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Knowledge of forage biomass is essential to the understanding of nutrient cycles and energy pathways for white-tailed deer (Odocoileus virginianus). Rapid, objective methods for assessing forage biomass can help managers integrate deer habitat information into resource management plans. Shrub leaves are among the most important summer deer foods (Cowan et al. 1957, McCaffery et al. 1974, Crawford et al. 1975, Mautz 1978, Harder 1980, Rogers et al. 1981). However, it is difficult to determine leaf biomass within reach of deer. Possible methods for estimating available leaf biomass include the clip and weigh method (Schwan and Swift 1941), which is too time-consuming for sufficient replication in extensive studies, and the weight estimation method (Pechanec and Pickford 1937), which is too subjective for statistical analysis.

Methods exist for estimating shrub density (Cottam and Curtis 1956, Catana 1963, Lyon 1968, Batcheler and Bell 1970, Oldemeyer and Regelin 1980). We found that estimates of shrub density may be converted to estimates of available leaf biomass if heights of the shrubs are known. We developed models for converting shrub height data to estimates of leaf biomass within reach of deer. We used shrub height as the independent variable because it is easily measured and it correlates well with leaf biomass on a whole shrub basis (Ohmann et al. 1976, Roussopoulos and Loomis 1979). In this paper, we present models for using shrub height (1) to estimate leaf biomass within reach of deer and (2) to predict whether leaf biomass within reach of deer will increase or decrease with further shrub growth. We focus here on 13 commonly browsed shrubs of the Upper Great Lakes Region (Rogers et al. 1981).

STUDY AREA AND METHODS

Data Collection

The study was conducted during July to early September of 1977 and 1978 in northeastern Minnesota (Lat. 47 45'N, Long. 91 30'W). To develop the models, we measured shrub heights, collected leaves within reach of deer, and weighed the leaves. Specifically, we measured each shrub to the nearest decimeter using a 6-m pole and collected the leaves in two strata—up to 0.91 m (3 ft) and 0.91 m to 1.52 m (5 ft) above ground level. The two bagged samples from each specimen were oven dried at 68°C for 48 hours and weighed.

Leaves up to 0.91 m above ground level were considered to be within reach of fawns, and leaves from the combined strata were considered to be within reach of yearling and adult deer. Observations of live fawns (Rogers 1981 and unpubl.), combined with measurements from front hoof to upstretched muzzle of 20 road-killed fawns (Wm. Peterson, Minnesota Department of Natural Resources, Grand Marais; unpubl. data), showed that fawns browsed to between 0.8 and 0.9 m in early July when extensive browsing began. By leaf-fall in October, fawns browsed to between 1.0 and 1.3 m; the 0.91-m point was arbitrarily selected because most fawns could reach that high most of the summer. Observations of older deer (Rogers 1981 and unpubl.) showed that mature bucks and some does browsed higher than the

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maximum clipping height of 1.52 m, but yearlings and most does that did so had to stand on their hind legs, which they did only in winter when food was scarce. The models were developed to assess leaf biomass available in summer.

To obtain shrub specimens, we searched through 32 aspen (Populus tremuloides) stands and 19 red pine (Pinus resinosa) stands ranging in age from <1 (newly clearcut) to >80 years old. We measured and clipped all live shrubs, regardless of vigor or shape, to avoid sampling biases with respect to variation in growth form. We sampled by moving across (rather than along) topographic contours, forest openings, or other environmental features that might influence growth. As sufficient samples were obtained for the most common shrub species and size classes, collection was narrowed to species and size classes needed to complete the study.

Data Analysis

Because available leaf biomass first increases with shrub growth and then decreases as crowns grow beyond reach of deer (Krefting et al. 1966), a nonlinear model was required to represent the pattern of increasing and then decreasing availability of leaves to deer. Six nonlinear statistical models that had the capability of producing this feature were investigated to determine which best predicted leaf biomass within reach of deer for each shrub species. Goodness of fit, measured by residual standard error, was the selection criterion. The model we selected produced smaller, or equally small, residual standard errors for all species than did the other models. The model has the following form:

$$E(Y) = \beta_1 X^\beta_2 \exp(\beta_3 X)$$

where $$E(Y)$$ is the expected value of dry weight (grams) of leaves to a height of 0.91 m for fawns or 1.52 m for older deer, $$X$$ is shrub height in meters, exp is the mathematical exponential function, and the $$\beta$$'s are parameters to be estimated. Estimates, $$\beta$$'s of the parameters $$\beta$$'s, were obtained by weighted nonlinear least squares regression and are shown in tables 1 and 2. After the model was fit to the data, further tests were performed to determine if removing specific parameters significantly ($$P=0.05$$) decreased the quality of fit. If not, the model was reduced accordingly. For some species, shrubs did not grow out of the reach of deer, and, thus, did not exhibit decreasing biomass for increasing height. For these species, the $$\beta_3$$ model parameter was not necessary, and no estimate is given (table 2).

