BIOMASS ESTIMATION FOR FIVE SHRUBS FROM NORTHEASTERN MINNESOTA[1]

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APPLICATION

Land managers and wildlife biologists sometimes need to determine the above-ground biomass of shrubs or the amount of shrub browse available for wildlife.

We have developed a series of values for use in an equation to predict biomass for five shrubs, green alder (*Alnus crispa*), beaked hazel (*Corylus cornuta*), juneberry (*Amelanchier* spp.), willow (*Salix* spp.), and mountain maple (*Acer spicatum*) which are common in northeastern Minnesota. The values and equation can be used to estimate the following: (1) biomass of leaves, (2) biomass of current year's twigs, (3) biomass of stems, and (4) total biomass of the above-ground parts. These biomass estimates could be used to predict available summer browse (leaves) and winter browse (current twigs) for deer and moose.

The values and equation are best used to predict shrub biomass in regenerated clearcuts because the data were obtained from such areas.[2] But even in nonclearcut areas, predictions from this equation should be reasonably accurate so long as the shrub measurements described below fall within the ranges listed in table 1.

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[2]*An exception are the data for mountain maple which were gathered from a mature forest community.*

HOW TO USE THE VALUES AND EQUATION

To predict any of the four kinds of biomass listed above, you can use any one of four different shrub measurements[3]:

(1) Plant height, cm (measure height to nearest 15 cm).

(2) Crown area, cm^2 (measure to nearest 15 cm the maximum crown diameter and the diameter 90 degrees to it; compute area of crown using formula $A = \frac{\pi}{4} (d_1) (d_2)$.

(3) Stem diameter, by 1-cm classes (measure diameter at 15 cm above ground and assign to nearest class; 1-cm class includes 0.5 to 1.4 cm).

(4) Stem diameter, cm (measure diameter to nearest 0.25 cm, 15 cm above the ground).

Suppose, for example, that you want to know the biomass (in grams) of this year's twigs on a single stem of green alder. To

[3]*Predictions using stem diameter will be slightly more accurate (higher R^2 values) but other measurements, such as plant height, are easier to make and are sufficiently accurate for many applications.*

Table 1.--*Ranges of shrubs measurements (x's) within which biomass predictions should be accurate*

Shrub species	Acceptable range of shrub measurements (x's)			
	Plant height	Crown area	Stem diameter classes	Stem diameter
	Cm	*Cm²*	*Cm*	*Cm*
Mountain maple	91 - 366	182 - 45,969	0.5 - 3.5	0.6 - 3.2
Green alder	91 - 290	182 - 6,384	.5 - 2.5	.6 - 2.1
Beaked hazel	91 - 213	182 - 5,108	.5 - 2.5	.6 - 2.3
Juneberry	91 - 274	182 - 7,661	.5 - 1.5	.5 - 1.9
Willow	91 - 305	365 - 19,154	.5 - 3.5	.7 - 3.8

predict this you need to take any one of the four measurements listed above, for example number 4--stem diameter. Suppose the stem measured 1.5 cm in diameter. First you check table 1 to see if 1.5 cm falls within the acceptable range (0.6 - 2.1) which it does. Then substitute 1.5 for x in the equation $Y = ax^b$.

Next look up the value of a and b in table 2. First run down the table to the section labeled "USING STEM DIAMETER AS x", find the "green alder" row, and look for the a and b values under the column headed "Current year's twigs." You will find that $a = 5.147$ and $b = 1.184$. When we substitute the values for x, a, and b in the equation, we get

$$Y = ax^b$$

$$Y = (5.147)(1.5)^{1.184}$$

Solving for the twig biomass (Y) is most easily done with logarithms.

