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RELATION OF CANOPY AREA AND VOLUME TO PRODUCTION OF THREE WOODY SPECIES[1]

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Abstract. Shrub canopy area, which more closely resembled an ellipse than a circle, shrub volume, and numbers of twigs per plant were highly correlated with weight of current leaves and twigs in aspen (*Populus tremuloides*), beaked hazel (*Corylus cornuta*), and pussy willow (*Salix discolor*). Lower correlations were obtained for shrub height with weight of current leaves and twigs. No appreciable change in correlations was obtained by using logarithmic regressions instead of linear regressions, except for weight versus height. Canopy area of shrub volume-weight relationships may be most applicable where floristics and production studies are combined.

INTRODUCTION

Most evaluations of shrub production are concerned with twigs which are available as winter forage for game or livestock, but evaluation of current production of both leaves and twigs is pertinent to studies of annual productivity of shrubs. Whether leaves and twigs or just production are to be estimated, however, it is conceded that such work is tedious (Pechanec and Pickford 1937*a*, Whittaker 1962). The possibility that shrub canopy cover could be used to estimate production was suggested by Daubenmire (1959) who stated that total canopy-coverage values for one union provide a comparative index of productivity at least for closely related ecosystems. However, he felt that relationships of canopy coverage to weight of production varied greatly depending on taxa, habitat type, growth state, and weather. If the relationship of canopy cover to weight of current twigs and leaves for a species is highly correlated, then canopy cover, already considered a valuable statistic for floristic studies (Lindsey 1956), could also provide productivity information. Recently, Lyon (1968) correlated twig production with crown volume in serviceberry (*Amelanchier alnifolia*), which further indicated that canopy cover could be correlated with twig and leaf production. This report is an evaluation of some relationships of canopy cover and shrub volume to production of twigs and leaves in aspen, beaked hazel, and pussy willow. The data were obtained in central Lake County, north of Lake Superior, in northeastern Minnesota.

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METHODS

Beaked hazel, pussy willow, and aspen were selected for study because they are common woody plants in northeastern Minnesota and they represent different growth forms, hazel being a clonal shrub, willow being a non-clonal shrub, and aspen being a clonal tree. Fifty plants of each species, 25 at each of two sites, were measured. Measurements included maximum height; two diameters taken at right angles to each other across the canopy of the plant, one of which was the maximum diameter for the plant; total number of twigs; and total weight of fresh twigs and leaves of current year's growth. The aggregating habit of hazel suggested that variation in canopy symmetry might be less if a whole clone was measured rather than individual rooted stems, so canopy areas for this species represent canopies of stem groups with overlapping canopies rather than individual stems. No aspen plants over 300 cm tall were sampled. Plants selected for study were growing on well-drained sites where the overstory was sparse or nonexistent and shading and crowding were minimized. All plants were considered to be typical in growth form for the species in the area. Data were obtained in late August 1969, after growth had ceased but before extensive leaf abscission occurred. Canopy, height, and weight measurements included leaves and twigs. No aments were measured or weighed. The area of each plant canopy was calculated from the formula for the area of a circle (area $=$ pi $\times$ radius^2) and from the formula for the area of an ellipse (area $=$ pi$/4d^1d^2$, where $d =$ diameter). Plant volumes were calculated by multiplying the canopy area by the height of the shrub. Ovendried weights were determined by drying ten 100-g samples of leaves and twigs of each species in a forced-air oven for 23 hr at 95°C (Horwitz 1965).

