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Production of Deerbrush and Mountain Whitethorn Related to Shrub Volume and Overstory Crown Closure

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Deerbrush (*Ceanothus integerrimus*) and mountain whitethorn (*C. cordulatus*) are important browse species for mule deer (*Odocoileus hemionus*) on migratory and summer ranges in the Sierra Nevada of California.¹ Both species are also used by cattle grazing on summer allotments.² In addition, both species are a concern of forest managers: dense stands can result from logging activities and delay conifer regeneration. As forest trees become reestablished, they shade out deerbrush and whitethorn shrubs³ reducing potential forage for deer and cattle.

In studying the effects of timber harvesting on response of deerbrush and mountain whitethorn in the understory, I needed to estimate annual production by the shrubs and utilization by browsing animals. This note reports a study relating production of deerbrush and mountain whitethorn to shrub volume and overstory crown closure. Sampling sites were established in a second-growth Sierra Nevada mixed conifer forest in central California. Sampling by regression models showed that shrub production increased as volume and volume squared increased, but decreased as overstory crown closure increased.

ESTIMATING SHRUB PRODUCTION

Two basic approaches to estimating the production by shrubs are direct and indirect. In the direct approach, all browse in three-dimensional plots of known size is clipped and weighed. Statistical analysis is

simplified, but sampling can be time consuming, and the technique is destructive, rendering it unsuitable for use on permanent plots.⁴

The indirect approach involves developing regression equations to predict browse production on the basis of other plant parameters such as twig counts and average twig weights, crown diameters, crown areas, or crown volumes. The indirect approach is nondestructive and can be used repeatedly on permanent plots. Properly constructed and applied predictive equations can provide accurate information at lower cost than can the direct approach.⁴

Close logarithmic relationships were found between crown diameter and dry leaf weight for two shrub species, including *Ceanothus crassifolius*, in southern California.⁵ A similar relationship was reported between mountain mahogany (*Cercocarpus montanus*) crown diameters and annual production in western Colorado.⁶ Shrub diameters, crown denseness, and crown depth were the most useful predictors of annual production in several shrubs in Nevada.⁷ Shrub volume was correlated with annual twig production in serviceberry (*Amelanchier alnifolia*) in Montana,⁸ and in several species in Minnesota.⁹ Net annual above-ground productivity was related to crown volume in creosote (*Larrea divaricata*) in New Mexico.¹⁰ In California, browse production in deerbrush was predicted on the basis of the diameter of second order stems,¹¹ and current year's growth in young mountain whitethorn shrubs was related to canopy area.¹²

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Annual production by deerbrush (*Ceanothus integerrimus*) and mountain whitethorn shrubs (*C. cordulatus*) in the south-central Sierra Nevada of California was related to shrub volume, volume squared, and overstory crown closure by regression models. Production increased as shrub volume and volume squared increased, and decreased as overstory crown closure increased. The log of production by individual twigs was a function of the log of air-dry twig diameter at point of current year's growth (allometric equation). These models were developed for a specific sample of shrubs, but the same independent variables may be of value in developing predictive equations for shrubs collected at other locations.

Retrieval Terms: *Ceanothus integerrimus*, *Ceanothus cordulatus*, shrub production, overstory-understory relationships, Sierra Nevada, California

Measurements of twig diameters at point of current year's growth and at point of browsing can be used to estimate shrub biomass removed by browsing animals.⁴ A random sample of such browsed twigs, along with an estimate of browsed versus unbrowsed twigs, can be used to estimate utilization of current year's growth for an entire shrub.¹³ Using twig weight and diameter information can result in more accurate utilization estimates than before and after twig length measurements, or simple counts of browsed and unbrowsed twigs.^{14,15}

STUDY AREA AND METHODS

The study area was located on the southeast flank of Dinkey Mountain, in the Sierra National Forest east of Fresno, California (37° 00' N, 119° 08' W). Sampling sites were located at about 1700 m elevation in second-growth Sierra Nevada mixed conifer forest, on Shaver series soils (Pachic Ultic Haploxerolls) characterized by gentle to moderately steep slopes (15–50 percent). Overstory tree species included white fir (*Abies concolor*), ponderosa pine (*Pinus ponderosa*), sugar pine (*P. lambertiana*), and incense-cedar (*Libocedrus decurrens*). The study sites represent the upper elevational limit for deerbrush and the lower limit for mountain whitethorn in the southern Sierra Nevada. The sites were used by mule deer primarily during spring (May–June) and fall (October–November) migration each year. Cattle had access to the sites from July to September.