<table>
<thead>
<tr>
<th>Species</th>
<th>n</th>
<th>$$R^2$$</th>
<th>$$b_1$$</th>
<th>$$b_2$$</th>
<th>$$b_3$$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Red maple</td>
<td>68</td>
<td>0.61</td>
<td>420.59</td>
<td>4.25</td>
<td>-4.63</td>
</tr>
<tr>
<td>Mountain maple</td>
<td>73</td>
<td>0.23</td>
<td>9.00</td>
<td>1.74</td>
<td>-1.35</td>
</tr>
<tr>
<td>Juneberry</td>
<td>65</td>
<td>0.32</td>
<td>17.65</td>
<td>2.89</td>
<td>-2.81</td>
</tr>
<tr>
<td>Roundleaf dogwood</td>
<td>56</td>
<td>0.45</td>
<td>2926.67</td>
<td>5.58</td>
<td>-5.38</td>
</tr>
<tr>
<td>Beaked hazel</td>
<td>72</td>
<td>0.40</td>
<td>461.72</td>
<td>5.09</td>
<td>-5.50</td>
</tr>
<tr>
<td>Hawthorn</td>
<td>36</td>
<td>0.64</td>
<td>889.94</td>
<td>4.40</td>
<td>-4.50</td>
</tr>
<tr>
<td>Quaking aspen</td>
<td>186</td>
<td>0.22</td>
<td>10.89</td>
<td>1.75</td>
<td>-1.11</td>
</tr>
<tr>
<td>Chokecherry</td>
<td>45</td>
<td>0.22</td>
<td>20.10</td>
<td>1.99</td>
<td>-1.81</td>
</tr>
<tr>
<td>Prickly rose</td>
<td>92</td>
<td>0.51</td>
<td>88.98</td>
<td>3.01</td>
<td>-2.76</td>
</tr>
<tr>
<td>Willow</td>
<td>74</td>
<td>0.31</td>
<td>156.74</td>
<td>4.60</td>
<td>-3.62</td>
</tr>
<tr>
<td>American mountain-ash</td>
<td>91</td>
<td>0.08</td>
<td>19.96</td>
<td>2.53</td>
<td>-2.07</td>
</tr>
</tbody>
</table>

1 Model: $$E(Y) = \beta_1 X^\beta_2 \exp(\beta_3 X)$$.
Table 2.—Parameter estimates for relationship\(^1\) between leaf biomass below 1.52 m and shrub height

<table>
<thead>
<tr>
<th>Species</th>
<th>n</th>
<th>(R^2)</th>
<th>(b_1)</th>
<th>(b_2)</th>
<th>(b_3)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Red maple</td>
<td>68</td>
<td>0.62</td>
<td>23.08</td>
<td>2.78</td>
<td>-1.41</td>
</tr>
<tr>
<td>Mountain maple</td>
<td>73</td>
<td>.56</td>
<td>3.26</td>
<td>1.31</td>
<td>(2)</td>
</tr>
<tr>
<td>Speckled alder</td>
<td>67</td>
<td>.22</td>
<td>42.96</td>
<td>3.97</td>
<td>-2.41</td>
</tr>
<tr>
<td>Juneberry</td>
<td>67</td>
<td>.60</td>
<td>10.88</td>
<td>3.10</td>
<td>-1.64</td>
</tr>
<tr>
<td>Roundleaf dogwood</td>
<td>56</td>
<td>.68</td>
<td>10.32</td>
<td>2.39</td>
<td>(2)</td>
</tr>
<tr>
<td>Beaked hazel</td>
<td>72</td>
<td>.53</td>
<td>48.49</td>
<td>3.88</td>
<td>-2.83</td>
</tr>
<tr>
<td>Hawthorn</td>
<td>36</td>
<td>.77</td>
<td>24.73</td>
<td>2.71</td>
<td>-0.82</td>
</tr>
<tr>
<td>Quaking aspen</td>
<td>186</td>
<td>.63</td>
<td>14.27</td>
<td>2.23</td>
<td>-0.70</td>
</tr>
<tr>
<td>chokecherry</td>
<td>45</td>
<td>.34</td>
<td>14.10</td>
<td>2.00</td>
<td>-1.08</td>
</tr>
<tr>
<td>Prickly rose</td>
<td>92</td>
<td>.53</td>
<td>7.63</td>
<td>1.66</td>
<td>(2)</td>
</tr>
<tr>
<td>Willow</td>
<td>74</td>
<td>.63</td>
<td>69.94</td>
<td>4.59</td>
<td>-2.52</td>
</tr>
<tr>
<td>American mountain-ash</td>
<td>91</td>
<td>.30</td>
<td>18.22</td>
<td>2.81</td>
<td>-1.38</td>
</tr>
<tr>
<td>Shortstalk arrowwood</td>
<td>23</td>
<td>.81</td>
<td>5.37</td>
<td>2.26</td>
<td>(2)</td>
</tr>
</tbody>
</table>

\(\beta_2\)

\(^1\) Model: \(E(Y) = \beta_1X \exp(\beta_3X)\).