(1) First find the natural logarithm of 1.5 either from tables or directly on some

Table 2.—*Values of a and b for substituting in regression equation $Y = ax^b$ to predict biomass*

Shrub species		Type of biomass: Leaves	Current year's twigs	Stem	Total aboveground parts
USING PLANT HEIGHT AS x					
Mountain	a	2.856E-05	2.639E-03	4.134E-05	1.747E-05
maple	b	2.599	1.409	2.835	3.047
Green	a	2.746E-03	1.739E-03	6.818E-03	1.899E-03
alder	b	1.738	1.600	1.806	2.120
Beaked	a	--	3.268E-03	2.089E-05	2.791E-04
hazel	b	--	1.373	2.980	2.520
Juneberry	a	6.124E-04	3.041E-04	1.989E-03	2.009E-03
	b	1.998	1.982	2.067	2.096
Willow	a	2.770E-05	1.875E-05	1.011E-05	1.303E-05
	b	2.735	2.571	3.163	3.175
USING CROWN AREA AS x					
Mountain	a	0.0115	0.3046	0.0132	0.0071
maple	b	.8834	.3215	1.064	1.138
Green	a	.2869	.2674	1.590	1.373
alder	b	.5858	.4496	.5354	.5937
Beaked	a	--	.3504	.8201	--
hazel	b	--	.2888	.5770	--
Juneberry	a	.0428	.0819	.7513	.2786
	b	.7849	.6072	.6250	.7641
Willow	a	.0084	.0047	.0157	.0115
	b	1.025	.9590	1.109	1.166
USING STEM CLASS AS x					
Mountain	a	12.69	3.581	47.88	64.38
maple	b	1.818	0.6826	2.486	2.320
Green	a	19.78	5.788	56.96	82.35
alder	b	.6824	.6727	1.052	1.038
Beaked	a	--	2.486	40.10	66.16
hazel	b	--	.3646	0.5878	0.6363
Juneberry	a	15.40	6.303	64.14	82.93
	b	.7386	1.128	1.204	0.9507
Willow	a	28.39	6.577	56.77	99.96
	b	1.362	1.602	2.266	1.936
USING STEM DIAMETER AS x					
Mountain	a	11.13	3.244	40.94	52.09
maple	b	2.123	.9149	2.781	2.724
Green	a	13.97	5.147	43.94	55.45
alder	b	1.682	1.184	2.214	2.409
Beaked	a	--	2.371	38.57	54.10
hazel	b	--	.7265	1.582	1.229
Juneberry	a	13.34	5.923	50.63	64.18
	b	1.547	1.685	2.547	2.322
Willow	a	21.59	5.823	56.09	87.79
	b	1.686	1.789	2.208	1.981

of the new electronic calculators.

(2) Multiply the log of 1.5 (0.4055) by *b* and find the antilog of that product. The product is 0.4801 and the antilog is 1.616.

(3) Then multiply the antilog by *a* (5.147 x 1.616) to obtain the value of Y, current year's twig biomass, 8.32 g. The steps are as follows:

(1) log 1.5 = 0.4055, substituting in the above equation we get

(2) Y = (5.147)(antilog of (0.4055)(1.184))
= (5.147)(antilog of 0.4801)

(3) = (5.147)(1.616)
= 8.32 grams

This value will be the same for each green alder stem with a diameter of 1.5 cm so that the calculation needs to be made only once for that diameter of green alder stem.

If you wish to determine biomass or browse biomass per acre or other unit of area, a sampling scheme using units such as milacre plots can be devised to determine number and size of shrubs. Multiplying the mass (Y) from the above equation by the number of shrub stems of each size and species on a certain area would yield the total mass of the stems of the species.

DOCUMENTATION

Indirect estimation of biomass of the shrub component of plant communities is becoming increasingly important in forest ecology and wildlife habitat research (McKell *et al.* 1972). Equations have been developed for estimating total biomass or biomass of some parts of boreal forest shrubs. Many of these equations either are based on dependent and independent variables that are measured in a variety of ways, or are designed to predict some aspect of biomass that is uniquely defined, or both.

Peek (1970) evaluated the relations of plant height, canopy cover, shrub volume, and number of twigs to twig biomass production in beaked hazel (*Corylus cornuta* Marsh.) and willow (*Salix discolor* Muhl.). For hazel, the independent variable, canopy cover, was defined as the cross sectional area of a clone of stems rather than the area of individual plant crowns. The dependent variable, twig biomass, was leaves and current year's twig growth. Tappeiner and John (1973) presented prediction equations for estimating total biomass and that of three components (leaves, aerial stems, and underground parts) of hazel per unit land area. Two of the independent variables used in their equations were shrub basal area/M^2, derived from stem diameter at 30 cm above ground, and number of stems/ha.

