forage densities for ~2-17 years longer than aspen. Finally, we provide a procedure to use the regression equations to estimate moose forage density from common forest regeneration survey data. Although the equations are suitable for monitoring, they should be used cautiously in high accuracy applications. Our findings suggest that diverse mixes of deciduous trees and shrubs resulting from post-harvest treatments likely provide abundant moose forage for longer durations than do nearly pure aspen stands often resulting from clearcutting alone in northeastern Minnesota.

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Moose (*Alces alces*; *Mooz* in Anishinaabemowin, the Anishinaabeg language) are a primary subsistence species used by the Gichi Onigaming Anishinaabeg (Grand Portage Band of Lake Superior Chippewa), a native community in northeastern Minnesota who exercise rights to hunt, fish, and gather across their traditional homeland (Stults et al. 2016). Maintaining subsistence species into perpetuity through the Anishinaabeg practice of seventh-generation planning (Vukelich 2023) and scientific inquiry are of high priority to the Tribal nation (Moore et al. 2024). As one of several strategies to maintain or increase moose numbers, the Gichi Onigaming Forestry Department conducts forest management projects at Gichi Onigaming intended to increase the abundance of woody forage preferred by moose. The data and research presented in this article were gathered with and for the Gichi Onigaming Anishinaabeg.

Moose populations in Minnesota have been declining (>50% decline since the 1990's) (Lenarz 2007, Severud et al. 2022), and population declines have impacted the Gichi Onigaming community's traditional way of life. To address these concerns, the Gichi Onigaming Anishinaabeg began a long-term moose research program in 2010 and have found that the decline has resulted from low survival rates of adults and calves (Wolf et al. 2021, Severud et al. 2022, Wehr et al. 2024, Garwood et al. 2025). Research in Minnesota during 2003–2022 by the Minnesota Department of Natural Resources (DNR) and others have indicated that parasites, disease, predation, and winter nutritional restriction are contributing to moose population declines, resulting in high mortality of adults and poor recruitment of calves (Severud et al. 2015, 2019, 2022; Wünschmann et al. 2015; DelGiudice et al. 2019; Carstensen et al. 2018).

Management to improve forage conditions may alleviate the negative effects of nutritional limitation on moose population dynamics in this region. Recent studies in other regions suggest that forest management decisions positively or negatively affect the abundance of preferred forage (Johnson and Rea 2024) and that the resulting "nutritional landscape" may contribute to moose population growth or decline (Schrempp et al. 2019; Peterson et al. 2020, 2022). Studies have found positive associations between preferred forage availability and calving success (Hayes et al. 2022) and between moose calf weights and a diverse diet of deciduous species (Felton et al. 2020). In Adirondack Park, New York, USA, moose densities were positively associated the abundance of summer forage with high digestible protein (Peterson et al. 2022), which was often a result of forest harvest. Also in Adirondack Park, local browsing intensity was associated positively with the density of preferred forage plant species and negatively with that of avoided species (Peterson et al. 2020). Together, these studies indicate that the abundance of diverse, high-quality preferred forage can influence moose at the population level.

In northeastern Minnesota, forest management practices are often directed at commercially valuable quaking aspen (*Populus tremuloides*; Anishinaabe language: Azaadi; De Pellegrin Llorente et al. 2020), which is preferred by moose (Portinga and Moen 2015). Aspen in northeastern Minnesota is commonly managed in even-aged stands harvested by clearcut with reserves (Perala 1977, David et al. 2001). Aspen typically regenerates after clearcutting through high densities of root suckers that grow rapidly (Perala 1977, David et al. 2001) and initially provide abundant moose forage. However, little is known about summer protein content in quaking aspen leaves relative to other forage species (but see Renecker and Hudson (1988)), and aspen forage quality is further complicated by seasonal variation in tannins (Lindroth 2001) that reduce protein availability (Robbins et al. 1987). Similarly, aspen's rapid height growth allows it to outcompete other forage species (Zenner and Puettmann 2008), reducing diversity while also potentially reducing its own accessibility over time. Recent research also suggests moose may prefer burned areas over harvested areas (Schrage 2023, Mumma et al. 2024), although the mechanisms are not clear. Overall, it is possible that modifications to forest management might produce more diverse, higher quality, or longer lasting forage for moose.

To improve the nutritional landscape for moose, managers need a better understanding of forage dynamics as well as rapid and practical methods to estimate forage abundance and quality. Ideally, forage quality and quantity could be incorporated into existing monitoring programs, such as post-harvest forest regeneration surveys. Such methods may need additional protocols to accurately estimate browse abundance that is available to moose. Moose typically eat twig ends during the dormant season and stripped leaves during summer (Renecker and Schwartz 2007). Twigs and leaves between 0.5 m to 2.5-3.0 m above the ground are used most heavily, presumably because they are easiest to reach (Renecker and Schwartz 2007). Although moose sometimes strip bark or push over large tree saplings to access twigs above 3 m, this is usually associated with exceptional conditions such as low food availability or difficult winters (Peek et al. 1976; Renecker and Schwartz 2007).

The only study to estimate browse production by individual woody plants for northeastern Minnesota (Grigal and Ohmann 1977) estimated leaf and twig biomass using measurements of plant diameter at 15 cm above ground for shrubs and trees. However, the power law equations used for these estimates do not account for whether twigs are within reach of moose, and many have poor coefficients of determination. For example, the Grigal and Ohmann (1977) equations estimate that a mature aspen tree 25 cm (~10 inches) in diameter at the base would have ~2,800 grams of current annual twig biomass. However, it is reasonable to expect that nearly all of that biomass would be well out of the reach of moose and thus unavailable. Increasing and then declining browse availability with the age of forage plants is consistent with multiple research studies showing that moose use of harvested or burned areas increases after the disturbance and then declines after about 10-20 years (Loranger et al. 1991, Fisher and Wilkinson 2005). Mechanisms behind this pattern may include changes in species composition as well as changes in plant height that create a disconnect between total biomass and accessible biomass. Instead of Grigal and Ohmann's allometric equation, the relationship between browse availability and plant size might be better modeled by a unimodal function that rises to a peak and then declines again to low values, which would account for reduced browse availability to moose beyond an upper limit in plant height. For example, similar browse biomass equations with unimodal properties have been recently developed in another ecological system within Adirondack Park (Peterson et al. 2022). The Grigal and Ohmann (1977) or Peterson et al. (2022) equations would also be difficult for foresters to apply to common field data because field foresters do not often measure plant basal diameter. Instead, foresters often collect tree regeneration and shrub competition data in terms of density by species and height (e.g., Minnesota DNR Forestry regeneration monitoring procedures [Minnesota DNR Forestry 2016], Wisconsin DNR forest regeneration metric [Wisconsin DNR 2021]).

Multiple studies have quantified species–specific characteristics of twigs eaten or available to be eaten by moose. Portinga and Moen (2015) provided tables of mean oven dry mass and diameter of twigs used by moose in northeastern Minnesota for 12 species in winter and 11 species in summer under open and closed canopies. Peek et al. (1976) provided estimates of mean browsing diameter and mean oven dry mass per twig of 10 species of forage eaten in fall and winter in northeastern Minnesota. Risenhoover (1987) provided estimates of mean browsing diameter and mean oven dry mass per twig of 17 species of forage eaten in winter in Isle Royale National Park (Minong). Given the availability of individual twig biomass data, determining the relationship between woody plant characteristics and the number of available twigs produced per plant may allow for more efficient models of biomass estimation per plant, and might also integrate seasonal and species corrections. Such an approach would not only account for biomass available to moose, but also meet the need for efficient data collection by foresters and managers.

Prior research also suggests that plant-level browse production may vary between species and with differences in canopy closure or browsing pressure. The variability among the coefficients of the Grigal and Ohman equations suggests production differences between species. De Jager and others working at Minong and in Sweden found that tree species differed in their response to browsing; some species increased twig production in response to moderate moose browsing whereas other species decreased production (De Jager 2008, 2009; De Jager and Pastor 2008). Portinga and Moen (2015) found differences in individual twig biomass between species and between open vs. closed canopy conditions within species. It is therefore possible that canopy closure may similarly affect the number of twigs produced.

To better understand the relationship between woody plant characteristics and the production of twigs available to moose, we developed a series of models using data from extensive moose browse vegetation surveys at Gichi Onigaming and Minong. We then verified the models against an independent data set and conducted a simple simulation of the forest management implications of our findings. Finally, we offer a brief worked example of how our models can be applied by field staff to rapidly estimate forage availability in the field. We hypothesized that: H1. Plant-level twig production within the accessible browse zone by trees and tall shrubs has a complex non-linear relationship with plant height, first increasing with height as the plant grows more branches, but then decreasing with height as lower branches senesce and new twigs are out of reach. H2. Plant-level twig production curves vary among species. H3. Plant-level twig production curves vary with forest overstory canopy cover.

STUDY AREAS

Grand Portage Indian Reservation (Gichi Onigaming Ishkonigan)

The Grand Portage Indian Reservation (Gichi Onigaming Ishkonigan in the Anishinaabe language) is located in the northeastern tip of Minnesota, USA (Figure 1). Gichi Onigaming encompasses approximately 22,600 ha of rugged terrain, ranging from 180 m at Lake Superior's shoreline to 550 m on ridge tops. (Kraft et al. 2014). Climate and vegetation are significantly influenced by Lake Superior. Soils originated after the last ice age and consist of red rock outcrops, glacial moraines, and glacial lake superior clay plains (Kraft et al. 2014). Moose are present across the study area (0.27/km^2), but their core range is inland away from Lake Superior (Oliveira-Santos et al. 2021).

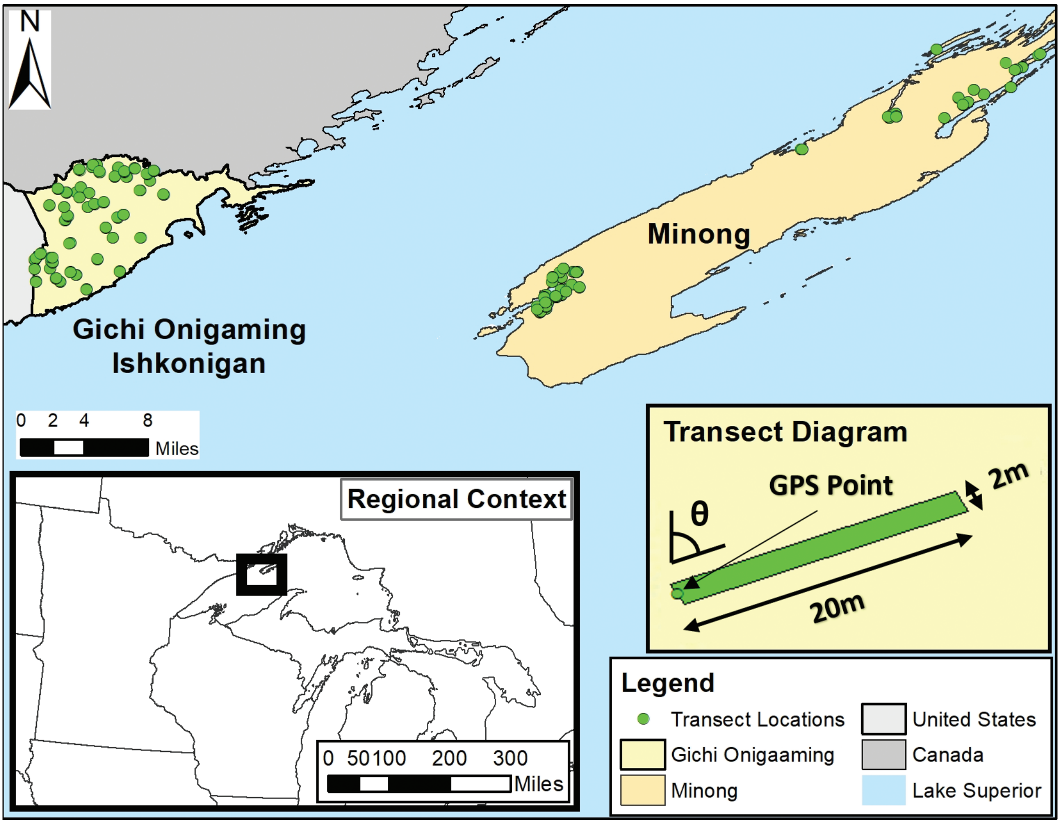

Fig. 1. Map of transect locations at Gichi Onigaming (Grand Portage Indian Reservation, Minnesota, USA) and Minong (Isle Royale, MI, USA) June–September 2019 with regional context and transect diagram (insets).