At four sites, a total of 30 deerbrush shrubs (12 in 1982, and 18 in 1983), and 30 mountain whitethorn shrubs (10 each in 1981, 1982, and 1983) were selected. They represented the range of shrub volume and overstory crown closure encountered in the study area. Shrub height, the largest shrub diameter, and diameter at right angles to largest shrub diameter were measured to the nearest 0.01 m. Shrub volume (VOL) was calculated from the average of the two diameters with the formula for a cylinder. Crown closure for overstory trees was obtained by taking a photographic slide with a 35-mm camera and a 28-mm wide-angle lens (75° field of view), held 1.5 m above the ground. The resulting slide was projected on to a grid of 150 points and the percentage of points

intersecting tree boles, branches, or crown was recorded as overstory crown closure (CROWN).

Each fall, all leaves and the current year's growth of twigs available to browsing animals (within 0.6 m from the edge of the shrub and not over 1.5 m above ground) were sampled. To reduce sampling time, only portions of the shrubs were clipped. Four randomly located, nonoverlapping wedges were delineated on each shrub, and only the current growth within these wedges was clipped. The angle of the wedge (range 10–90°) chosen was a function of the size of the shrub. Larger angles were used on smaller shrubs. About one-third of all shrubs were small enough that each wedge subtended a full 90 degrees, and the entire shrub was clipped. If the wedge angle was less than 90 degrees, the resulting forage weights were expanded to represent a full quarter of the shrub. Forage weights from each wedge were combined to arrive at a value for the shrub as a whole.

A sample of individually tagged twigs on shrubs not clipped as part of this study indicated that both deerbrush and whitethorn ceased twig elongation by late August. To avoid missing some of the current year's growth because of leaf fall, deciduous deerbrush shrubs were clipped in late August and early September each year. Evergreen whitethorn shrubs were not clipped until October each year. Twigs and leaves were separated, oven-dried at 55–60 °C for 48 hours, and weighed to the nearest 0.1 g. The largest basal stem of each shrub was sectioned for age determination.

To develop predictive equations for individual twigs, leaf and twig component weights for 862 unbrowsed deerbrush twigs (462 in 1982, 400 in 1983) and 787 unbrowsed whitethorn twigs (400 in 1981, and 387 in 1982) were measured to the nearest 0.01 g. In addition, air-dry diameter at point of current year's growth (ADD) was recorded to the nearest 0.05 mm.

Data for all years and sites were pooled. Predictive equations were developed by using multiple linear regression (PIR) and all possible subsets regression (P9R) programs available with BMDP.¹⁶ For variables expressed as percentages, arcsin transformations were used.

RESULTS AND DISCUSSION

Shrub Production

The deerbrush shrubs in this study averaged 7.67 years of age (range 2–14 years), 9.33 m³ in volume (range 0.57–45.87 m³), and grew under an average overstory crown closure of 33 percent (range 0–72 percent). The whitethorn shrubs averaged 9.63 years of age (range 5–20 years), 18.59 m³ in volume (range 0.11–103.34 m³), and grew under an average overstory crown closure of 27 percent (range 6–71 percent).

Oven-dry weight of twigs (TWIGS) and oven-dry weight of leaves (LEAVES), in both deerbrush and mountain whitethorn, increased with increasing shrub age and volume. Combined twig and leaf weights (TOTAL) also increased as a function of shrub volume (VOL) (fig. 1). These increases did not appear to be linear, however, showing a convex-downward functional relationship. TWIGS, LEAVES, and TOTAL in both deerbrush and whitethorn also tended to decrease with increasing overstory crown closure (CROWN) (fig. 1).

To determine the best subset of independent variables with respect to precision of estimates, I used all possible subsets regression. Separate equations were developed for TWIGS, LEAVES, and TOTAL for both species, using AGE, VOL, VOL², and CROWN as independent variables. The criterion used to select the best subset was the lowest Mallows's CP value.¹⁷

In deerbrush, the best subsets for all dependent variables (TWIGS, LEAVES, and TOTAL) consisted of the independent variables VOL, VOL², and CROWN (table 1). In each case, the b value for VOL² was negative (which accounted for the convex-downward shape of the production-volume curve), as was the b value for CROWN (indicating decreasing production as overstory crown closure increased).

For whitethorn LEAVES, the best subset of independent variables was again VOL, VOL², and CROWN (table 1). However, the best subset for whitethorn TWIGS was VOL and AGE, and the best subset for TOTAL was VOL and CROWN. But the use of the expanded model (including VOL, VOL², and CROWN as in-