TABLE 1. Height, weight, number of twigs, and canopy area and volume of *Populus tremuloides, Corylus cornuta,* and *Salix discolor* plants

Measurement	*Populus tremuloides*		*Corylus cornuta*		*Salix discolor*	
	Mean	Range	Mean	Range	Mean	Range
Ovendry weight/plant (g)	43	(6-206)	79	(4-203)	141	(5-1,209)
Canopy area/plant (cm^2)[a]	3,171	(506-14,772)	6,284	(153-47,676)	10,284	(324-62,431)
Canopy area/plant (cm^2)[b]	3,073	(461-14451)	6,092	(121-47,351)	10,121	(243-62,385)
Volume/plant (cc)[c]	688,018	(40,155-4,726,463)	764,365	(8,409-9,445,590)	1,554,460	(14,826-1,179,804)
Volume/plant (cc)[d]	666,117	(36,541-4,648,160)	745,774	(6,672-9,381,341)	1,530,447	(14,595-1,178,942)
Number twigs/plant	32	(5-156)	89	(1-552)	192	(5-771)
Height/plant (cm)	158	(79-365)	90	(39-185)	119	(45-210)

[a]Area=pi x radius^2
[b]Area=pi/4 x d^1 d^2, where d=diameter
[c]Volume=pi x radius^2 x height
[d]Volume=pi/4 x d^1 d^2 x height, where d=diameter

RESULTS

Willow plants exhibited the greatest mean canopy area, mean volume, mean weight, and number of twigs per plant; these four measurements were lowest in aspen (Table 1). Variation in number of twigs, size of canopy area, volume, and weight per plant was greatest in hazel and least in aspen (Table 1). Hazel produced the greatest weight of twigs and leaves per unit of canopy and volume, illustrating the compactness of the foliage within each hazel aggregation and the more sparse foliage of willow and aspen.

Regression coefficients differed significantly between species ($P = .01$), but not between sites for each species (Table 2). No increase in correlation between weight and canopy area was obtained by using the elliptical area formula rather than the formula for the area of a circle. However, the shortest diameter averaged 92% of the longest diameter for willow, 77% for aspen, and 80% for hazel, indicating that the actual canopy shape resembled an ellipse more than a circle. Neither correlation nor sampling efficiency was improved by using logarithmic regressions for determining weight on canopy area. In all cases correlations were highest for willow and lowest for aspen.

Regressions of twig and leaf weight on plant volume showed relationships similar to weight on canopy area. Regression coefficients again differed significantly between species, but not by site within species. Correlation coefficients for weight on volume were also similar to those of weight on canopy area. No improvement in either correlation coefficients or sampling efficiency was obtained by using volume to predict weight of current twigs and leaves rather than canopy area. The elliptical volume formula did not increase accuracy of weight predictions over the cylinder formula. However, elliptical volume undoubtedly approaches the actual shape of the plant more closely than cylindrical volume. Curvilinear regression did not increase accuracy of the predictions. Again, correlations were highest for willow and lowest for aspen. The data reflect to some extent the different growth forms of the two shrub species when compared to aspen. Curvilinear equations were slightly more efficient than linear equations for aspen: an improvement in correlation coefficients from .89 for weight on elliptical volume to .92 for $\log_e$ weight on $\log_e$ elliptical volume occurred, with slightly smaller standard error of the logarithmic regression coefficient as well. Also, height was more highly correlated with volume, area, and weight in aspen than in hazel or willow. This suggests that for a sapling, where a great portion of the growth is concentrated in an increase in height, the curvilinear response is more pronounced than in shrub species where height extension may be a smaller portion of the total growth. However, the greatest increase in correlation, when curvilinear regression of weight on height was used instead of linear regression, occurred with willow, the tallest shrub form.

High correlations were obtained between numbers and weight of twigs and leaves per plant in each species. This tends to corroborate Shafer's (1963) findings of high correlations between numbers and weights of twigs without leaves in 100-ft^2 plots for aspen and four other woody species. Logarithmic equations did not improve the relationship. Sampling efficiency and correlation coefficients were similar for the two shrub species, but decreased for aspen. Generally, the sampling efficiency was below that obtained for either crown area or volume.