Gichi Onigaming was about 80% forested and contained several forest cover types. In 2019, quaking aspen-paper birch (*Betula papyrifera;* Wiigwaas) forest represented 56% of forest cover, with the remainder composed of upland spruce-fir (*Picea* spp.- *Abies balsamea***;** *Mina'ig – Zhingob*) forests (~12%), sugar maple (*Acer saccharum*; Ininaatig) forests (~6%), lowland swamp conifers (~5%), white cedar (*Thuja occidentalis*; Giizhik) swamps (~5%), and miscellaneous other forest types (Gichi Onigaming Forestry, unpublished 2019 GIS data). The Gichi Onigaming Forestry Department actively manage Reservation forests for multiple Tribal uses including commercial timber, firewood, moose habitat, and traditional gathering. Forests were managed using timber harvest, prescribed fire, tree planting, and a variety of tree tending practices such as mechanical release, pre-commercial thinning, and pruning.

Isle Royale National Park (Minong)

Part of the ancestral homeland of the Gichi Onigaming Anishinaabeg is Minong (now known as Isle Royale National Park), an archipelago of islands in northwestern Lake Superior near the USA-Canada border. The Gichi Onigaming Anishinaabeg are the historical occupants of Minong and have stewarded it for centuries. This relationship was recognized in 2019 when the Federal Government designated Minong a "Traditional Cultural Property" of the Gichi Onigaming Anishinaabeg (U.S. National

Park Service 2019). Over the last decade, the Gichi Onigaming Anishinaabeg and Isle Royale National Park administration have established a working co-stewardship relationship.

The climate and vegetation of Minong are heavily influenced by Lake Superior. Long ridges and valleys that run the length of the island also influence the vegetation and micro-climate. Forests are a mix of mesic sugar maple, yellow birch (*Betula alleghaniensis*; Wiinizik), and white cedar on the western end of the island, mixed paper-birch spruce-fir forests in the central part of the island, and spruce and fir boreal woodlands on the eastern end of the island and in a narrow band along Lake Superior (Sanders and Kirschbaum 2023). Moose have inhabited the island since the early 1900s and have influenced the vegetation in significant ways through browsing (De Jager et al. 2020). Moose density on Minong was higher than on the mainland during the study period.

The humid influence of Lake Superior, Park Service regulations, and fire suppression have limited the extent and severity of disturbances such as wildfire, timber harvest, and development over the last 85 years. Although wildfires have occurred since 1940, they are not frequent or large (Kraft et al. 2010). Logging and development are prohibited by the Park Service.

METHODS

Sampling Design and Data Collection

Model fitting data: Gichi Onigaming and Minong browse survey data. – We selected potential sampling site polygons in areas known to be used by moose within 400 m of a road or trail to increase survey crew efficiency, stratified to be evenly distributed across cover types, treated/untreated areas, and treatment types. At Minong, accessible moose use areas were stratified by ecosystem group (Nature Conservancy 1999). At Gichi Onigaming, accessible moose use areas were stratified into areas with recent management ("Treated": timber harvest, shearing, planting release, or precommercial thinning) and those without ("Untreated") using 2008–18 Gichi Onigaming treatment history maps (Gichi Onigaming Forestry, unpublished data). Untreated areas were then further stratified by cover type (deciduous forest, evergreen forest, mixed forest, shrub/scrub, woody wetlands) using US National Land Cover Database (Homer et al. 2015) and treated areas by treatment type. Once these strata were identified, at least 3 site polygons were chosen from each stratum using visual selection in ArcGIS Pro such that sites were well distributed across study areas, resembling systematic random sampling. Site polygons ranged from 0.8 ha to 319.7 ha (mean 36.3 ha) at Gichi Onigaming, and from 0.6 ha to 644.7 ha (mean 75.3 ha) at Minong. A minimum of 3 transect start points were visually placed within each site polygon. Start points were placed such that transects would not overlap.

Field crews collected vegetation data at 297 transects across 97 sites (Table 1) between 6 June and 7 September 2019 in Gichi Onigaming, and between 15 July and 2 August 2019 on Minong. Of these, 150 transects across 47 sites were at Gichi Onigaming, and 147 transects across 50 sites were on Minong (Fig. 1). At Gichi Onigaming, one very large treated site contained nine transect start points, and three large treated sites received six transect start points each. Due to human error and difficult terrain, one Minong site had only two transects and another Minong site had only one transect. Map errors during stratification required site reclassification after data collection, resulting in an unbalanced design (Table 1).

Table 1. Cover type and treatment status of moose browse study sites at Gichi Onigaming (Grand Portage Indian Reservation, Minnesota, USA) and Minong (Isle Royale, MI, USA) June–September 2019. Cover types and ecosystems reclassified per Severud et al. (2023) at Gichi Onigaming.

Place	Ecosystem Type	Treated	Cover Type	*n*
Gichi Onigaming	Rock Outcrop	No	Rock Outcrop	2
Gichi Onigaming	Shrub Wetland	No	Alder Swamp	3
Gichi Onigaming	Boreal Forest	No	Mature Boreal Conifer	3
Gichi Onigaming	Boreal Forest	No	Mature Boreal Mix	12
Gichi Onigaming	Boreal Forest	No	Mature Aspen/Birch	2
Gichi Onigaming	Maple Forest	No	Mature Maple Hardwood	3
			Subtotal	25
Gichi Onigaming	Boreal Forest	Yes	Boreal Clearcut	11
Gichi Onigaming	Boreal Forest	Yes	Managed Conifer	10
Gichi Onigaming	Maple Forest	Yes	Maple Clearcut	1
			Subtotal	22
Minong	Wetland Forest	No	White Cedar Swamp	2
Minong	Boreal Forest	No	Mature Boreal Conifer	13
Minong	Boreal Forest	No	Mature Boreal Mix	14
Minong	Boreal Forest	No	Mature Aspen/Birch	7
Minong	Maple Forest	No	Mature Maple Hardwood	14
			Subtotal	50
			Grand Total	97

We established transects (20-m x 2-m) beginning at the start points, with azimuths determined by a random number (0-360) generated on a cell phone application (Fig. 1). We recorded visual estimates of canopy cover to the nearest 5% at the center of each transect. Following Portinga and Moen (2015), plants on transects with 0–50% canopy closure were considered open canopy, and plants from transects with 51–100% canopy closure were considered closed canopy. For each tree within a transect, we recorded the tree species, total height, and total number of twigs. Due to time constraints, full measurements of shrubs were collected on only a subset of transects collected by one crew member. These transects were well distributed across possible sites and transects, resembling systematic random sampling. Of 3,191 observed shrubs, we measured 542 shrubs (17%) across 127 transects on 62 sites (31 on Gichi Onigaming, 31 on Minong). We recorded shrub species, total height, and total number of twigs. Total number of twigs for both trees and shrubs was defined as the count of all twig ends within the browse zone (0.5-2.5 m above the ground), including both intact twig ends and twig ends that had been recently browsed or stripped of leaves. Total height was visually estimated. Trees with foliage overhanging the transect plots were also recorded, even if no twigs were within the browse zone.

Validation data: Gichi Onigaming thinning project monitoring data. – We used an independent, out-of-sample moose browse monitoring data set to assess the validity of our twig production equations. These data were collected during fall 2021 to monitor moose browsing and vegetation response to an experimental pre-commercial aspen strip-thinning treatment conducted at Gichi Onigaming. Thinning sites were high productivity (aspen height at 50 yrs > 21.3 m [70 ft]) young aspen forests that had been clearcut 9-19 years prior and thinned in 2020 or early 2021.

We collected browse monitoring data on 120 transects across 4 sites. At each site, we installed 10 transects in cut strips, 10 transects in leave strips (uncut strips adjacent to cut strips), and 10 transects in control areas (contiguous areas without any treatment), for a total of 30 transects per site. Data were collected similarly to those described above, except that transects were 10 m x 2 m, treated area transects were oriented diagonally across strips, all shrubs were measured, and twigs counts over 15 were estimated to the nearest five twigs.

Statistical Analysis

Regression model forms. – We fit non-linear regression models to our data to determine which relationship with plant height and which species and canopy cover covariates best explained variation in accessible twig production, quantified by total twig count. Candidate model forms (Table 2) were a non-linear unimodal curve representing Hypothesis 1 (unimodal model), an allometric growth curve representing the Grigal and Ohman equations (allometric model), and an intercept only model representing the null hypothesis of no relationship between twigs and height (null model).

We modeled the unimodal non-linear height relationship using a custom variant of the exponentiated exponential function (i.e. $y = \alpha\lambda(1\text{-}e^{-\lambda x})^{\alpha} e^{-\lambda x}$), which is used in survival analysis as an alternative to Weibull and gamma distributions (Gupta and Kundu 2001, Aslam et al. 2010, Nadarajah 2011). For our model, we used an order α = 1 function, exponentiated the x-terms, and added normalizing and scaling parameters (Bolker 2008). Our parameterization took the form:

$$y_{s,i} = 4T_s \left(e^{-(\ln 2)\left(\frac{x_{s,i}}{H_s}\right)^{\frac{c}{\ln\left(1+\frac{B_s}{H_s}\right)}}} - e^{-2(\ln 2)\left(\frac{x_{s,i}}{H_s}\right)^{\frac{c}{\ln\left(1+\frac{B_s}{H_s}\right)}}} \right) \tag{1}$$

where $y_{s,i}$ is the total twig count of observation i of group s, T_s is a fitted coefficient for group s representing the mean peak (maximum) twig count, $x_{s,i}$ is the height (in meters) of observation i of group s, H_s is a fitted coefficient for group s representing the mean height at which twigs peak, B_s is a fitted coefficient for group s representing the mean height increment above peak at which twig production declines by 90% (i.e. the reciprocal of the rate at which twig production declines with height), c is a fixed normalizing coefficient, in this case $c = \ln(5.284428)$ (Supplementary Material 1), $\varepsilon_{(s,i)}$ is the random error of observation i of group s, and s is a group determined by some combination of categorical covariates (e.g. species × canopy). This parameterization allows biologically meaningful comparisons between parameters of differing species or canopy status. It can be mathematically proven that the fitted parameters of equation 1 represent the location of the curve maxima at (H, T) and the height increment after the peak at which twig production declines by 90% (i.e. to 10% of maxima; H+B,0.1T) (Figure 2, Supplementary Material 1).