Lyon (1968) related twig production in juneberry (*Amelanchier* Medic.) to crown volume. The dependent variable in the equations was current year's twig growth (exclusive of leaves) of individual plants. Shafer (1963) reported a twig-count method to determine weight per unit area of available and utilized winter browse, based on the average diameter at the point of browsing for an unbiased sample of twigs of several species. Telfer (1969) presented prediction equations for twig weights based on twig diameters at point of browsing for each of 22 species of plants.

We recently described changes in biomass from mid-June through early December for five shrub species from northeastern Minnesota (Ohmann *et al.* in press). In the present report we further examine a portion of those data to develop prediction equations for total aboveground biomass and for biomass of certain parts of shrubs. Some of the relations we examine are between commonly measured parameters in forest ecology and wildlife habitat studies thus the equations we present could also be used to predict biomass using data from past habitat studies in northeastern Minnesota.

METHODS

Data Collection

Five shrubs, mountain maple (*Acer spicatum* Lam.), green alder (*Alnus crispa* (Ait.) Pursh.), juneberry (*Amelanchier* spp. Medic.), beaked hazel (*Corylus cornuta* Marsh.), and willow (*Salix* spp.L.), were sampled at about 2-week intervals from 15 June through 8 December 1971 (Ohmann *et al.* in press). Nine stems of each shrub were cut at ground level and randomly collected on each of the 13 sample dates (12 for willow). Even-aged stems of all shrubs except maple were collected from a 1-hectare clearcut having homogenous soils and topography. Mountain maple was collected from a similar area in a nearby uncut forest and was also nearly even-aged (Ohmann *et al.* in press).

For each stem we recorded: height above ground (plant height), length of crown (crown depth), maximum crown diameter and diameter at right angles to it (to compute crown area), two measures of stem diameter at 15 cm above ground (diameter class and stem diameter), stem diameter at crown base (base diameter), stem length, and number of annual rings at the stem base. Plant height, crown depth, and diameter used to compute crown area were measured to the nearest 15 cm; diameter class to the nearest centimeter; stem diameter and base diameter to the nearest 0.25 cm; and stem length to the nearest 3 cm. All the above parameters are hereafter referred to as predictor variables.

Leaves, current year's twig growth, last year's twig growth, stem, fruits, and buds were all separated. Each component was bagged, dried at 75° for a minimum of 48 hours, and its mass was determined to the nearest 0.01 gram. The five biomass variables analyzed were leaves, this year's twigs, last year's twigs, stem (excluding fruits and buds), and total aboveground mass (including fruits and buds).

We sampled stems throughout the growing season and into the early winter dormant period. Therefore, phenological development differed over the entire sample period. Only data collected on five sample dates (7 July through 1 September when mature leaves were present) were used to examine the relations involving leaf biomass and total aboveground biomass. Data from 10 collection dates (21 July through 8 December) were used to examine relations involving this year's twig, last year's twig, and stem biomass. This was the period during which twig elongation was essentially complete (Ohmann *et al.* in press).

Data Analysis

We first analyzed five biomass variables and eight predictor variables for each of the five species. To determine which combinations of single variables would yield useful prediction equations, and to gain insight as to the appropriate form of the equation, we screened all possible single combinations using four functional relations (Crow 1971). A regression was calculated for each combination of biomass and predictor variable for each species using four equations in their linearized form:

Linear $Y = A + BX$ (1)

Exponential $Y = Ae^{BX}$

$\ln Y = \ln A + BX$ (2)

Allometric $Y = AX^{B}$

$\ln Y = \ln A + B \ln X$ (3)

Hyperbolic $Y = X/(A + BX)$

$1/Y = B + A(1/X)$ (4)

To assess the resulting 800 regressions, we first compared the results from each of the four models. The index of fit, R^2, is a poor criterion for comparing and choosing between regression models with different dependent variables. Hafley (1969) and Furnival (1961) suggest the use of a maximum likelihood function as an alternative means of comparing models. Because we were more interested in selecting a single model for suitable predictions based on the many possible relations between predictor and biomass variables for all five species, rather than the best model for each specific relation, we used the simpler measure of relative error, e, $(S_{y \cdot x}/\bar{Y})$ (Whittaker and Woodwell 1968) to evaluate the four functions.