Correlation coefficients for linear regression of plant weight on height were the lowest obtained and showed greatest improvement when curvilinear regression was used. Plant height, which shows the least correlation with weight, appears to account for the slightly lower sampling effi-

TABLE 2. Regression equations and correlation coefficients for weight of current year's growth of twigs and leaves on various external plant-form measurements and plant height and number of twigs

Relationship	Species	Regression equation[e]	Correlation coefficient
Weight on canopy area[a]	*Salix discolor*	$Y=-33.56+0.017(0.00073)\ X$	96
	Corylus cornuta	$Y=-11.26+0.014(0.00067)\ X$	95
	Populus tremuloides	$Y=\ 2.55+0.013(0.00082)\ X$	91
Weight on canopy area[b]	*Salix discolor*	$Y=-32.74+0.0172(0.00071)\ X$	96
	Corylus cornuta	$Y=-10.58+0.0147(0.00069)\ X$	95
	Populus tremuloides	$Y=\ 2.88+0.0131(0.00088)\ X$	91
$\log_e$ weight on $\log_e$ canopy area[b]	*Salix discolor*	$Y=-4.51+1.012(0.0426)\ X$	96
	Corylus cornuta	$Y=-3.43+0.876(0.0517)\ X$	93
	Populus tremuloides	$Y=-3.68+0.922(0.0571)\ X$	92
Weight on shrub volume[c]	*Salix discolor*	$Y=-1.64+0.000092(0.0000033)\ X$	97
	Corylus cornuta	$Y=\ 15.82+0.000083(0.0000040)\ X$	95
	Populus tremuloides	$Y=\ 17.79+0.000037(0.0000027)\ X$	89
Weight on shrub volume[d]	*Salix discolor*	$Y=-1.05+0.000093(0.0000032)\ X$	97
	Corylus cornuta	$Y=\ 17.02+0.000083(0.0000043)\ X$	94
	Populus tremuloides	$Y=\ 17.94+0.000038(0.0000029)\ X$	89
$\log_e$ weight on $\log_e$ shrub volume[d]	*Salix discolor*	$Y=-6.41+0.797(0.0299)\ X$	97
	Corylus cornuta	$Y=-5.47+0.727(0.0373)\ X$	94
	Populus tremuloides	$Y=-4.96+0.659(0.0392)\ X$	92
Weight on number of twigs	*Salix discolor*	$Y=-15.86+0.820(0.0413)\ X$	94
	Corylus cornuta	$Y=-4.49+0.937(0.0576)\ X$	92
	Populus tremuloides	$Y=\ 3.25+1.255(0.109)\ X$	86
$\log_e$ weight on $\log_e$ number of twigs	*Salix discolor*	$Y=-1.81+0.897(0.0386)\ X$	96
	Corylus cornuta	$Y=-0.67+0.797(0.0459)\ X$	93
	Populus tremuloides	$Y=\ 0.36+0.959(0.0811)\ X$	86
Weight on plant height	*Salix discolor*	$Y=-207.6+2.933(0.498)\ X$	65
	Corylus cornuta	$Y=-146.2+2.504(0.361)\ X$	70
	Populus tremuloides	$Y=-43.6+0.548(0.0502)\ X$	84
$\log_e$ weight on $\log_e$ plant height	*Salix discolor*	$Y=-9.47+2.910(0.229)\ X$	88
	Corylus cornuta	$Y=-7.15+2.415(0.234)\ X$	76
	Populus tremuloides	$Y=-6.08+1.893(0.169)\ X$	85

[a]Computed with the circle area formula.
[b]Computed with the elliptical area formula.
[c]Computed with the cylinder area formula.
[d]Computed with the elliptical volume formula.
[e]Standard error of regression coefficient in parenthesis.

ciency in volume-weight regressions when compared with canopy-weight. Twig length, rather than plant height, has been highly correlated with twig weight by Basile and Hutchings (1966) and Telfer (1969).

Ovendry weights of aspen, hazel, and willow twigs and leaves averaged 38% of the fresh green weight, with no significant differences between species. Whittaker (1962) reported that twigs constituted 4–17% and leaves 77–91% of the total dry weight of leaves and twigs combined for some deciduous shrubs in the Great Smoky Mountains.