For the allometric equation representing the Grigal and Ohman (1977) methodology, we used the equation:

$$y_{s,i} = A_s x_{s,i}^{P_s} + \varepsilon_{s,i} \tag{2}$$

Table 2. Candidate models to estimate mean twig count within reach of moose per woody plant from height, species, and canopy cover at Gichi Onigaming (Grand Portage Indian Reservation, Minnesota, USA) and Minong (Isle Royale, MI, USA) June–September 2019. The B coefficient represents the mean height increment above peak to 90% decline in twig production within moose browse zone (i.e. the reciprocal of the rate of decline in twig production with height). Variables are defined as: $y_{s,i}$ is the total twig count of observation i of group s, $x_{s,i}$ is the height (in meters) of observation i of group s, c is a fixed normalizing coefficient, in this case $c = \ln(5.284428)$. Max(y_s) is the maximum observed twig count of group s, and max(x_s, 4) is the maximum observed height of group s or 4, whichever is greater. Possible random error distributions (ε_s) were Poisson, normal with standard deviation σ_s, or negative binomial with size parameter K_s.

Model	Equation	Parameters			
		Symbol	Meaning	Constraints	Maximum Possible Covariates
Unimodal	$y_{s,i} = 4T_s\left(e^{-(\ln 2)\left(\frac{x_{s,i}}{H_s}\right)^{\frac{c}{\ln\left(1+\frac{B_s}{H_s}\right)}}} - e^{-2(\ln 2)\left(\frac{x_{s,i}}{H_s}\right)^{\frac{c}{\ln\left(1+\frac{B_s}{H_s}\right)}}}\right)$	T_s	mean peak twig count	$0.1 \le T \le \max(y_s)$	Species x Canopy
		H_s	mean height at peak count	$0.5\text{ m} \le H \le \max(x_s)$	Species
		B_s	mean height to 90% production decline	$2 \le B_s \le \max(4, x_s)$	Species
	(Eq.1)	$\varepsilon_{s,i}$	random error (K_s or σ_s)	$0.001 \le \sigma_s \le \max(y_s)$ $0.01 \le K_s \le 100$	Species
Allometric	$y_{s,i}= A_s * x_{s,i}\,\hat{}\,(P_s) + \varepsilon_{s,i}$ (Eq.2)	A_s	slope	$0.001 \le A_s \le 100$	Species x Canopy
		P_s	power	$0.001 \le P_s \le 20$	Species
		$\varepsilon_{s,i}$	random error (K_s or σ_s)	$0.001 \le \sigma_s \le \max(y_s)$ $0.01 \le K_s \le 100$	Species
Null	$y_{s,i}= \mu_s + \varepsilon_{s,i}$ (Eq.3)	μ_s	mean twig count	$0.001 \le \mu_s \le \max(y_s)$	Species x Canopy
		$\varepsilon_{s,i}$	random error (K_s or σ_s)	$0.001 \le \sigma_s \le \max(y_s)$ $0.01 \le K_s \le 100$	Species

where $y_{s,i}$, $x_{s,i}$, $\varepsilon_{s,i}$ and s are as above, and A_s and P_s are a fitted allometric coefficients for group s. These coefficients are not comparable to the coefficients of equation 1.

Finally, the null model took the simple form $y_{s,i} = \mu_s + \varepsilon_{s,i}$ where μ_s is the mean of group s and $\varepsilon_{s,i}$ is the random error as above. We considered 3 potential error distributions (ε_s): Poisson, normal with standard deviation σ_s, and negative binomial with size parameter K_s. See below for error distribution selection procedure.

Regression model covariates. – To test hypotheses 2 and 3, we allowed model parameters related to magnitude (T, A, or μ) to vary according to species and canopy cover (open vs. shaded) covariates (group s) (Table 2). Options for magnitude parameter covariates were Species only, Canopy only, Species + Canopy, Species × Canopy, and intercept only. To prevent overfitting of species with small sample sizes, we only allowed curve shape and error distribution parameters to vary with either species or an overall intercept. We defined the fully saturated (i.e., all possible covariates) model as the model where magnitude parameters varied with the species x canopy interaction, and curve shape and error distribution parameters (if present) varied with species.

Regression model fitting and selection. – All models were fit using the maximum likelihood `mle2` function of the R package `bbmle` (Bolker et al. 2023), the package

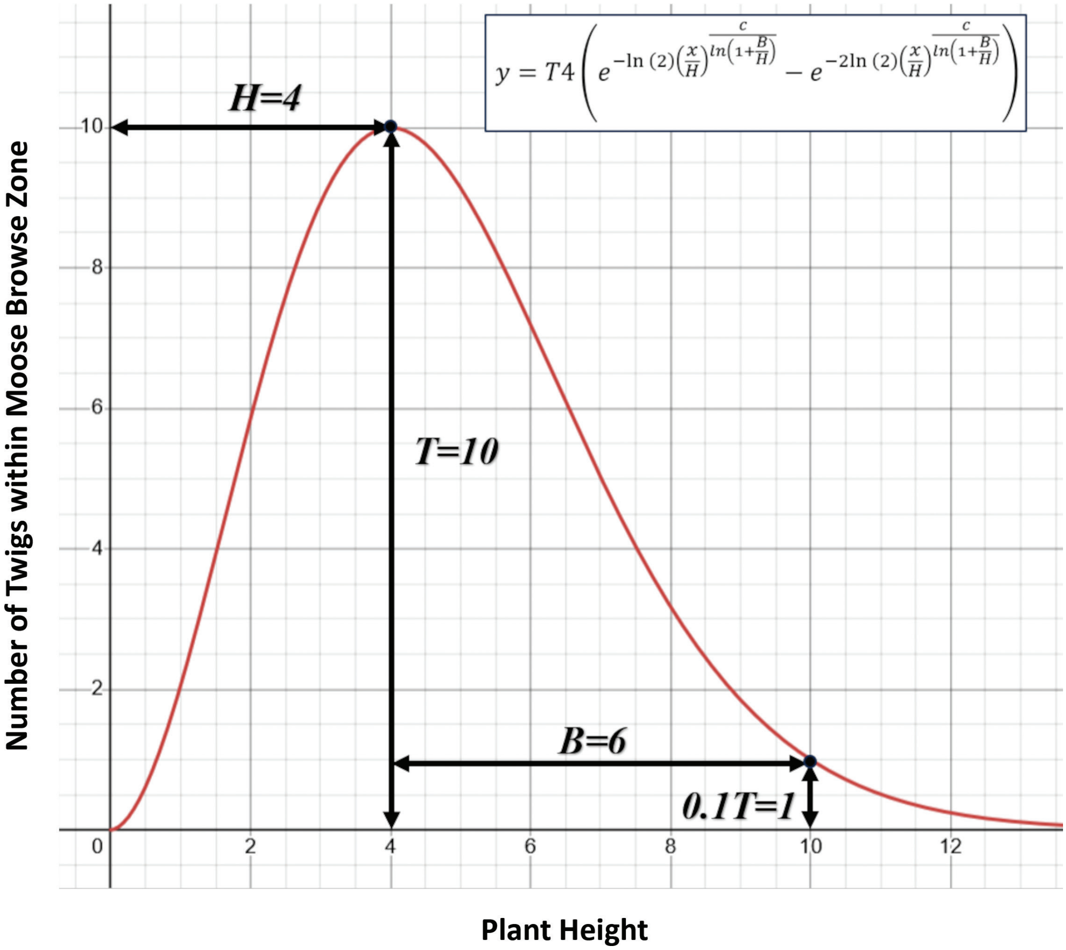

Fig. 2. Interpretations of the parameters (*T*, *H*, *B*) and locations of critical points of Equation 1. Small *B* values indicate a high rate of production decline with height. Large *B* values indicate a low rate of production decline with height.

`optimx` (Nash 2014), and the L-BFGS-B bounded optimizing algorithm (Byrd et al. 1995). Models were evaluated using Akaike's Information Criterion for small sample sizes (AIC$_c$; Burnham and Anderson 1998). Before fitting, we dropped species with fewer than 10 observations to prevent model non-convergence. We constrained model parameters between lower and upper bounds (Table 2) to ensure model convergence and keep parameters within observed values (Table 3). Notably, constraints of 2 and 4 for *B* prevented extreme values that crashed the statistical software.

Fitting occurred in two stages following Zuur et al. (2009) and Bolker (2008): 1) error distribution fitting; 2) backwards selection of covariates. In the first stage, we fit a fully saturated version of each of the 3 model forms with the 3 possible random error distributions (Poisson, normal, or negative binomial). We then selected the best fit random error distribution for each of the 3 model forms using AIC$_c$. In the second stage, we performed backwards selection separately on each of the three fully saturated model forms with the error distribution selected in the first stage. Each possible

Table 3. Summary statistics of tree and shrub data used to fit models from moose browse study sites at Gichi Onigaming (Grand Portage Indian Reservation, Minnesota, USA) and Minong (Isle Royale, MI, USA) June–September 2019.

Species Common Name	Species Scientific Name	*n*	Height (m)				Twigs Per Plant			
			Med†	*σ*	Min	Max	Med†	*σ*	Min	Max
Balsam Fir	*Abies balsamea*	2092	1.00	2.3	0.1	20	8	27.0	0	240
Red Maple	*Acer rubrum*	24	1.90	1.7	0.5	5	24	20.1	4	102
Sugar Maple	*Acer saccharum*	1217	0.60	1.9	0.1	18	4	10.1	0	110
Mountain Maple	*Acer spicatum*	1709	0.80	1.1	0.1	8	6	11.0	0	114
Alder Spp.	*Alnus* spp.	35	4.00	2.1	0.5	8	10	13.3	0	52
Juneberry Spp.	*Amelanchier* spp.	83	1.20	0.7	0.3	3	5	11.2	0	46
Yellow Birch	*Betula alleghaniensis*	197	1.30	2.8	0.5	15	8	10.1	0	91
Paper Birch	*Betula papyrifera*	446	2.00	4.2	0.2	25	16	38.3	0	400
Beaked Hazelnut	*Corylus cornuta*	66	1.00	0.9	0.2	6	12	18.4	0	122
Red Osier Dogwood	*Cornus sericea*	59	1.20	0.2	0.4	1.2	5	2.5	1	21
Hawthorn	*Crataegus* spp.	16	0.90	1.7	0.5	7	6	5.5	2	19
Bush Honeysuckle	*Diervilla lonicera*	64	0.50	0.1	0.5	1	3	9.1	1	51
Black Ash	*Fraxinus nigra*	249	1.50	3.3	0.2	18	14	19.4	0	142
Canada Honeysuckle	*Lonicera canadensis*	27	1.00	0.4	0.5	1.8	6	13.0	3	70
White Pine	*Pinus strobus*	20	2.00	2.2	0.2	8	30	47.9	0	150
Balsam Poplar	*Populus balsamifera*	33	1.50	1.6	0.5	8	11	15.6	3	74
Quaking Aspen	*Populus tremuloides*	948	2.00	3.7	0.1	20	8	15.3	0	113
Fire Cherry	*Prunus pensylvanica*	62	1.25	0.9	0.3	5	13	20.8	0	100
Chokecherry	*Prunus virginiana*	176	1.00	1.2	0.2	7	13.5	14.6	1	104
Willow Spp.	*Salix* spp.	22	1.75	1.8	0.5	6	16	16.0	0	52
Red Elderberry	*Sambucus racemosa*	10	1.50	0.9	0.6	4	12	5.1	1	18
Mountain Ash	*Sorbus* spp.	776	0.70	0.7	0.1	7	4	5.0	1	47
White Cedar	*Thuja occidentalis*	187	1.50	3.3	0.3	20	12	28.0	0	230

†Median

categorical covariate (or interaction) was sequentially removed from each parameter of each model form and the results evaluated by AIC$_c$. The variable removal with the greatest improvement in fit was selected, and the process repeated until no more variables could be removed without worsening fit. If removing a variable did not worsen fit by more 2 AIC units, we considered that variable uninformative and removed it (Arnold 2010).