\(^2\) The shrub, on average, did not grow out of reach and therefore did not require the \(\beta_3\) parameter in the model or, equivalently, \(\beta_3=0\).

To estimate the shrub height that produces maximum leaf biomass within reach of deer, the mathematical derivative of the model was determined with respect to height. For each species, the resulting expression was set equal to zero and solved for shrub height. However, minimum values for these estimates were established as the height the deer could reach. Estimates less than the height the deer could browse were considered anomalous and were attributed to sampling error. Variances of estimates of optimum height were approximated using propagation of error techniques based on Taylor’s series approximations (Rao 1952).

**RESULTS AND DISCUSSION**

Although the models did not account for a large proportion of variability in the observations, the relationship between leaf biomass and shrub height was still estimated quite well for many species. The estimated relationship and its 95 percent confidence interval are shown for each species in figures 1 and 2 and provide estimates of shrub leaf biomass within reach of deer in summer. This information can be used in two ways: (1) to estimate available browse for shrubs of a given size and species and (2) to estimate the size of shrub that produces the maximum browse for deer, on the average. The latter information can help managers schedule habitat improvement programs by revealing when forests have reached a stage where further shrub growth would result in declining browse availability.

Scatter in individual browse measurements is assumed to be due to differences in shading, soil moisture, soil pH, slope, aspect, and other factors that influence form and vigor in plants. Including those factors in the model would undoubtedly improve the precision of individual estimates, but would render the method too cumbersome for extensive use. Shading may produce especially large variability in shade intolerant species such as willow and aspen (Baker 1949). Shade had less effect on round-leafed dogwood and mountain-ash. These fairly
shade-tolerant species (Gill and Healy 1974) were collected from both shaded and sunny locations, but intraspecific differences in browse availability below 1.52 m were not significant. The remaining species were collected from partially shaded sites typical for the species, and the sites did not differ sufficiently to allow testing for shade effects.

Because of the large amount of scatter in the leaf biomass observations as discussed in the preceding paragraph, our models do not always account for large proportions of variability. Thus, this method of estimating available leaf biomass is intended for use in intensive surveys where overall estimates of biomass are needed for large numbers of plants. It is not intended for use in intensive surveys where leaf biomass of individual plants must be accurately estimated. Estimates using this method will approximate the annual productivity of leaf biomass available to deer because data for the models were collected in middle to late summer when leaf growth was complete or nearly complete (Ohmann et al. 1974) and because study plants were essentially unbrowsed due to very low deer densities (<0.33 deer/km) for 6 to 10 years before the study (Mech and Karns 1977, Floyd et al. 1979). In areas of high deer density, heavy browsing and mainstem breakage may cause increased branching and higher leaf biomass within reach of deer (Krefting et al. 1966).
Predicting Trends in Browse Production

Table 3 lists for each species the shrub size that produced maximum biomass of leaves within reach of deer. Shorter or taller specimens, on the average, produced less leaf biomass within reach of deer. Thus, in stands where plants are shorter, on the average, than those indicated in table 3, available leaf biomass would be expected to increase with shrub growth. Where plants are taller than those indicated in table 3, browse availability would be expected to decrease as crowns grow out of reach. Shrub heights that produced the greatest predicted leaf biomass within reach of deer were fairly similar (1.37 to 3.30 m) among species (table 3) even though maximum height differed widely among species.

Availability of current annual stems should follow trends similar to those for leaves because leaves and current annual stems are similarly distributed; shrub leaves grow only on current annual stems. However, in winter, additional browse is available because fawns are taller by then and deer can reach higher when standing on packed snow.