The relative error estimate is analogous to the coefficient of variation, thus a value of 0.10 for e suggests an expected error for a given estimate of Y of $\pm$ 10 percent at $\bar{X}$ (Whittaker and Woodwell 1968). Relative error has another advantage over the traditional index of fit, R^2; it is not sensitive to scale, so it is a suitable criterion for comparing results based on data such as these (table 1) that vary considerably in size. We examined the relative error associated with regressions of all combinations of a predictor and a biomass variable, using each of the four functions derived from the linearized form. However, we calculated e after transforming the variables back to their original form. To further evaluate the models we plotted the residual sums of squares for a number of regressions to determine if there were significant trends away from the best-fit regression line.

After the functional form of the equation was chosen, we selected predictor and biomass variables that either showed the best relation based on relative errors, or that were of particular interest to our study. The data were then re-analyzed using an iterative nonlinear least squares technique to derive the prediction equations.

RESULTS AND DISCUSSION

Basic Data

Our equations are most suitable as predictors for other data sets when the size ranges of those sets fall within the size ranges of our variables (table 3).

Crown area varied (as measured by standard deviation) more than most of the other predictor variables, and also showed the greatest difference within species when data from 5 sampling dates were compared to those from 10 dates (table 3). The variation in crown area--as well as that in the other variables--results in part from biomass changes in these shrubs over the growing season (Ohmann *et al.* in press). Even though these changes are somewhat obscured

Table 3.--*Means, standard deviations, ranges, and number of stems collected for independent and dependent variables, for five shrub species*

Species	Stems collected	Independent variables: Plant height[1] Mean (SD)	Plant height Range	Crown area Mean (SD)	Crown area Range	Stem diameter class[2] Mean (SD)	Stem diameter class Range	Stem diameter Mean (SD)	Stem diameter Range	Dependent variables: Leaf biomass Mean (SD)	Leaf biomass Range	Current year's twig biomass Mean (SD)	Current year's twig biomass Range	Stem biomass Mean (SD)	Stem biomass Range	Total aboveground biomass Mean (SD)	Total aboveground biomass Range
	No.	*cm*		*cm²*		*cm*		*cm*		*grams*							
Mountain maple	[3]45	186 (66)	91-366	7,321 (9,086)	182-45,969	1.3 (0.77)	0.5-3.5	1.4 (0.62)	0.7-3.2	28 (33)	3-153	— (—)	—	— (—)	—	198 (286)	15-1,461
	[4]90	185 (67)	91-366	5,892 (7,387)	182-45,969	1.4 (0.66)	0.5-3.5	1.4 (0.57)	0.6-3.2	— (—)	—	4.3 (3.84)	0.2-22.6	148 (205)	9-1,236	— (—)	—
Green alder	45	166 (42)	91-259	1,658 (1,406)	365-6,384	1.1 (0.58)	0.5-2.5	1.2 (0.33)	0.7-2.1	21 (13)	5-54	— (—)	—	— (—)	—	103 (75)	19-372
	90	162 (39)	91-290	1,336 (1,189)	182-6,384	1.2 (0.52)	0.5-2.5	1.2 (0.31)	0.6-2.1	— (—)	—	6.2 (4.13)	0.2-17.2	69 (46)	9-260	— (—)	—
Beaked hazel	45	115 (27)	91-213	1,022 (1,107)	182-5,108	0.7 (0.44)	0.5-2.5	0.9 (0.30)	[5]0.6-2.3	11 (9)	2-50	— (—)	—	— (—)	—	50 (64)	11-351
	90	113 (23)	91-213	681 (681)	182-5,108	0.8 (0.47)	0.5-2.5	0.9 (0.24)	0.6-2.3	— (—)	—	2.2 (1.32)	0.4-8.6	33 (42)	7-300	— (—)	—
Juneberry	45	151 (41)	91-259	1,837 (1,536)	[5]182-7,661	1.0 (0.51)	0.5-1.5	1.1 (0.31)	0.5-1.9	15 (11)	3-54	— (—)	—	— (—)	—	82 (65)	10-270
	90	153 (47)	91-274	1,732	[6]182-7,661	1.1 (0.50)	0.5-1.5	1.1 (0.32)	0.5-1.9	— (—)	—	7.0 (6.24)	0.1-34.6	72 (57)	6-272	— (—)	—
Willow	36	165 (54)	91-305	3,821 (4,443)	547-19,154	1.2 (0.76)	0.5-3.5	1.4 (0.67)	0.8-3.8	40 (59)	4-307	— (—)	—	— (—)	—	192 (271)	28-1,152
	90	171 (47)	91-305	3,577 (3,490)	365-19,154	1.4 (0.58)	0.5-3.5	1.5 (0.53)	0.7-3.8	— (—)	—	12.0 (14.86)	0.6-95.8	150 (164)	13-884	— (—)	—