Moose browsing preferences. – To aid interpretation of our results, we classified tree and shrub species by moose browse preferences reported by Portinga and Moen (2015; Tables 1, 8), realizing this is a coarse filter and many finer-scale variables influence forage quality. For simplicity, we synthesized summer and winter preferences to classify overall preference. Species used significantly more often than available in at least one season were classified as preferred. Species not used significantly more often than available in at least one season and used according to abundance in at least one season were classified as neutral. Species appearing in Portinga and Moen (2015; Tables 1, 8) and not classified as preferred or neutral were classified as avoided/rarely used. Species not included in Portinga and Moen (2015; Tables 1, 8) were classified as not evaluated.

Within sample model assessment. – We assessed in-sample accuracy and precision by calculating the bias (mean error), RMSE (standard deviation of the error), Pearson correlation, and a pseudo-R^2 (square of Pearson correlation) for the best fit model and leading alternative models. We calculated approximate RMSE confidence intervals using the square root of variance confidence intervals $[((n-1)*\sigma^2)/\chi^2_{(0.975,(n-1))} \leq \sigma^2 \leq ((n-1)*\sigma^2)/\chi^2_{(0.025,(n-1))}]$. Differences in bias and RMSE between alternative models were assessed using repeated measures analysis of variance (ANOVA), Mauchley's test for sphericity, and post-hoc t-tests in R package `rstatix` (Kassambara 2023). To control for the false discovery rate of multiple comparisons, we used the YB correction (Benjamini and Yekutieli 2001).

Production differences among species and canopy cover. – To understand twig production differences between species and canopy cover, we conducted post-hoc comparisons on parameters from the final model using the `glht` and `cldList` functions in the `multcomp` and `rcompanion` R packages, respectively (Hothorn et al. 2023, Mangiafico 2024). To control for multiple comparisons, we used the fdr method (Benjamini and Hochberg 1995) for comparisons between species and the YB method for canopy comparisons within species.

Out-of-sample model validation. – To validate the model, we applied the final model equations to the independent Gichi Onigaming thinning project browse monitoring data and evaluated out-of-sample model performance at the population level. Regression equations have at least 2 sources of error: the prediction error of individual observations and the estimation error of population parameters (Pardoe 2020). In applications such as monitoring concerned with population means, individual observation errors are unimportant because opposing errors cancel out. Therefore, we evaluated performance at the population level using summed transect data. We used open canopy equation coefficients for cut strips, closed canopy equation coefficients for leave strips and control areas. We evaluated the accuracy and precision of the best fit model and alternative models using the same statistical measures as within-sample model assessment, as well as by fitting linear regression lines to the modeled vs. observed data.

All data analyses were conducted in the R statistical environment version 4.3.3 (R Core Team 2024). We determined significance according to $P < 0.05$ and estimated 95% confidence intervals.

Simulation of Forest Management Implications

To understand the forest management implications of our results, we coupled our moose forage equations with tree age-height curves to simulate forage dynamics over time for three tree species (quaking aspen, paper birch, and red maple (*Acer rubrum*; *Zhiishiigimewanzh*) known to be preferred by moose (Irwin 1985, Portinga and Moen 2015). For simplicity, we assumed pure even-aged stands with no understory shrubs and no tending treatments. We used site index equations for the lake states (Michigan, Minnesota, Wisconsin) to model tree height growth as a function of age and site quality (Carmean et al. 1989). We assumed an aspen site index of 18.3 m (60 ft) at 50 years, typical of average sites in northeastern Minnesota, and calculated equivalent site indexes for other species using equations in Carmean et al. (2013). We assumed initial stem densities and mean annual self-thinning mortality rates (Supplementary Material 2, Table S2.1) based on USFS silviculture guides (Leak et al. 1969, Perala 1977, Safford 1983). We multiplied twig densities by estimates of average mass per twig (Portinga and Moen 2015) to calculate forage biomass densities for both winter and summer. We compared simulation results to a published minimum forage density threshold for moose use of 50 kg/ha (Allen et al. 1987).

RESULTS

We identified and modeled 23 species (11 trees and 12 shrubs) from 8,518 total observations (Table 3). Trees and shrubs were identified to species-level except for willows (*Salix* spp., Oziisigobiminzh), juneberries (*Amelanchier* spp.; Gozigwaakominagaawanzh; alders (*Alnus* spp.; Wadoop), hawthorns (*Crataegus* spp.; Miinensagaawanzh), and mountain ash (*Sorbus* spp.; Makominagaawanzh), which were identified to genus only.

Best Fit Model: Relationship Between Twig Production and Covariates

Negative binomial error distributions fit best across all 3 model forms (Table 4). The unimodal model best described the relationship between twig production and woody plant height (Table 5). The top 3 unimodal models fit better than the best allometric or null models in all cases and by a large margin (Table 5).

The saturated unimodal model fit best overall, indicating that peak number of twigs per plant (*T*) varied with the interaction between canopy and species, and all other parameters (*H*, *B*, *K*) varied by species (Figure 3, Table 5). The saturated model fit significantly better than the next closest model (Likelihood ratio test $\chi^2 = 218.74$, $P < 0.001$). The saturated unimodal model had a moderately strong correlation between observed and predicted data (0.58 ± 0.02), explained roughly a third of the observed variance, and had a higher correlation than the saturated allometric or null models (Supplementary Material 3, Table S3.1). RMSE varied significantly among models (Mauchley's test $w = 0.39$, $P < 0.001$), and the unimodal model had the lowest RMSE among models (Table S3.1).

Bias differed significantly among models (repeated measures ANOVA $F = 10.5$, $adj.DFn = 1.93$, $adj.DFd = 16428.7$, $P < 0.001$). Bias was not significant for the unimodal and null models (Supplementary Material 3, Table S3.2). The allometric model had significant over-estimation bias and significantly greater bias than the unimodal and null models. Unimodal model bias and RMSE varied among species (Table 6). Species-level bias ranged from + 0.99 for juneberry to -1.08 for red elderberry (*Sambucus racemosa*; Bibigwewanashk), but was not significant for any species.

Table 4. Measures of fit (AIC_c) of 3 error distributions applied to 3 models used to estimate mean twig count within reach of moose per woody plant at Gichi Onigaming (Grand Portage Indian Reservation, Minnesota, USA) and Minong (Isle Royale, MI, USA) June–September 2019. All models fit with fully saturated parameter covariates (see text).

	Model		
	Unimodal	Allometric	Null
Error Distribution	AIC_c	AIC_c	AIC_c
Negative Binomial	55,287.7	56,725.6	59,594.7
Normal	66,396.9	68,186.2	69,853.1
Poisson	109,710.8	132,381.4	156,544.8

Table 5. Measures of fit (AIC$_c$ and likelihood ratio tests) for models and parameter covariates used to estimate mean twig count per plant within moose browse zone at Gichi Onigaming (Grand Portage Indian Reservation, Minnesota, USA) and Minong (Isle Royale, MI, USA) June–September 2019. Only the top three models for each equation form are displayed. *K* is the size parameter of the negative binomial distribution, df is number of model parameters. χ^2, Δdf, and *P*-value are for the likelihood ratio tests for difference between top 3 models (1 vs. 2 and 1 vs.3).

Equation Form	Parameter Covariates				Model Fit					
	T	*H*	*B*	*K*	df	AIC$_c$	ΔAIC$_c$	Chi-Sq	Δdf	*P*
Unimodal	Spp x Canopy	Spp	Spp	Spp	115	55,288	0			
Unimodal	Spp + Canopy	Spp	Spp	Spp	93	55,461	174	218.7	22	<0.001
Unimodal	Spp x Canopy	Spp	1	Spp	93	55,675	387	432.3	22	<0.001
	A	P		K						
Allometric	Spp x Canopy	Spp		Spp	92	56,726	1,438			
Allometric	Spp + Canopy	Spp		Spp	70	56,959	1,671			
Allometric	Spp x Canopy	1		Spp	70	57,022	1,735			
	μ			*K*						
Null	Spp x Canopy			Spp	69	59,595	4,367			
Null	Spp + Canopy			Spp	47	59,757	4,529			
Null	Spp x Canopy			1	47	60,382	5,153			

Of 23 modeled species, all coefficients were within bounds for 11 species, indicating good predictive value (Table 6). Eight species had *B* coefficients (rate of decline with height) at an upper bound and other coefficients within bounds, indicating reasonable predictive value except at large heights (Table 6). The remaining 4 shrub species (red osier dogwood [*Cornus sericea*; Miskwaabiimizh], hawthorn, red elderberry [*Sambucus racemosa*; Bibigwewanashk], and bush honeysuckle [*Diervilla lonicera*]) had 2 coefficients at a bound, indicating limited predictive or inferential value (Table 6). Of these, bush honeysuckle had a *B* coefficient with an undefined standard error, indicating poor model convergence for this species.

Differences in Peak Twig Production (*T*) Between Species and Canopy Cover

Peak number of twigs was significantly greater in the open than under shade for 7 species (mountain maple, quaking aspen, mountain ash, balsam fir, black ash (*Fraxinus nigra*; Baapaagimaak), white cedar, yellow birch; Figure 4, Table 6). There was no significant difference in peak twig production between open and closed canopy for the other 16 species.

Under open canopy conditions, mean peak number of twigs per plant (T_{open}) varied considerably among species, with seven species having greater peak production than aspen. In the open, 3 preferred species (paper birch, red maple, chokecherry (*Prunus virginiana*; Asasaweminagaawanzh) and 4 avoided