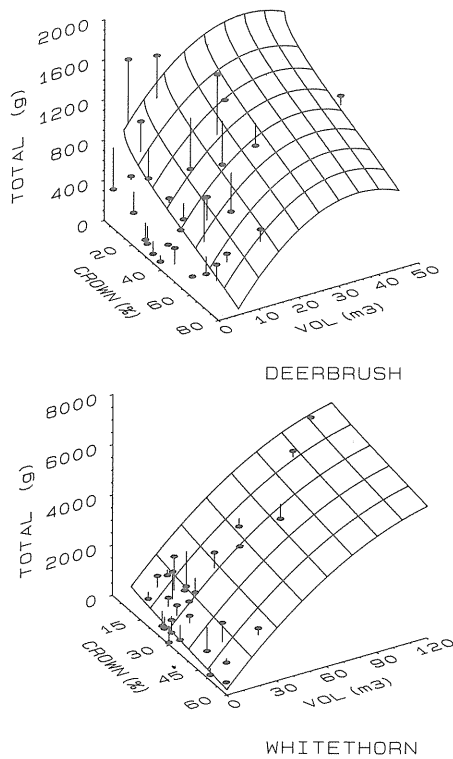


Figure 1—Relationships between oven-dry weight of current year's production (TOTAL), shrub volume (VOL), and overstory crown closure (CROWN) in deerbrush and whitethorn shrubs. Response surface is in the form of $TOTAL = b_0 + b_1VOL + b_2VOL^2 + b_3CROWN$, with coefficients as shown in *table 1*. Points are connected to response surface with vertical lines.

dependent variables), although not adding much to R^2 , did not result in large increases in CP ($TWIGS\ CP = TOTAL\ CP = 4.00$) (*table 1*). Therefore, the parameters for the full model are given (*table 1*). Measurements of VOL and CROWN are relatively easy to obtain and do not require destruction of the shrub, unlike AGE.

Twig Production

Models were constructed for the production, by individual twigs, of twigs alone (TWIGWT), leaves (LEAFWT), and twigs and leaves combined (TOTALWT) as functions of air-dry diameter at point of current year's growth (ADD). TOTALWT was related to ADD in both deerbrush and mountain whitethorn in a convex-upward function (*fig. 2*). The relationship was portrayed by the allometric equation $Y = aX^b$. Natural log transformations were used and least squares solutions found for the models:

$$LN(Y) = LN(a) + bLN(X),$$

where separate equations were calculated for LN(TWIGWT), LN(LEAFWT), and LN(TOTALWT) as dependent variables, and LN(ADD) was used as the independent variable.¹⁸ Direct conversion back to untransformed units is biased and requires that the antilog of the estimated Y values be multiplied by a correction factor (CF):

$$CF = \exp((S_{y,x})^2/2),$$

where $S_{x,y}$ is the standard error of the estimate for the regression model.^{18,19} Models developed for deerbrush and mountain whitethorn twigs resulted in r^2 values shown (*table 2*). Standard errors of the estimates are provided for calculation of the correction factor necessary to convert back to untransformed scales.

Utilization by Browsing Animals

Individually tagged twigs on both deerbrush and mountain whitethorn shrubs indicated that migrating deer browsed about 25 percent of the new twigs before mid-June, as they were starting to elongate.

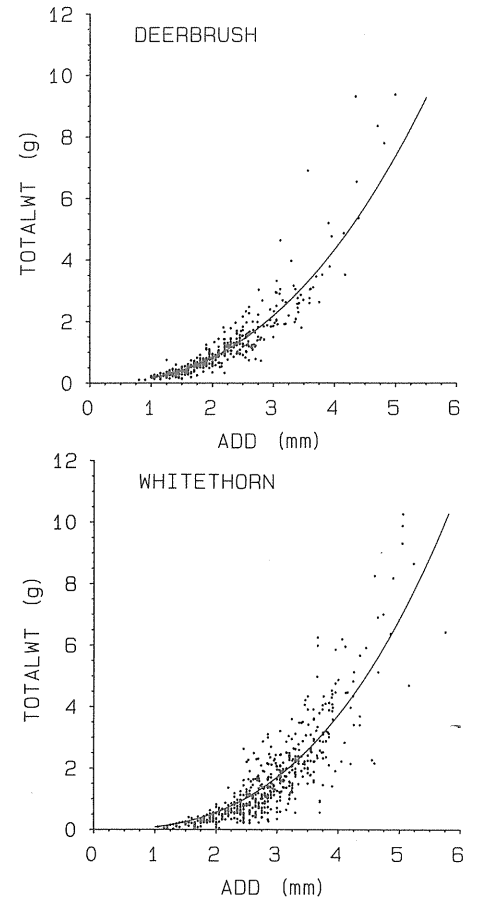


Figure 2—Relationship between oven-dry weight of current year's production (TOTALWT) and air-dry diameter at point of current year's growth (ADD) in deerbrush and whitethorn twigs. Plotted line is in the form of $LN(TOTALWT) = LN(a) + bLN(ADD)$, with coefficients as shown in *table 2*. For clarity, not all points with ADD less than 3 mm are plotted.