[1]Minimum height sampled 91.4 cm.
[2]Minimum class 0.5 cm.
[3]Collected over five sample periods.
[4]Collected over 10 sample periods.
[5]Based on only 44 stems.
[6]Based on only 89 stems.

when the data are "blocked" over time periods in the analyses, they probably contribute to the variability (high relative and standard errors) of the resulting equations. On the other hand, most extensive surveys of vegetation or browse require sampling over much of the growing season (or winter). So the extent to which seasonal change in biomass is included in our analyses (because of the long sampling period) may make our equations more applicable to such extensive vegetation surveys.

Selection of Equation Form

The relative errors associated with the 800 linearized equations indicated that the linear and allometric forms were superior to the exponential and hyperbolic forms for describing relations between predictor and biomass variables. For each species we ranked the four functions (1 through 4, lowest to highest) according to relative error associated with each predictor-biomass regression. These rankings were averaged for all species--a total of 200 ranks for each function. The resulting average ranks in ascending order were: linear (1.2), allometric (2.2), exponential (2.7), hyperbolic (3.9).

We expected the linear function to perform better than the other functions in describing some relations (e.g., that between last year's twig biomass and number of annual rings), but we did not expect the linear function to give a consistently small (in terms of relative error) but better description of the relations for almost all variables. We selected the allometric function to derive the prediction equations because: (1) its relative errors were very close to those of the linear function; (2) it is widely accepted for estimating biomass where a curvilinear trend is expected as the predictor variable increases.[4]

Selection of Predictor Variables

Stem diameter was the best predictor of biomass. For each species the eight predictor variables were ranked one through eight from the lowest to highest relative error associated with each combination of variables. The rank of each predictor variable was then averaged for all species.

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[4]*The linear function could also have been used for further analyses (Ovington* et al. *1967, Post 1970).*

The resulting average rank in ascending order was stem diameter (3.2), plant height (3.4), stem length (3.6), crown area (3.7), base diameter (3.7), crown depth (5.0), diameter class (6.1), and annual rings (7.4). The rankings were very similar for mountain maple, willow, and green alder; the ranking for juneberry was more similar to those three species than to beaked hazel which had much different rankings. If hazel is excluded from the calculations, average rank of relative error becomes stem diameter (2.9), base diameter (3.0), crown area (3.3), plant height (3.7), stem length (4.1), crown depth (5.2), diameter class (6.3), and annual rings (7.6).

Some of the predictor variables are closely related--such as those in each of the following groups: base diameter, stem diameter, and diameter class; stem length and plant height; and crown area and crown depth. We decided to continue the analyses with the diameter measures taken at 15 cm above ground because they could be applied more consistently in the field. Plant height rather than stem length was retained because it, too, could be more readily measured in the field. Crown area was retained because Peek (1970) suggested its use as an indirect measure of biomass for beaked hazel and willow. Finally, diameter class had been used in recent vegetation surveys in the area (Ohmann and Ream 1971, Ohmann *et al.* 1973) and was of particular interest to us, so it was retained although its relative error was higher than in most of the other predictor variables. Crown depth and annual ring count were eliminated from further analysis.

Selection of Biomass Variables

Of the five biomass variables, stem biomass was best predicted by the linearized equations using the allometric function. For each species, each combination of biomass-predictor variable was ranked one through five, lowest to highest, according to its relative error. The ranks for all equations containing a given biomass variable were averaged for all species. The resulting average rank was stem (2.4), this year's twig (2.8), leaf (2.9), total above ground (3.0), and last year's twig biomass (4.0). The ranking of best-estimated biomass variables were most similar for juneberry and green alder, followed by willow and mountain maple. All of these species were more similar to one another than they were to beaked hazel, which had a different average ranking of errors. If beaked hazel is excluded from the average, the order becomes stem (2.0), leaf (2.4), total above ground (2.5), this year's twig (3.2), and last year's twig biomass (4.4).