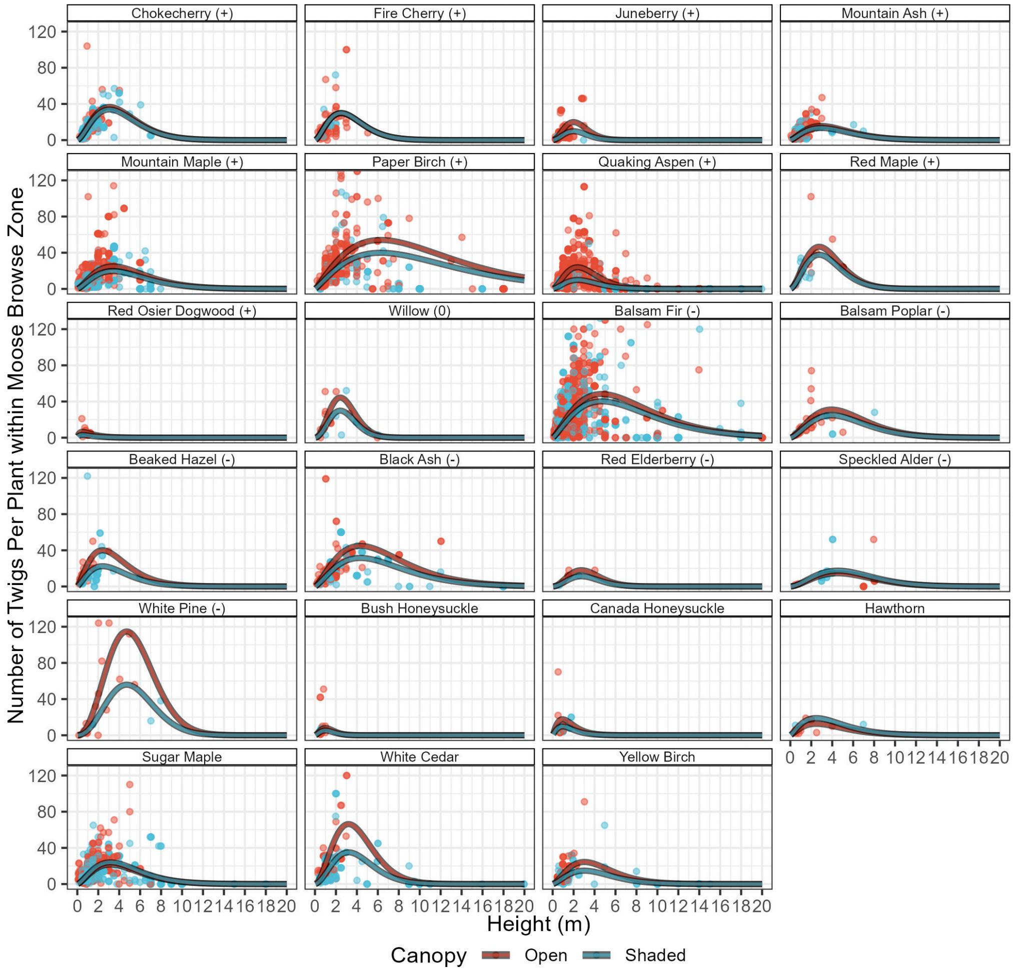

Fig. 3. Observed data and best fit model prediction of mean number of twigs per plant within moose browse zone as a function of height, species, and canopy cover at Gichi Onigaming (Grand Portage Indian Reservation, Minnesota, USA) and Minong (Isle Royale, MI, USA) June-September 2019. Point color intensity is proportional to number of observations. Canopy cover is open (0-50%) or shaded (51-100%). Equation is $y = 4T(\exp(-\ln(2)(x/H)\text{\textasciicircum}(c/\ln(1+B/H))) - \exp(2\ln(2)(x/H)\text{\textasciicircum}(c/\ln(1+B/H))))$, where y is mean number of twigs per plant, x is total height in meters, and coefficients are in Table 6. Symbols after species names indicate moose preference (+), proportional use (0), avoidance/rare use (-) or not evaluated (no symbol) in Portinga and Moen (2015). Observations beyond $x = 20$ and $y = 120$ not shown.

or not evaluated species (white pine, balsam fir, white cedar, black ash) had a significantly greater peak number of twigs than quaking aspen (Figure 4, Table 6). Of these, paper birch, white pine, and white cedar were the most productive. In the open, one preferred shrub (mountain ash) had a significantly lower peak number of twigs than quaking aspen.

Under a shaded canopy, mean peak number of twigs per plant (T_{closed}) also varied considerably among species. Six preferred species (paper birch, red maple, chokecherry, fire cherry (*Prunus pensylvanica*; Bawa'iminagaawanzh), mountain maple, mountain ash), 3 avoided species (balsam fir, black ash, beaked hazel), and 2 not

Table 6. Coefficients (β) and standard errors (SE) and RMSE of best fit unimodal regression equation to predict mean number of twigs per plant within moose browse zone as a function of height, species, and canopy cover at Gichi Onigaming (Grand Portage Indian Reservation, Minnesota, USA) and Minong (Isle Royale, MI, USA) June–September 2019.

Species	T (Open)		T (Shaded)		ΔT			H		B		K		Error	
Common Name	β	SE	β	SE	$\Delta\beta$	SE	p	β	SE	β	SE	β	SE	*RMSE*	Bias
Balsam Fir	48.3	2.3	40.2	2.2	8.1	2.0	0.003	4.7	0.1	12.5	0.6	1.1	0.0	23.1	-0.32
Red Maple	46.5	8.4	37.7	10.4	8.8	10.5	1.000	2.8	0.2	4.9	1.1	5.5	1.9	16.3	0.05
Sugar Maple	21.6	1.1	24.0	1.3	-2.4	1.1	0.206	3.2	0.1	7.0	0.3	2.6	0.1	8.0	-0.17
Mountain Maple	25.0	0.9	19.7	0.7	5.3	0.8	< 0.001	3.4	0.1	8.0#	0.5	3.7	0.2	8.6	-0.17
Speckled Alder	14.5	8.1	17.5	3.8	-2.9	9.4	1.000	4.5	0.9	8.0#	3.2	1.2	0.4	12.4	0.26
Juneberry Spp.	19.9	3.2	9.8	3.6	10.1	3.7	0.079	2.0	0.2	3.0#	0.5	1.4	0.3	11.1	0.99
Yellow Birch	24.4	3.7	14.8	1.7	9.6	2.9	0.016	3.0	0.2	6.5	0.6	2.5	0.3	8.9	0.17
Paper Birch	54.1	5.1	39.9	4.8	14.2	5.2	0.076	6.3	0.3	19.0	1.7	1.0	0.1	34.2	-0.98
Beaked Hazelnut	40.0	10.3	22.4	3.4	17.6	9.1	0.430	2.4	0.4	6.0#	1.5	2.0	0.4	17.3	0.51
Red Osier Dogwood	6.4	1.1	3.0	1.8	3.4	2.1	0.656	0.5#	0.2	3.0#	1.1	56.4	68.3	2.4	0.00
Hawthorn	12.6	2.6	19.0#	6.1	-6.4	6.2	1.000	2.5	0.3	7.0#	1.3	6.3	4.6	4.5	-0.78
Bush Honeysuckle	7.9	2.0	5.3	1.7	2.7	1.6	0.656	1.0#	0.3	2.0#	NA	1.6	0.3	8.9	-0.09
Black Ash	44.9	4.3	31.5	2.7	13.4	3.7	0.009	4.3	0.2	10.8	0.8	2.4	0.2	16.9	0.47
Canada Honeysuckle	17.7	7.0	9.7	2.3	8.0	8.1	1.000	0.9	0.5	3.0#	1.1	1.7	0.5	13.3	0.74
White Pine	114.7	35.8	55.9	30.9	58.9	41.8	0.925	4.7	0.6	5.6	1.7	1.7	0.6	32.5	0.90
Balsam Poplar	31.1	7.9	24.6	7.9	6.4	11.1	1.000	3.9	0.6	8.0#	1.8	2.7	0.7	14.4	0.60
Quaking Aspen	23.9	1.1	9.9	1.2	14.0	1.5	< 0.001	2.4	0.1	4.5	0.2	1.1	0.1	13.0	-0.18
Fire Cherry	29.7	4.7	29.9	8.2	-0.2	8.3	1.000	2.5	0.4	5.0#	1.5	1.8	0.3	18.9	0.34
Chokecherry	36.6	3.6	33.9	2.7	2.8	3.1	1.000	3.1	0.2	6.2	0.8	4.3	0.6	11.5	0.16
Willow Spp.	44.3	16.6	29.9	9.8	14.5	19.2	1.000	2.4	0.3	3.2	0.5	2.4	0.9	13.2	0.65
Red Elderberry	18.0#	3.1	11.3	3.5	6.7	4.2	0.656	2.7	0.2	4.0#	1.2	66.0	77.7	2.4	-1.08
Mountain Ash	15.6	0.9	13.5	0.7	2.2	0.6	0.009	2.9	0.1	7.0#	0.6	8.8	1.1	3.7	0.00
White Cedar	66.3	11.0	35.1	4.4	31.2	9.6	0.018	3.2	0.1	5.3	0.3	1.4	0.2	23.5	0.66

Equation is $y = 4T(\exp(-\ln(2)(x/H)^\wedge(c/\ln(1+B/H))) - \exp(-2\ln(2)(x/H)^\wedge(c/\ln(1+B/H))))$ where y is mean number of twigs per plant, x is height in meters, T is the mean peak number of twigs per plant for the species and canopy combination, H is the mean height at which number of twigs peak, B is the mean height increment above peak to 90% decline in twig production (i.e. the reciprocal of the rate of decline in twig production with height), and $c = \ln(5.284428)$. K is the dispersion parameter of negative binomial error. Canopy cover is defined as open (0-50%) or shaded (51-100%). ΔT values are post-hoc comparisons corrected by Benjamini-Yekutieli (BY) method. Underlined ΔT values significant ($p < 0.05$). Underlined β values not significantly different from zero ($p > 0.05$). "#" indicates coefficient at boundary. "NA" indicates undefined.

evaluated species (white cedar, sugar maple) had significantly greater peak production than quaking aspen under canopy shade (Figure 4, Table 6).

Species Differences in Height at Peak Production (*H*)

Mean height at peak number of twigs per plant (*H*) varied considerably among species, with most species having a greater mean height at peak than aspen. Five preferred or used species (paper birch, mountain maple, chokecherry, mountain ash, willow), and 8 avoided or not evaluated species (white pine, balsam fir, speckled alder, black ash, balsam poplar, white cedar, sugar maple, yellow birch) had significantly greater mean height at peak than quaking aspen (Figure 5, Table 6). One preferred shrub (juneberry) and 1 not evaluated shrub species (Canada honeysuckle) had significantly lower height at peak than quaking aspen.

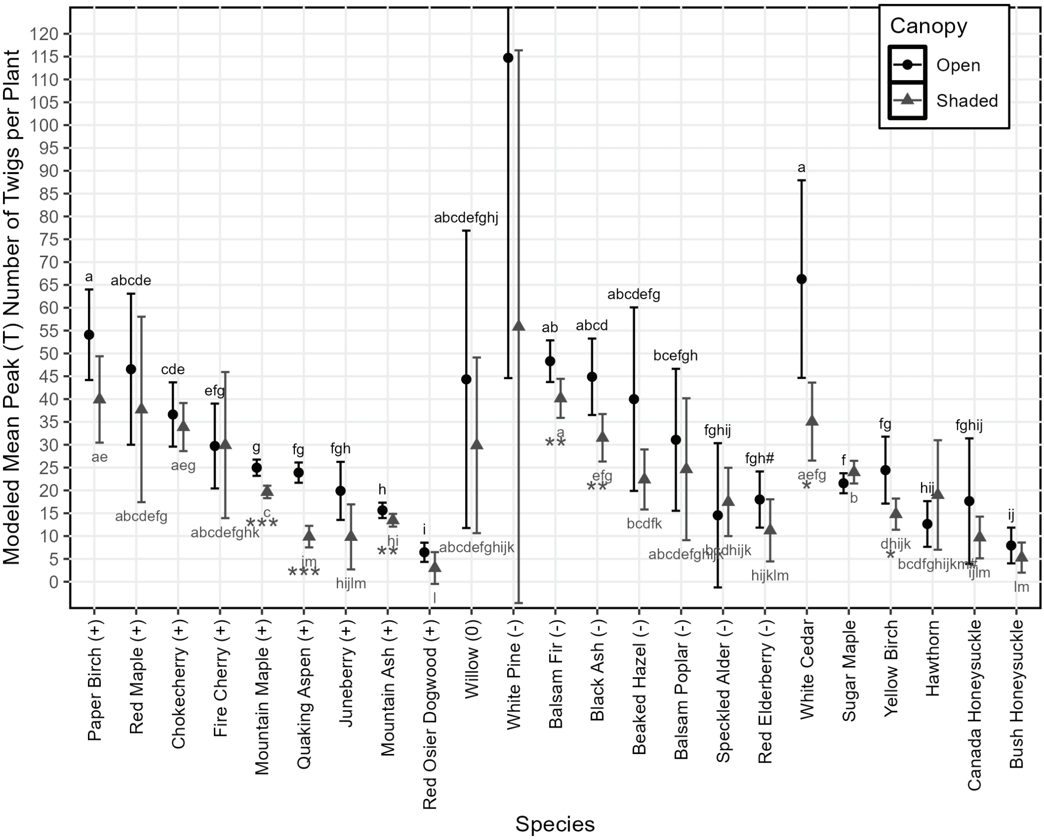

Fig. 4. Modeled peak (*T*) of mean number of twigs per plant within moose browse zone by species and canopy cover at Gichi Onigaming (Grand Portage Indian Reservation, Minnesota, USA) and Minong (Isle Royale, MI, USA) June–September 2019. Symbols after species names indicate moose preference (+), proportional use (0), avoidance/rare use (-) or not evaluated (no symbol) in Portinga and Moen (2015). Letters indicate differences between species within the same canopy condition. Species not sharing any letter are different by Tukey-test with "fdr" correction ($P < 0.05$). Asterisks indicate differences between open and shaded conditions within species by Tukey-test with "YB" correction (*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$). "#" indicates estimate at boundary.