The usual shrub response was for a remaining lateral twig to take over terminal growth. This early browsing by deer did not appear to affect final production estimates, but further research is needed.

Table 1—Regression coefficients and their standard errors for the subsets of equations ($TWIGS, LEAVES, TOTAL$) = $b_0 + b_1VOL + b_2VOL^2 + b_3CROWN$; standard errors of the estimates ($S_{y,x}$); squared multiple correlation coefficients (R^2); and Mallow's CP values; for deerbrush and whitethorn shrubs

Y	b_0	VOL (m^3) $b_1 (\pm SE_{b_1})$	VOL ² $b_2 (\pm SE_{b_2})$	CROWN (pct)* $b_3 (\pm SE_{b_3})$	$S_{y,x}$	R^2	CP
Deerbrush (n = 30 shrubs)							
TWIGS (g)	290.98	22.12 (± 7.09)	-0.449 (± 0.173)	-6.14 (± 1.78)	140.79	0.46	3.04
LEAVES (g)	251.37	41.53 (± 9.19)	-0.464 (± 0.224)	-6.12 (± 2.30)	182.43	0.69	4.96
TOTAL (g)	542.35	63.65 (± 15.30)	-0.913 (± 0.374)	-12.26 (± 3.84)	303.90	0.61	3.84
Whitethorn (n = 30 shrubs)							
TWIGS (g)	711.12	35.98 (± 9.41)	-0.040 (± 0.102)	-12.15 (± 6.61)	380.86	0.86	4.00
LEAVES (g)	736.08	34.35 (± 9.95)	-0.197 (± 0.108)	-12.07 (± 6.98)	402.53	0.64	4.02
TOTAL (g)	1447.20	70.33 (± 15.87)	-0.236 (± 0.172)	-24.22 (± 11.10)	642.16	0.84	4.00

*Arcsin transformed (degrees)

Table 2—Regression coefficients and their standard errors for the equations $LN(TWIGWT, LEAFWT, TOTALWT) = LN(a) + bLN(ADD)$, where ADD is twig air-dry diameter; standard errors of the estimates ($S_{y,x}$); and squared correlation coefficients (r^2); for deerbrush and whitethorn twigs

Y	LN(a)	LN(ADD) b (± SE _b)	S _{y,x}	r ²
Deerbrush (n = 862 twigs)				
LN(TWIGWT) (g)	−3.334	3.093 (±0.066)	0.600	0.72
LN(LEAFWT) (g)	−2.254	2.003 (±0.051)	0.461	0.64
LN(TOTALWT) (g)	−1.898	2.386 (±0.038)	0.348	0.82
Whitethorn (n = 787 twigs)				
LN(TWIGWT) (g)	−3.614	3.296 (±0.062)	0.577	0.78
LN(LEAFWT) (g)	−2.967	1.994 (±0.061)	0.566	0.58
LN(TOTALWT) (g)	−2.597	2.729 (±0.054)	0.508	0.76

Little additional summer use of sample shrubs was observed during this study. However, at higher elevations on deer summer ranges, whitethorn leaves are an important component in deer diets.¹ Whitethorn twigs become sharply spine-scent by late June, and deer normally pick individual leaves off the twigs. Similarly, because sheep often strip leaves from snowberry (*Symphoricarpos oreophilus*) twigs, percentage of twigs browsed did not accurately estimate browsing intensity. Therefore, the use of a model based on leaf weight as a function of twig diameter was recommended.¹⁵

CONCLUSIONS

Production of twigs and leaves by deerbrush and mountain whitethorn shrubs was a function of shrub volume and overstory crown closure. Net production, defined as the annual growth available to browsing animals, increased as shrub volume increased. Increasing crown closure was related to decreased production of leaves and twigs.

In a previous study, basal stem diameters from 60 secondary stems in deerbrush were used to develop predictive models for leaf weight and total weight per secondary stem.¹¹ Using that technique, several basal stem diameter measurements would be required for each shrub. Shrub height and diameter may be obtained from data taken for other purposes, and would yield the necessary estimate of shrub volume for the models presented here.

Models presented here were developed for a specific sample of shrubs, and should not be used to estimate production by shrubs in other areas. Growth patterns of both deerbrush and mountain whitethorn

undoubtedly vary as a function of latitude and elevation. Whitethorn shrubs growing at higher elevations, for example, are likely to produce less during the shorter growing season and leaves may be smaller. However, measurements of shrub volume and overstory crown closure can be used to develop equations for shrubs growing elsewhere.

Shrubs, particularly those growing in more xeric locations, often show annual differences in production related to precipitation and available moisture patterns.¹⁹ Production per shrub and production per twig did not differ between years in this study; however, the study was not designed to test for such differences. Also, precipitation, primarily snowfall in winter, was normal or above normal during the 3 years of this study. Production would likely be lower during drought years.

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