Because the average ranking of relative error for last year's twig biomass was high in comparison to the other variables, and because it seemed a less important component to consider separately, it was dropped from further analysis.

After screening we retained four biomass variables (leaf, this year's twig, stem, and total aboveground biomass) and four predictor variables (plant height, crown area, diameter class, and stem diameter) for further analysis.

Prediction Equations

All of the prediction equations, except a few for hazel, accounted for statistically significant (0.05 level) amounts of variation in the dependent variable. The equation parameters along with their associated R^2's and standard errors of estimate are presented in table 4. The index of fit, R^2, is appropriate for use in comparing data for the same dependent variable in table 4. A correction factor for bias due to logarithmic transformation of the data was unnecessary because a nonlinear technique on untransformed data was used to determine the parameters for each equation.

Biomass Variable Relations

Leaf biomass of mountain maple, juneberry, and willow was most closely related to crown area (in terms of highest R^2 and lowest Sy.x), while leaf biomass of alder was better related to stem diameter than to crown area. None of the relations between leaf biomass and predictor variables was statistically significant for hazel. The relations between leaf biomass and the predictor variables, measured by R^2, were highest for maple, while those for the other three species were similar and considerably lower (table 4).

Biomass of this year's twig was most closely related to plant height in all species except willow, where it was better related to crown area (table 4). For maple, alder, and hazel, crown area was the second-best predictor, and for juneberry

Table 4.--*Regressions for estimation of biomass of shrubs from northeastern Minnesota (allometric relation* $Y = ax^b$*)*

Item		Mountain maple	Green alder	Beaked hazel	Juneberry	Willow
REGRESSIONS ON PLANT HEIGHT (cm)						
Leaf biomass (g)	a	2.856E-05	2.746E-03	---	6.124E-04	2.770E-05
	b	2.599	1.738		1.998	2.735
	R^2	0.70	0.49		0.54	0.43
	S y.x	18.4	9.4		7.7	44.6
This year's twig biomass (g)	a	2.639E-03	1.793E-03	3.268E-03	3.041E-04	1.875E-05
	b	1.409	1.600	1.373	1.982	2.571
	R^2	0.33	0.40	0.23	0.55	0.31
	S y.x	3.2	3.2	1.2	4.2	12.4
Stem biomass (g)	a	4.134E-05	6.818E-03	2.089E-05	1.989E-03	1.011E-05
	b	2.835	1.806	2.980	2.067	3.163
	R^2	0.67	0.46	0.37	0.67	0.58
	S y.x	117.8	33.8	33.7	32.9	106.7
Total above-ground biomass (g)	a	1.747E-05	1.899E-03	2.791E-04	2.009E-03	1.303E-05
	b	3.047	2.120	2.520	2.096	3.175
	R^2	0.65	0.53	0.36	0.52	0.68
	S y.x	170.3	52.1	51.7	45.6	154.9
REGRESSIONS ON CROWN AREA (cm^2)						
Leaf biomass (g)	a	0.0115	0.2869	---	0.0428	0.0084
	b	0.8834	0.5858		0.7849	1.025
	R^2	0.86	0.58		0.66	0.66
	S y.x	12.3	8.6		6.7	34.8
This year's twig biomass (g)	a	0.3046	0.2674	0.3504	0.0819	0.0047
	b	0.3215	0.4496	0.2888	0.6072	0.9590
	R^2	0.22	0.35	0.11	0.35	0.56
	S y.x	3.4	3.4	1.2	5.1	10.0
Stem biomass (g)	a	0.0132	1.590	0.8201	0.7513	0.0157
	b	1.064	0.5354	0.5770	0.6250	1.109
	R^2	0.82	0.48	0.13	0.51	0.84
	S y.x	86.2	33.2	39.6	40.4	65.2
Total above-ground biomass (g)	a	0.0071	1.373	---	0.2786	0.0115
	b	1.138	0.5937		0.7641	1.166
	R^2	0.89	0.48		0.61	0.91
	S y.x	96.9	54.8		40.9	84.6
REGRESSIONS ON STEM CLASS (cm)						
Leaf biomass (g)	a	12.69	19.78	---	15.40	28.39
	b	1.818	0.6824		0.7386	1.362
	R^2	0.64	0.34		0.27	0.54
	S y.x	20.1	10.7		9.8	40.3
This year's twig biomass (g)	a	3.581	5.788	2.486	6.303	6.577
	b	0.6826	0.6727	0.3646	1.128	1.602
	R^2	0.17	0.28	0.11	0.32	0.26
	S y.x	3.5	3.5	1.2	5.2	12.8
Stem biomass (g)	a	47.88	56.96	40.10	64.14	56.77
	b	2.486	1.052	0.5878	1.204	2.266
	R^2	0.82	0.40	0.07	0.44	0.67
	S y.x	87.3	35.8	40.9	43.0	94.4
Total above-ground biomass (g)	a	64.38	82.35	66.16	82.93	99.96
	b	2.320	1.038	0.6363	0.9507	1.936
	R^2	0.79	0.56	0.09	0.38	0.67
	S y.x	132.0	50.3	61.6	51.6	158.1
REGRESSIONS ON STEM DIAMETER (cm)						
Leaf biomass (g)	a	11.13	13.97	---	13.34	21.59
	b	2.123	1.682		1.547	1.686
	R^2	0.80	0.63		0.47	0.54
	S y.x	15.0	8.1		8.7	40.3
This year's twig biomass (g)	a	3.244	5.147	2.371	5.923	5.823
	b	0.9149	1.184	0.7265	1.685	1.789
	R^2	0.22	0.29	0.11	0.37	0.48
	S y.x	3.4	3.5	1.2	5.0	10.8
Stem biomass (g)	a	40.94	43.94	38.57	50.63	56.09
	b	2.781	2.214	1.582	2.547	2.208
	R^2	0.93	0.87	0.20	0.90	0.92
	S y.x	53.4	16.7	38.1	17.9	47.9
Total above-ground biomass (g)	a	52.09	55.45	54.10	64.18	87.79
	b	2.724	2.409	1.229	2.322	1.981
	R^2	0.92	0.94	0.13	0.83	0.87
	S y.x	80.0	18.3	61.1	27.0	99.3