Species Differences in Rate of Twig Decline with Height (*B*)

Among species with *B* coefficients within the range of observed values, one preferred tree (paper birch) and five avoided or not evaluated trees (balsam fir, black ash, sugar maple, and yellow birch) had significantly greater *B* coefficients than aspen, indicating lower rates of twig decline with height. One neutral shrub (willow) had a significantly lower *B* coefficient than aspen (Figure 6, Table 6), indicating a higher rate of twig decline with height. Among species with *B* coefficients at the boundary, indicating limited inferential value, mountain maple and mountain ash had a greater *B* coefficient than aspen, whereas juneberry had a lower *B* coefficient than aspen.

Out-of-Sample Model Validation at the Population Level

The validation data set contained 18 of the 23 species fit in the original model, and bias and RMSE could be assessed for 17 species (Supplementary Material 4, Table S4.3). Unimodal estimates of out-of-sample number of twigs per transect explained 54.7% of the variance (Figure 7, Supplementary Material 4, Table S4.1). Correlations were higher for the unimodal model than the allometric and null models, although confidence intervals overlapped. Population level out-of-sample RMSE differed significantly among models (Mauchley's test $w = 0.249$, $p < 0.001$). Unimodal model RMSE was greater than the null model and less than the allometric model.

All models had significant out-of-sample overprediction bias at the population level (Figure 7, Supplementary Material 4, Table S4.2,). Bias differed significantly among models (repeated measures ANOVA $F = 183.9$, $adj.DFn = 1.7$, $adj.DFd = 207.1$, $P < 0.001$). The unimodal model had significantly higher bias than the null model and significantly lower bias than the allometric model. Out-of-sample bias and RMSE varied between species (Table S4.3). Overestimation bias was significant for 12 of 17 species.

Simulation Model Results

Simulation results for pure even-aged stands of 3 preferred forage species on average sites indicated that whereas quaking aspen produced ~1.4-2.2 times more peak forage biomass than paper birch or red maple, paper birch and red maple produced usable forage densities for ~1.2-2.9 times longer (Table 7, Figure 8). In summer, quaking aspen had the highest, red maple the middle, and paper birch the lowest peak forage density. Summer paper birch forage was above the usable density threshold for 26 years, red maple for 15 years, and aspen for 10 years. In winter, quaking aspen had the highest, paper birch the middle, and red maple the lowest peak forage density. Winter paper birch forage was above the usable density threshold for 26 years, red maple for 11 years, and aspen for 9 years.

DISCUSSION

This study and its implications support the cultural and ecological stewardship priorities of the Gichi Onigaming Anishinaabeg to advance moose restoration. This study's species-specific twig production models offer a tool to evaluate and anticipate how different forest treatments influence moose forage dynamics over time, thereby supporting Indigenous-led strategies that seek to balance biodiversity, habitat health, and cultural continuity. Moose are a key species ecologically and foundation of Indigenous food sovereignty, ceremonial practice, and intergenerational knowledge transmission (Stults et. al 2016, Garwood et al. 2023, Moore et al. 2024, Severud et al. 2023). Forest management decisions involving timber harvest and post-disturbance regeneration have significant implications for the viability of culturally essential moose populations.

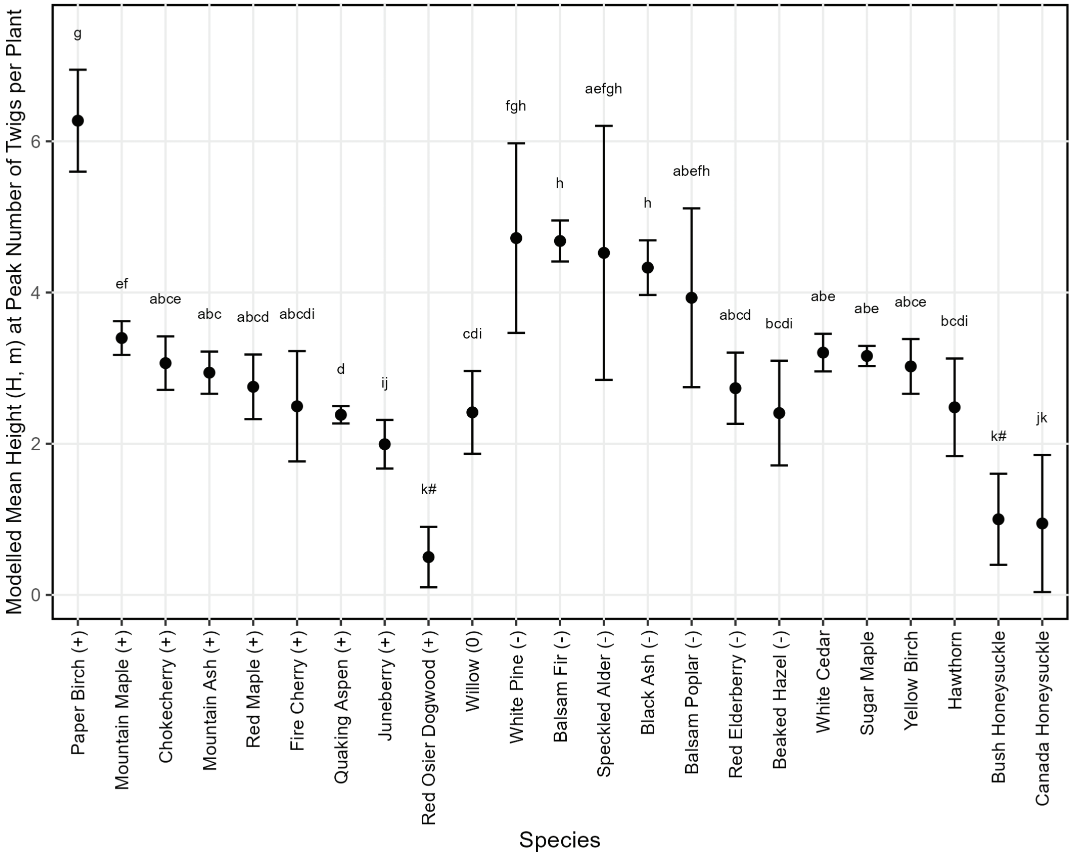

Fig. 5. Modelled mean height (*H*) at peak number of twigs per plant within moose browse zone by species at Gichi Onigaming (Grand Portage Indian Reservation, Minnesota, USA) and Minong (Isle Royale, MI, USA) June-September 2019. Species not sharing any letter are significantly different by Tukey-test ($P < 0.05$) with "fdr" correction. "#" indicates estimate at boundary. Symbols after species names indicate moose preference (+), proportional use (0), avoidance/rare use (-) or not evaluated (no symbol) in Portinga and Moen (2015).

Differences in Available Twig Production Between Species

We have shown that production of twigs available to moose varies considerably among tree and shrub species (H2); that twig production is sometimes greater under open canopies (H3); that twig production increases, peaks, then declines as stem height increases (H1); and that the rate of decline with height varies somewhat among species (H1 and H2). Paper birch and balsam fir generally had the greatest peak twig production, greatest heights at peak production, and slowest rates of production decline. In contrast, quaking aspen generally had lower peak twig production, lower height at peak production, and faster rates of decline with height than most other trees and some tall shrubs. Two large shrubs (mountain maple, fire cherry) often preferred by moose (Miquelle and Jordan 1979, Belovsky 1981, Irwin 1985, Ricard and Doucet 1999, Portinga and Moen 2015) also performed favorably compared to quaking aspen. Mountain maple had similar peak twig production under open canopies, greater peak production under closed canopies, and greater height at peak production compared to aspen. Fire cherry had similar peak twig production

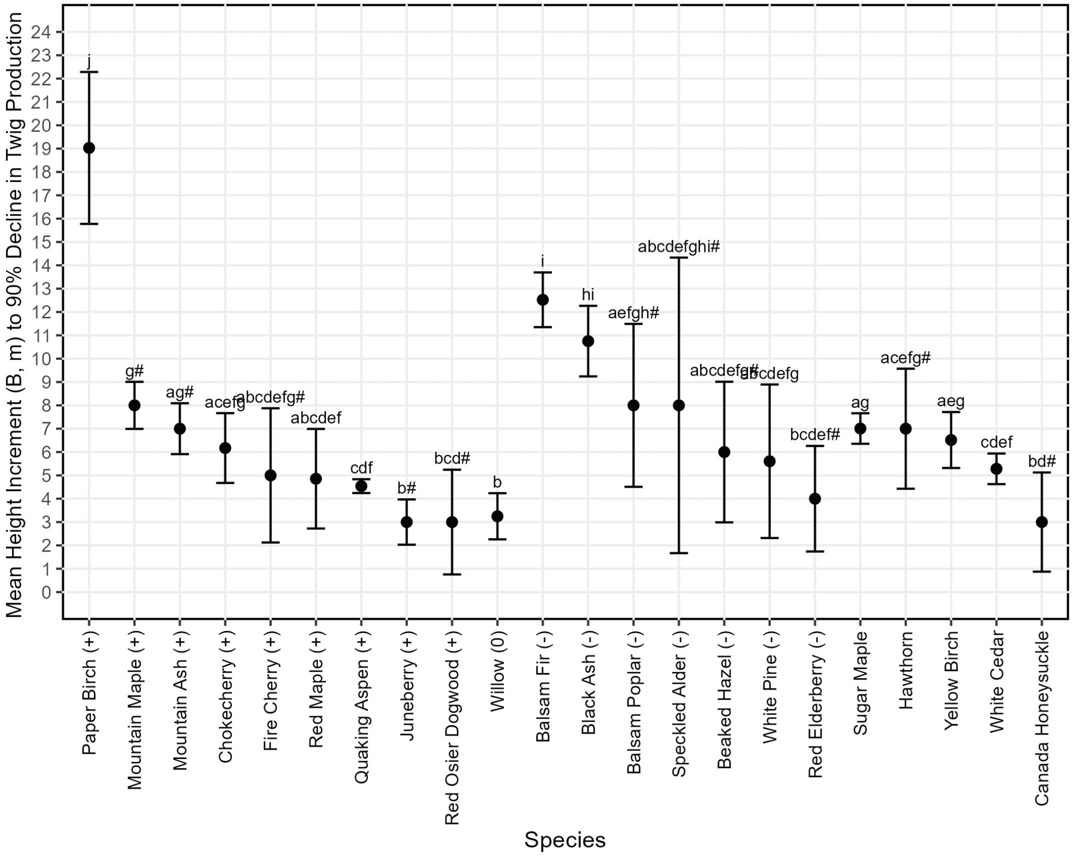

Fig. 6. Height to 90% production decline (*B*) by species at Gichi Onigaming (Grand Portage Indian Reservation, Minnesota, USA) and Minong (Isle Royale, MI, USA) June-September 2019. The *B* coefficient represents the mean height increment above peak to 90% decline in twig production (i.e. the reciprocal of the rate of decline in twig production with height). Species not sharing any letter are significantly different by Tukey-test ($p < 0.05$) with "fdr" correction. "#" indicates estimate at boundary. Bush honeysuckle excluded because estimate had undefined standard error. Symbols after species names indicate moose preference (+), proportional use (0), avoidance/rare use (-) or not evaluated (no symbol) in Portinga and Moen (2015).

under open canopies, greater peak production under closed canopies, and similar heights at peak production compared to aspen. This suggests that these shrubs, with typically slower height growth than aspen and ability to persist in the understory, have the potential to be significant and long persisting sources of preferred moose browse.