Table 3.—Species, maximum observed height, and heights producing maximum available white-tailed deer summer-browse from specimens sampled in northeastern Minnesota during middle to late summer, 1977 and 1978

<table>
<thead>
<tr>
<th>Species</th>
<th>Maximum observed height</th>
<th>Height yielding maximum browse</th>
<th>Fawns</th>
<th>Adults</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Ht</td>
<td>SE(Ht)</td>
<td>Ht</td>
</tr>
<tr>
<td>Red maple (Acer rubrum)</td>
<td>13.5</td>
<td>0.92</td>
<td>0.04</td>
<td>1.97</td>
</tr>
<tr>
<td>Mountain maple (Acer spicatum)</td>
<td>7.0</td>
<td>1.29</td>
<td>0.23</td>
<td>1.65</td>
</tr>
<tr>
<td>Speckled alder (Alnus rugosa)</td>
<td>6.0</td>
<td>(3)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Juneberry (Amelanchier spp.)</td>
<td>7.5</td>
<td>1.03</td>
<td>0.11</td>
<td>1.89</td>
</tr>
<tr>
<td>Roundleaf dogwood (Cornus rugosa)</td>
<td>3.5</td>
<td>1.04</td>
<td>0.06</td>
<td>2.18</td>
</tr>
<tr>
<td>Beaked hazel (Corylus cornuta)</td>
<td>3.5</td>
<td>0.93</td>
<td>0.07</td>
<td>1.52</td>
</tr>
<tr>
<td>Hawthorn (Crataegus spp.)</td>
<td>2.0</td>
<td>0.98</td>
<td>0.05</td>
<td>3.30</td>
</tr>
<tr>
<td>Quaking aspen (Populus tremuloides)</td>
<td>13.5</td>
<td>1.58</td>
<td>0.10</td>
<td>3.19</td>
</tr>
<tr>
<td>Chokecherry (Prunus virginianus)</td>
<td>4.0</td>
<td>1.10</td>
<td>0.13</td>
<td>1.85</td>
</tr>
<tr>
<td>Prickly rose (Rosa spp.)</td>
<td>1.8</td>
<td>1.09</td>
<td>0.13</td>
<td>(3)</td>
</tr>
<tr>
<td>Willow (Salix spp.)</td>
<td>5.0</td>
<td>1.27</td>
<td>0.08</td>
<td>1.82</td>
</tr>
<tr>
<td>American mountain-ash (S. americanus)</td>
<td>5.0</td>
<td>1.22</td>
<td>0.09</td>
<td>2.04</td>
</tr>
<tr>
<td>Shortstalk arrowwood (V. rafinesquianum)</td>
<td>1.7</td>
<td>(3)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

1 Plant names follow Petrides (1972) except for prickly rose and American mountain-ash that follow Scott and Wasser (1980).
2 The shrub, on average, did not grow out of reach.
3 No relationship between leaf biomass and shrub height was detected.
4 Estimate was lower than the height the deer could reach.

G. Kie, K. R. McCaffery, A. N. Moen, L. F. Ohmann, and J. M. Sweeney for helpful comments on the manuscript.

LITERATURE CITED


Figure 2.—Dry weight of leaves within reach of yearling and adult doe white-tailed deer.
2b. Mountain maple

- predicted biomass
- upper and lower bounds of 95% confidence interval for predicted biomass

2c. Speckled alder

- predicted biomass
- upper and lower bounds of 95% confidence interval for predicted biomass
2d. Juneberry

Shrub height (m) vs. Leaf biomass (g)

- Predicted biomass
- Upper and lower bounds of 95% confidence interval for predicted biomass

2e. Roundleaf dogwood

Shrub height (m) vs. Leaf biomass (g)

- Predicted biomass
- Upper and lower bounds of 95% confidence interval for predicted biomass
2f. Beaked hazel

- predicted biomass
- upper and lower bounds of 95% confidence interval for predicted biomass

2g. Hawthorn

- predicted biomass
- upper and lower bounds of 95% confidence interval for predicted biomass

Shrub height (m) vs. Leaf biomass (g)
2h. Quaking aspen

- predicted biomass
- upper and lower bounds of 95% confidence interval for predicted biomass

2i. Chokecherry

- predicted biomass
- upper and lower bounds of 95% confidence interval for predicted biomass
2j. Prickly rose

- predicted biomass
- upper and lower bounds of 95% confidence interval for predicted biomass

2k. Willow

- predicted biomass
- upper and lower bounds of 95% confidence interval for predicted biomass
2l. American Mountain-ash

- Predicted biomass
- Upper and lower bounds of 95% confidence interval for predicted biomass

2m. Shortstalk arrowwood

- Predicted biomass
- Upper and lower bounds of 95% confidence interval for predicted biomass
Rogers, Lynn L.; McRoberts, Ronald E.

Describes an objective method for using shrub height to estimate leaf biomass within reach of deer. The method can be used in conjunction with surveys of shrub height, shrub density, and shrub species composition to evaluate deer habitat over large areas and to predict trends in forage availability with further forest growth.

KEY WORDS: Odocoileus virginianus, habitat evaluation, forest growth, browsing height, shrub height, leaf biomass prediction, annual leafy browse production.