and willow, stem diameter was related second best (table 4). Although relations were statistically significant, none of the R^2's was very high; for example, R^2's for equations predicting current twig biomass were above 0.50 only for willow and juneberry.

Stem biomass was most closely related to stem diameter in all species except hazel, where it was most closely related to plant height. However, for hazel, this R^2 was lower than those related to stem diameter for the other species (table 4). The R^2's for the stem biomass-stem diameter relations (with the exception of hazel) were high and very similar, ranging from 0.87 to 0.93. Crown area also appeared to be closely related to stem biomass in maple and willow.

Total aboveground biomass was most closely related to stem diameter in maple, alder, and juneberry, with R^2's from 0.83 to 0.94. In willow the R^2 for prediction of total biomass based on crown area was slightly higher than that based on stem diameter (R^2 = 0.91 versus 0.87). Crown area also related well to total biomass in maple (R^2 = 0.89). In hazel, R^2's relating total biomass to all predictor variables were low (largest was 0.36 for relation with plant height), and the relation of crown area to total biomass was not statistically significant.

Performance of Predictor Variables

Plant height.--Plant height is easily measured in the field, especially when it is recorded to the nearest 15 cm as in this study. Unfortunately, measurements by large class intervals influence the resulting regression estimates, their standard errors, and R^2's. However, the relative errors associated with plant height in the linearized set of regressions were lower than those for stem length, presumably a more precise measure of the same parameter. We suspect that if height had been measured more precisely, it would have performed more nearly like stem diameter as a predictor variable. A combination of a more precise measure of plant height and of stem diameter as predictor variables in a multiple regression would probably account for much of the variation in shrub biomass, just as it does in the case of biomass in tree species.

In spite of the possible effect of imprecise measurement, an R^2 of 0.70 was obtained for the regression of leaf biomass on plant height in maple, and except for twig biomass, most of the R^2's for this predictor were in the 0.50 to 0.60 range.