Our twig production model appears reasonably consistent with observed growth-form characteristics of many tree and shrub species. The low peak twig production and rapid decline in twig production of quaking aspen among deciduous trees is consistent with findings that aspen have strong apical dominance (Farmer 1962), tend toward vertical rather than horizontal canopy extension when young (Harper 2008) and self-prune lower branches more rapidly than other species (Puettmann and Reich 1995). In contrast, conifers such as balsam fir and white cedar have conical crown structure

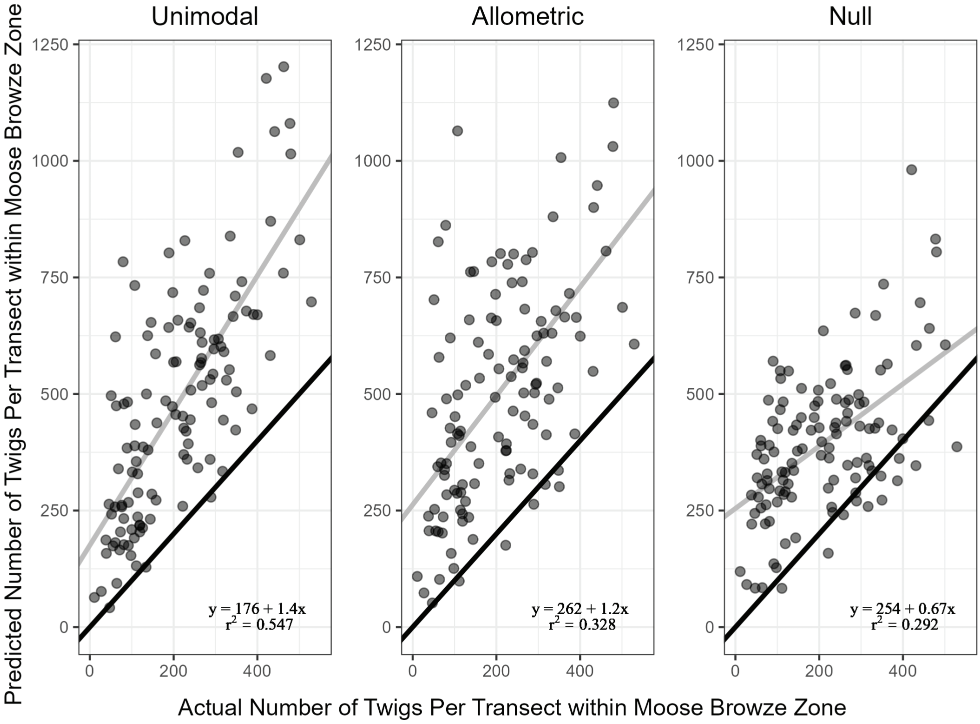

Fig. 7. Comparison of predictions by the 3 alternative models with out-of-sample (validation) observations of number of twigs per transect within moose browse zone at Gichi Onigaming (Grand Portage Indian Reservation, Minnesota, USA), September 2021. Black line is 1:1 line. Gray line is the predicted regression line, with regression equation and coefficient of determination listed on plot.

and tend to retain their lower branches. White pine also has a conical crown and tends to delay self-pruning until at least 15 years old, after which it may self-prune aggressively (Burns and Honkala 1990). Moreover, evergreen conifer needles live longer than deciduous leaves. Theoretically, these factors together should result in more twigs within the browse zone. The higher peak twig production for these species in our model is consistent with this observation (Figure 3, Table 6). Similarly, the slow decline in twig production of balsam fir relative to other trees in our model (Figure 5) is consistent with the field observation that, of these three conifers, balsam fir tends to retain its lower branches the longest, retaining some lower twigs even at very tall heights. This may be in part due to the extremely high shade tolerance of balsam fir. Other studies have found that shade tolerant evergreens tend to maximize leaf longevity to survive under low light conditions (Walters and Reich 1999).

Although somewhat surprising for an early successional species, the high peak twig production and slower decline in twig production of paper birch is also consistent with the known biology of paper birch. When grown on the same site, paper birch generally have slower height growth than quaking aspen (Carmean et al. 2013), suggesting less allocation of resources to height growth. Moreover, paper birch also produce abundant stump and epicormic sprouts when stressed or harvested (Burns and Honkala 1990). Based on field observations, we further speculate that although paper birch self-prune (Zenner and Puettmann 2008), they may do so more slowly than aspen.

Table 7. Comparison of simulated forage density (kg/ha) from ages 0-30 years between paper birch, quaking aspen, and red maple in winter and summer for aspen site index of 18.3 m (60 ft) at 50 years in northeastern Minnesota using best-fit unimodal model.

Species	Summer			Winter		
	First Year ≥ 50 kg/ha	Last Year ≥ 50 kg/ha	Max. Density (kg/ha)	First Year ≥ 50 kg/ha	Last Year ≥ 50 kg/ha	Max. Density (kg/ha)
Paper Birch	2	27	131	2	27	131
Quaking Aspen	1	10	294	1	9	189
Red Maple	2	16	195	3	13	98

The production of twigs available to moose may also be augmented by the effects of browsing itself. Previous research at Minong and in Sweden has shown that birch and aspen respond to light to moderate moose browsing by increasing the production of fine branches and foliage (De Jager and Pastor 2008, De Jager et al. 2009, Pastor 2016). For deciduous species with slower height growth, such as paper birch or red maple, this effect might amplify available twig production over time relative to faster growing species. Consistent with this explanation, our study observed greater peak twig production for both paper birch and red maple (Figure 1, Table 6). Interestingly, birch also had greater variability in twig production than aspen, despite a smaller sample size (Table 3, Figure 1). Although other explanatory mechanisms are possible, such a pattern might result if birch responds more strongly than aspen to variability in browsing pressure across the landscape.

Differences in Twig Production with Canopy Cover

Our finding that trees and shrubs generally produced more twigs in the open than under shade and that the difference varies between species is generally consistent with a large body of tree physiology studies and prior moose forage research (see reviews by Lusk et al. 2008 and Walters and Reich 1999). In general, the tree physiology literature finds that shade grown woody plants tend to reduce photosynthetic capacity (e.g. number and size of leaves) relative to open grown plants of the same species in order to manage the balance between photosynthesis and respiration (Lusk et al. 2008). Further, differences in allocation in full sun vs. shade between species are related to shade tolerance, evergreen vs. deciduous leaves, leaf longevity, and leaf mass (Walters and Reich 1999). An earlier study of moose browse found that mean moose bite mass is often – but not always – larger for open-grown plants than for shaded plants (Portinga and Moen 2015). Although size may also be related to other factors such as moose selectivity or optimal foraging, the Portinga and Moen (2015) result is consistent with the idea that shaded plants allocate less mass to leaves and twigs. Taken together, these bodies of work suggest that our model is biologically reasonable.

Model Validation and Limitations

We have also shown that unimodal twig production-height equations perform better than allometric equations, and that our equations performed reasonably well with independent out-of-sample data as quantified with some of our validation metrics. Unimodal equations consistently had higher pseudo-R^2, lower bias, and lower RMSE than allometric equations on both fitting and validation data. The unimodal model was also consistently better correlated with actual twig counts

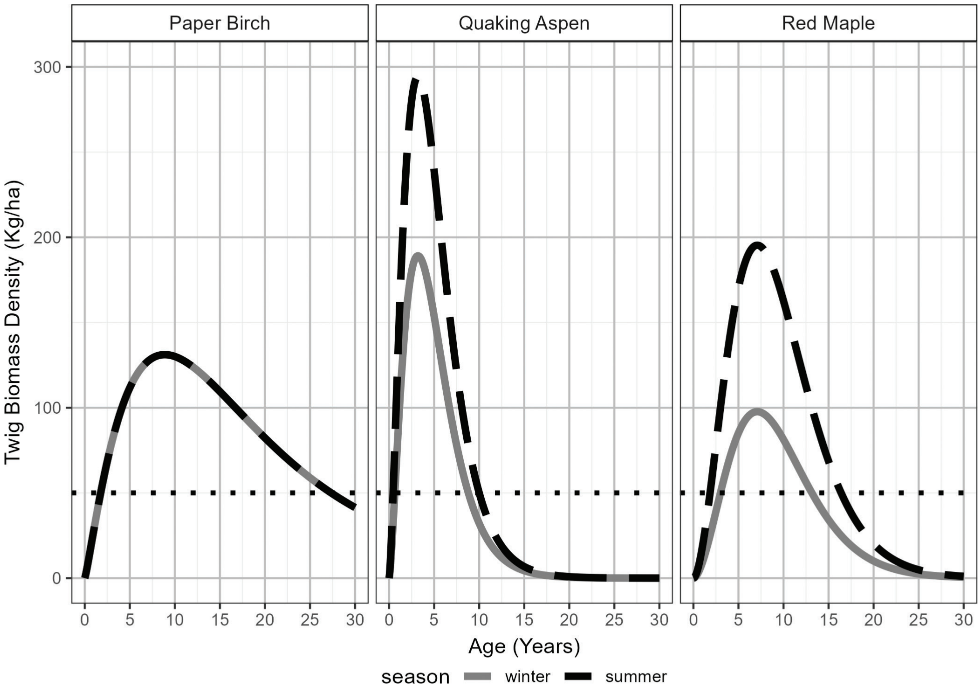

Fig. 8. Comparison of simulated forage density (kg/ha) from ages 0-30 years between paper birch, quaking aspen, and red maple in winter and summer for aspen site index of 18.3 m (60 ft) in northeastern Minnesota using best-fit unimodal model. Solid gray line indicates winter density. Dashed black line indicates summer density. Dotted line represents minimum forage density for moose use of 50 kg/ha. Paper birch winter and summer curves overlap because biomass/twig is the same.

than the species-cover average model for both fitting and validation data. These results demonstrate the greater predictive ability of unimodal models over Grigal and Ohmann (1977) style allometric models. However, although our unimodal model did a good job reflecting differences in forage density between plots, it appeared to have a significant bias that consistently overestimated the absolute forage density of the validation data. This suggests that although the model was adequate for monitoring relative differences between sites or changes in sites over time, it should be used with caution in applications requiring high accuracy such as calculating moose carrying capacity.

The model's apparent lack of accuracy and ability to explain only 54.7% of variability is likely related to limited sample sizes, poor sampling balance, protocol deficiencies, missing covariates and biological process variance. Several shrubs and trees had less than 50 samples, which limited the precision of parameter estimates. For these species, fitting data was poorly balanced with respect to height and site factors such as canopy cover, productivity, and past management. For trees, small sample sizes were due to species rarity. For most shrubs, small sample sizes were due to our subsampling of twig counts. Our measurement of multi-stemmed plants as one individual likely increased count variability and reduced estimate precision. Lack of identification to species for some shrubs may have pooled counts across species with divergent growth forms. For example, *Salix discolor* reaches heights of 10 m, whereas *Salix humilis* only reaches heights of 3 m (Smith 2008). Other covariates that might also influence twig production, such as stem diameter, neighboring stem density, browsing pressure, and abiotic factors affecting site productivity were not explicitly included in the model. Conversely, apparent bias might have resulted from an unrepresentative set of validation data; validation data were collected at sites that all had above average site productivity (aspen height at 50 yrs > 21.3 m (70 ft)) and high stem densities resulting from past clearcutting. Compared with unmanaged sites with average productivity, the validation sites might have had above average rates of branch senescence from rapid height growth and heavy competition. It is possible our model may perform better or underestimate twig production elsewhere.