Discussion

Relationships of plant canopy area and volume with weight have practicality for several reasons. First, the sampling procedure involves actual measurement rather than estimation. Although weight estimation gives satisfactory results with grasses (Pechanec and Pickford 1937*b*), Shafer (1963) concluded that ocular estimates of weight in shrubs were of doubtful utility and accuracy. Second, a large sample of shrub heights and canopy diameters can be readily obtained. Finally, canopy area is a valuable estimate of the influence a plant has upon its community (Daubenmire 1959), and comparisons of such data among species are valuable in themselves.

Drawbacks include the need for some clipping to derive the appropriate regressions. This may be necessary each year in situations where shrub growth is rapid. Also, when judging production on an area basis, a separate sampling for species composition and density is required, and regressions may have to be developed for each species of interest. Thus the application of these relationships would be most appropriate in stands comprised of few woody species, or where production of individual shrubs or woody species is to be measured, or where only a few species are of interest in stands consisting of many species, and when shrub density and composition determinations are to be made for several reasons, including production estimates. Whittaker (1962) reported that production of mature or canopy shrubs so far overshadows that of the smaller individuals that net annual production for the dominant shrubs is close to that for the whole shrub stratum. This suggests that even in stands of greater diversity, annual production estimates could be simplified by considering only dominant species and individuals in certain situations.

Our data suggest that 25 plants or less can be clipped and measured to obtain reliable regressions for canopy area: weight determinations for one species in one stand. This sample can be obtained by one person in less than an hour. The 25 plant samples per site established regression coefficients accurate to within 10% of the point estimate for willow, 13% for hazel, and 18% for aspen, at the 95% level of significance, with accuracy for volume regressions slightly lower. The actual numbers of plants required to develop a satisfactory regression depend upon variation in sizes and densities, plus the desired level of accuracy. A selection of a representative sample of all sizes of a species is necessary to obtain a reliable regression. Lyon (1968) felt that 10–20 plants would suffice to determine a reliable regression for weight of twigs without leaves on crown volume in serviceberry.

Although there were no significant differences in regressions within each species which could be attributable to site, this merely indicates the similarity of the sites upon which the plants were collected. The regressions are considered applicable only to those sites upon which they were obtained. Such factors as degree of overstory closure, annual precipitation, soil productivity, degree of hedging attributable to browsing, shrub density, and shrub form may well affect these relationships. Since shrub production commonly decreases as overstory crown closure increases, a regression developed for shrubs on a site when closure is minimal will undoubtedly change as closure progresses. However, when a reasonably stable overstory canopy has developed, or when a shrub community has matured to where further growth is minimal and decadence is not appreciable, it seems likely that a rather stable relationship between shrub canopy area and weight would then occur. Whittaker (1962) reported that the proportion of growth of a shrub which is distributed in current twigs and leaves decreases as the shrub matures, which would also affect the canopy area: weight relationships.

A wide range of shrub sizes was measured to account for as much variation in the stands as possible. However, Shafer (1963) stated that sprout clumps of the same species, even when similar in shape and total numbers of twigs, often differed in mean weight per twig by as much as 40%. This type of variation was readily apparent to us also, but did not seem to appreciably affect the relationships. It is possible that leaves, included in our measurements but not Shafer's, could account for some of this difference. Whittaker (1962) reported that about 40–50% of a deciduous shrub's growth above ground is in leaves. The shrub volume calculations are overestimations of the true space occupied by the shrub. Overestimation was greatest for aspen, where the canopy is usually contained in the upper half of the plant, and the lower half is the rooted stem. Further, the sampling error for the canopy area equations appears to be somewhat less than for the volume equations, so shrub canopy area may be a more practical parameter than volume. Assessment of between-stand variation within species, between-species variation, and annual variation in these relationships would help to determine the utility of using shrub canopy area to assess current twig and leaf production.

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