Peek (1970) reported correlations coefficients of r = 0.88 and r = 0.76 for allometric regressions of twig weight (including both wood and leaf material) on plant height in willow and hazel. Because of a difference in twig definition, direct comparison is impossible. We found equivalent correlations of r = 0.66 and r = 0.56 in willow; and r = 0.21 and r = 0.48 in hazel for leaf and twig biomass regressions on plant height, respectively. In addition to the definition problem, there are methodological differences in the two studies that might account for the differences. Our material was sampled over time and consisted of all twig and leaf material present on each plant. Peek collected subsamples of twigs only once.

Crown area.--As expected, crown area performed well in comparison to the other predictor variables in accounting for leaf biomass. It also related well to total aboveground biomass. The highest R^2's for this variable occurred in regressions of total biomass on crown area (R^2=0.89 in maple and R^2 = 0.91 in willow), but total biomass was accounted for better in most cases by stem diameter. Leaf relations with crown area resulted in R^2's ranging from 0.58 to 0.86. Except for leaf equations in hazel and all those related to twig biomass, most R^2's involving crown area were above 0.50.

Peek (1970) also used crown area to predict twig weight (again including wood and leaf material). Correlations from our study for leaf (r = 0.81) and twig (r = 0.75) are lower than Peek's (r = 0.96) for willow. Our values for hazel (r = 0.22 for leaf and r = 0.33 for twig) are much lower than those reported by Peek (r = 0.93). The difference in this case is probably due to the definition of canopy area. Peek used the crown area of clones of stems while we used the canopy area of individual stems as the predictor variable.

Based on Lyon's (1968) finding that crown volume in juneberry is a more accurate predictor of twig production than is crown surface area, a multiple regression of crown depth and area might be appropriate for estimating twig biomass.

Stem class.--Like plant height, stem class suffers from lack of precision that influences the resulting estimates, their standard errors, and R^2's. In this study, stem diameter differed from stem class only in that it was a more precise measure (nearest 0.25 cm versus nearest cm). The standard errors of estimate for regressions using stem class as a predictor variable are always larger than those which use stem diameter (the standard errors of twig biomass estimates based on stem class average 1.05 greater than those using stem diameter; leaf 1.20 greater; stem 1.82 greater; and total 1.78 greater). Thus, although stem class is a convenient field measure, it should be used only if a more precise measure of diameter is not feasible. Where twig biomass estimation is of special interest, plant height is a better field predictor.

Stem diameter.--For leaf, stem, and total aboveground biomass estimation, this variable was a better predictor than the other variables, and for estimation of twig biomass it ranked second for three of the species. The highest R^2 associated with this predictor was 0.94 for the relation to total biomass in alder, but R^2's in the low 90's and high 80's were common for both total and stem biomass estimates. The R^2's tended to be lower for leaf and twig biomass estimates.

Tappeiner and John (1973) presented allometric regression equations for hazel using basal area based on stem diameter measured at 30 cm above ground. They found both aerial stem biomass (R^2 of 0.93) and leaf biomass (0.97) were related to basal area. Both the dependent and independent variables in their case were defined per unit land area, in contrast to variables based on individual stems in this study. Use of basal area for prediction of individual stem biomass was not examined here, but in the allometric form basal area and stem diameter differences only affect the size of the parameters and not the relation, so the results should have been similar.

In this study hazel stem biomass was related to stem diameter with an R^2 of 0.20, and to leaf biomass with a statistically nonsignificant R^2 of 0.03. We have no explanation for these widely varying results between our study and Tappeiner and John (1973). We presumed that the growth form and clonal nature of hazel make it difficult to predict biomass of individual plants or plant components from parameters measured on individual stems. Apparently biomass estimates in hazel should be tied to area or clonal measures.

CONCLUSIONS

(1) Except for hazel, a random sample of weights of individual stems or stem components combined with rather simple, rapid, field measurements of heights, crowns, or stems will provide relatively good biomass estimates for single plants. These estimates can then be related to density or to other shrub or community characteristics. In the case of hazel, however, estimates should be based on either clones or unit area.

(2) At least three (plant height, crown area, stem diameter) of the four predictor variables used here are useful for predicting either total aboveground biomass or biomass of stem components. Also, for four (mountain maple, green alder, juneberry, and willow) of the five species the various relations were similar enough that a single overall equation based on those four species might serve to estimate shrub biomass for purposes such as reconnaissance studies. The fact that the R^2's of many of the final prediction equations are lower than might be expected may be partly because biomass changes were incorporated into the analysis by sampling over time.

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