Model accuracy could likely be improved by collecting additional fitting data with improved methods. In the future, twigs should be counted on all shrubs, rather than subsampling. Sampling should intentionally seek out species used by moose that were under-sampled in this study and better identify shrubs (e.g., willow, juneberry) to species or species groups. Improved protocols for dealing with multi-stemmed plants should be developed. Accounting for additional factors such as neighboring stem density and site productivity should be explored.

Using Models with Forestry Field Surveys to Estimate Moose Forage Density

Despite the limitations of our unimodal model noted above, the high correlation with validation data and consistency with published literature suggest the model is a useful first approximation to estimate twigs available to moose for forestry and wildlife monitoring purposes. Applying these equations to common forest regeneration survey data (e.g. plot tallies of tree and shrub stems by species and height class) and multiplying by published twig mass values, a practitioner can estimate moose forage densities (e.g., kg per hectare or lbs per acre) by species. Forage densities can then be further grouped by moose preference (and avoidance) to estimate total acceptable browse.

We developed a detailed protocol and worked example of the application of these equations to forest regeneration survey data (Supplementary Material 5, Table S5.1). The tally data used in that exercise were slightly modified from an actual plot taken during a routine regeneration survey in a dense part of a 6-year-old clearcut at Gichi Onigaming. Our estimate of 595 kg/ha, although not representative of the overall stand due to very high stem density on this plot, was similar to other high forage density estimates in the literature (Crête 1989; Peterson et al. 2022). Our experience suggests that estimating forage availability by applying our equations to already occurring forest regeneration surveys may be more efficient than conventional forage transect methods. It took less than 14 minutes to collect the forest regeneration plot used in this example (Table S5). In contrast, it took on average ~60 minutes to collect the 2 m x 20 m forage transects used for fitting and ~30 minutes to collect the 2 m x 10 m transects used for validation. This suggests a more efficient use of field time, albeit with lower accuracy.

Implications for Moose and Forest Management

If abundance of diverse, high-quality forage can influence moose at the population level (Schrempp et al. 2019, Felton et al. 2020, Hayes et al. 2022, Peterson et al. 2022), then our results indicate that the assumption that aspen management alone is sufficient to maintain moose populations should be re-examined. To the extent that moose preference is a proxy for nutritional quality, our finding that quaking aspen's low twig production per stem and rapid rate of decline with height relative to other preferred tree and shrub species suggests that aspen alone may not provide a sufficient forage base for moose over time. Our simulation further supports the idea that quaking aspen's rapid decline in twig production may scale up to the stand level, with consequences for moose forage availability on the landscape over time. Although aspen in our simulation produced a huge pulse of dense forage, the pulse was short-lived (9-10 years); paper birch and red maple provided forage for longer periods of time (11-25 years). This illustrates an important paradox: although quaking aspen is preferred by moose (Irwin 1985, Portinga and Moen 2015), commercially valuable, and easy to regenerate by clearcutting, each stem does not provide many twigs, nor do they provide twigs once they have grown beyond a certain height. Although aspen's low twig production per stem is offset by high stem densities in clearcuts, aspen's rapid early height growth and self-pruning soon moves twigs out of the reach of moose.

Conversely, our simulation suggested that young red maple and paper birch, two species preferred by moose but with low commercial value in northeastern Minnesota, may provide moose forage for longer periods of time than aspen. Managers in northeastern Minnesota have not historically managed specifically for paper birch due to low stumpage values and regeneration difficulties. More often, paper birch has been viewed as an incidental companion species and sometimes as a weed competing with more commercially valuable species. Red maple, less common and not typically found in pure stands in northeastern Minnesota, has similarly often been viewed as a competing species to be eliminated. However, our results suggest that maintaining these tree species on the landscape, despite their low commercial value, may be important to sustaining moose populations.

Similarly, our results indicating favorable performance of fire cherry and mountain maple relative to aspen suggest that maintaining preferred shrubs on the landscape may also be important to sustaining moose populations. Foresters have historically viewed shrubs as a barrier to tree establishment, using herbicides and mechanical release to reduce shrub density. Our results suggest that a shift in perspective from "shrubs as competition" to "preferred shrubs as wildlife asset" may benefit foresters managing for moose. Such a shift would be consistent with the Anishinaabeg understanding that all species have value (Davidson-Hunt et al. 2005). Similarly, our results suggest that stands with a mix of preferred deciduous tree and shrub species may benefit moose more than stands with low species diversity. If, as our simulation found, different species produce peak forage at different times, then mixed stands would have several forage peaks resulting in more sustained forage availability. This might in turn benefit moose populations through improved calving success, associated with high preferred browse density (Hayes et al. 2022), and/or enhanced calf weight gain, which has been associated with higher deciduous browse diversity (Felton et al. 2020).

Although our results also suggest that balsam fir may provide abundant moose forage for long periods of time, we caution that moose appear to avoid eating fir when other options are available (McNicol and Gilbert 1980, Cumming 1987, Risenhoover 1987, Hodgson 2010, Portinga and Moen 2015). Although high density moose populations on Minong often browse fir heavily in winter (Brandner et al. 1990), studies on Minong found that fir is eaten less than available (Hodgson 2010), browsed at lower rates than deciduous species (Risenhoover 1987), or are browsed more than cedar but less than deciduous species (Belovsky 1981). Similarly, several studies of moose in Minnesota and northwest Ontario found that moose eat fir less than available (McNicol and Gilbert 1980, Cumming 1987, Portinga and Moen 2015), although one study in central Ontario found moose preferred fir (Routledge and Roese 2004). Possible reasons for avoidance are that fir has lower digestibility than deciduous browse (Risenhoover 1987, Parikh et al. 2016) and contains terpenes (Terra-Berns 1993) that may be energetically costly for moose to detoxify (Parikh et al. 2016; but see also Hoy et al. 2022).

Overall, our results suggest the importance of managing intentionally for a diversity of preferred deciduous tree and shrub species in areas intended for moose forage, such as timber harvests. Post-harvest treatments such as mechanical site preparation, burning, shearing, and mechanical release could be used to increase the abundance, diversity, and longevity of preferred moose forage species. Mechanically releasing paper birch from aspen can shift stand composition towards birch (Zenner and Puettmann 2008). Light shearing or brush-sawing can also stimulate vigorous re-growth of red maple, mountain maple, fire cherry, aspen, and paper birch from stump or root sprouts (Krefting et al. 1956, Scheiner et al. 1988, Burns and Honkala 1990). Fire cherry and paper birch regenerate well from seed following more severe mechanical site preparation or prescribed fire (Burns and Honkala 1990). At least one Anishinaabeg community in what is now Canada historically burned specifically to improve moose forage (Theriault 2006), and many Tribal nations elsewhere in North American burn to increase forage for ungulates (Kimmerer and Lake 2001, Aguilar 2005, Connor et al. 2022, Hoagland and Albert 2023). Using prescribed fire to improve moose forage would support restoration of Anishinaabeg cultural burning, which was widely practiced historically (Larson et al. 2021, Johnson et al 2022). Conversely, herbicide use for release or site preparation should be avoided were possible because it can reduce the density of preferred deciduous browse species (Lautenschlager 1992, Johnson and Rea 2024). Other methods should be evaluated for impact on preferred forage density over time.

Although promising, managing for prolonged availability of preferred moose forage rests on the assumption that moose prefer forage of high nutritional quality. Although other studies have drawn links between forage quality and moose preference (e.g. Belovsky 1981, Peterson et al. 2020), our study does not address either preference or quality. Measurement of forage quality and moose preference is also notoriously complex. Forage quality (e.g. energy, protein, and mineral content) varies considerably across plant parts, species, seasons, and geographic regions, and is subject to complicating factors such as tannins and secondary metabolites that can limit uptake (Robbins et al. 1987, Lindroth 2001, Wam et al. 2018). Methods in moose preference studies vary considerably, often lacking quantitative rigor (e.g., Peek et al. 1976) or using measures such as Ivlev's electivity (e.g. Irwin 1985) which may be biased and unreliable (Manly et al. 2002). As noted in the case of balsam fir, conflicting results between preference studies are common. More research is needed to better understand moose forage quality and its relationship to moose forage preferences in the western Lake Superior region.

Managing for prolonged forage availability may also have downsides. Quaking aspen can sometimes be browsed so heavily and repeatedly that it cannot mature, to the detriment of species reliant on mature and old aspen (Mathisen et al. 2017, Painter et al. 2018). Prolonged use in concentrated areas might also facilitate parasite transmission (Ellingwood et al. 2020, Hoy et al. 2021).

Care must be taken to ensure an abundance of forage across the landscape to prevent animal concentration and over browsing.

Post-harvest treatments such as burning, shearing, and/or mechanical release may also reduce parasites such as brainworm (*Parelaphostrongylus tenuis*) and winter tick (*Dermacentor albipictus*) implicated in the decline of moose in northeastern Minnesota (Wünschmann et al. 2015, Carstensen et al. 2018, Severud et al. 2019, 2022; Oliveira-Santos et al. 2021). Prescribed fire can reduce densities of some slug and snail (gastropod) species that transmit brainworm to moose, while increasing densities of others (Nekola 2002). Prescribed burning can also reduce winter tick densities when litter and duff layers are sufficiently consumed (Drew et al. 1985), although winter tick populations might also rebound if enhanced forage increases moose abundance and density (Ellingwood et al. 2020, Hoy et al. 2021). At Gichi Onigaming, forestry treatments within the last 5 years (including mechanical release only) reduced overall gastropod densities and specifically densities of *Deroceras* spp., a frequent brainworm host (Severud et al. 2023).

Finally, our results indicate that canopy openness is critically important to stimulating high density moose forage. Managers should be mindful of light conditions as we seek to improve moose forage. Reserve areas in timber harvests, although important for winter snow refuge (Mastenbrook and Cumming 1989) and summer cooling (Street et al. 2016), should not be so close together that they create excessive shade. In some mixed wood stands, early, heavy, and frequent thinning might also be used to maintain high densities of preferred forage over time while retaining mature trees for cover.

In summary, our findings suggest that young, open canopied forests with a diverse mix of deciduous trees and shrubs likely provide abundant moose forage for longer durations than do the nearly pure aspen forests that often follow clearcutting alone in northeastern Minnesota. Species used and preferred by moose such as paper birch, red maple, mountain maple, and fire cherry may be of particular importance due to equal or greater peak forage production and/or slower rates of forage decline. In many aspen-dominated forests, promoting tree and shrub diversity to sustain adequate moose forage will likely require additional post-harvest treatments such prescribed fire, site preparation, winter shearing, or mechanical (brush saw) release. These treatments may also benefit moose by reducing parasite densities on the landscape.

Our findings reinforce the value of heterogeneous post-disturbance regeneration in supporting sustained moose forage availability, especially when guided by species-specific forage production curves. These outcomes align closely with Indigenous co-stewardship principles that prioritize ecological resilience, interspecies relationships, and culturally grounded resource governance (Moore et al. 2024). Collaborative research such as this study exemplifies how Indigenous science and western methodologies can be integrated to inform adaptive management. Future applications of these equations, when paired with ongoing monitoring of moose health, predation, and parasitism pressures (Wolf et al. 2021, Garwood et al. 2023, Severud et al. 2023, Weesies, in review) serve as a powerful co-management tool. They offer the potential to tailor silvicultural prescriptions in a way that supports both moose recovery and food sovereignty goals of the Gichi Onigaming Anishinaabeg and affirm the vital role of Indigenous leadership in shaping forest futures that are ecologically functional and culturally enduring.

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SUPPLEMENTARY MATERIAL

Supplementary data are available with the article at https://alcesjournal.or/indexphp/alces/article/view/1961.

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