Koedoe 21:67–76 (1978)

STANDING CROPS OF DOMINANT *COMBRETUM* SPECIES AT THREE BROWSING LEVELS IN THE KRUGER NATIONAL PARK

B. R. DAYTON
Biology Department
State University College
Oneonta
New York 13820
U.S.A.

Abstract – In red bushwillow veld near the Sand River in the Kruger National Park, Republic of South Africa, a determination was made of the standing crops of *Combretum apiculatum* and *C. zeyheri* at browsing levels delineated by the maximum feeding heights of impala (1,5 m), kudu (2,5 m) and giraffe (5,5 m). Using harvested sample trees, logarithmic or linear regression equations were generated which related basal diameter or stem height to biomass or percentage of total biomass at the different levels. Biomass was divided into two components: current shoots and wood plus bark. Regression forms and variables which produced the highest correlation coefficients changed with changes in species or browsing level, however, most equations were logarithmic with basal diameter as the independent variable.

Nine per cent of the estimated standing crop was current shoots, biomass considered potentially edible. Although the preferred browse species, *C. apiculatum,* comprised 67% of the total current shoot standing crop, only 2% of the total consisted of *C. apiculatum* below 2,5 metres. The low availability of preferred browse to impala and kudu may have in part resulted from prolonged overbrowsing by impala congregating near a perennial water supply.

Introduction

Woody vegetation has been managed in the Kruger National Park (KNP) since the 1950s. The thrust of the management has been to control "bush encroachment" through periodic burning in order to maintain a balance between populations of grazing and browsing ungulates, as well as to minimize the possibility of accidental fires (Brynard, 1964).

Some management has also been necessary in the KNP to protect, rather than reduce, woody plant growth. Culling of elephant herds has been carried out in part to prevent overutilization of woody species (Pienaar 1972). Further decisions about culling of browsing species may be necessary in the future. Widespread pruning of knobthorn (*Acacia nigrescens*) due to giraffe browsing is now apparent in the knobthorn-marula (*Sclerocarya caffra*) veld (S.C.J. Joubert, Division of Nature Conservation, Skukuza, *pers. comm.*). Impala herds, already subject to culling (Pienaar 1972), are causing browse lines in red bush willow (*Combretum apiculatum*) and mopane (*Colophospermum mopane*) veld, as they congregate near perennial streams during the dry season.

Throughout the world, decisions to reduce densities of browsing ungulates have often been based on the degree of utilization of browse plants. Typically, ranges have undergone degradation of carrying capacity before action was taken. However, regression techniques, coupled with methods for determining forage intake by ungulates (Van Dyne 1968), now provide the potential for estimating range carrying capacities before they are approached by browsing populations. Regression techniques allow the calculation of woody plant standing crop and productivity, utilizing stem diameter and length measurements in sample plots (Whittaker and Woodwell 1968).

In 1977 a study was undertaken to devise methods for investigations of woody plant productivity in the KNP, relating to the availability of browse. The study was designed to answer the following questions: (1) What is the standing crop of the dominant woody species in a major habitat type (red bushwillow veld)? (2) What portion of the standing crop is composed of edible tissue (twigs, leaves, fruits)? (3) What portion of edible tissue is produced by the species preferred by browsing ungulates? (4) What portions of the edible tissues are, by virtue of their height above ground, unavailable to major browsing species?

Study Sites

Two replicate sites, 8 km northeast of Skukuza and judged to be floristically and structurally representative of red bushwillow veld in the KNP, were selected. The sites are situated approximately 1 km apart on the tops of topographic undulations, and occupy granitic soils of the Portsmouth series. The dominant species on both sites are *Combretum apiculatum* and *C. zeyheri*. A Braun-Blanquet vegetation sample (taken by B. J. Coetzee, Division of Nature Conservation, Skukuza) indicated that *C. apiculatum* and *C. zeyheri* comprised 57% and 28% of the crown coverage, respectively. According to Van Wyk (1974), *C. apiculatum* leaves are eaten by bushbuck *Tragelaphus scriptus*, eland *Taurotragus oryx*, giraffe *Giraffa camelopardalis*, kudu *Tragelaphus strepsiceros*, klipspringer *Oreotragus oreotragus*, elephant *Loxodonta africana*, impala *Aepyceros melampus* and steenbok *Raphicerus campestris*. *Combretum zeyheri* foliage was reported to be little utilized, although sometimes eaten by elephant and giraffe.

The sites are within 2 km of the Sand River and approximately 250 m from the western boundary fence. Proximity to a perennial water supply and the "edge" caused by the cleared area along the fence provide ideal habitat for impala. Browse lines at 1,5 m on fallen *C. apiculatum* stems and severe pruning of other palatable woody species (*Gardenia spatulifolia, Dichrostachys cinerea* and *Commiphora africana*) indicated that the impala were exerting heavy browsing pressure on both sites. Giraffe and kudu were also frequently observed feeding in the area.

Methods

At each site a 50 m × 50 m plot was established, with a 30 m × 30 m plot nested inside. Measurements were made on *C. apiculatum* stems within the entire 50 m × 50 m plot on each site, while *C. zeyheri* stems were measured only within the 30 m × 30 m plots. In February, stem diameter above the basal swell was determined to the nearest 0,1 cm on all stems $\geq$ 1 cm in diameter, and height was estimated to the nearest 0,5 m with a measuring rod.

During March and April, 14 stems of *C. apiculatum* and 25 stems of *C. zeyheri* were cut at the basal swell. Stems were selected from around the sample plots to represent the range of sizes and growth forms at both sites. Prior to felling, basal diameter and height measurements were made, and height permitting, stems were marked at 1,5 m and 2,5 m above the ground. After taller stems were felled, approximate 5,5 m levels were marked in the crowns after aligning a measuring rod with the 1,5 and 2,5 marks. These heights were chosen to represent the maximum feeding levels of impala, kudu and giraffe, respectively and also correspond to canopy height levels now employed by Coetzee and Gertenbach (1977) in describing woody vegetation composition in the Kruger National Park.

Each stem was cut into browsing levels delineated by the above heights. Each browsing level was then divided into two live biomass components: "current shoots" (twigs, leaves and fruits of the current season) and "wood plus bark". Dead material was removed. In the case of large *C. apiculatum* stems it was not practical to clip current shoots from all branches. Here, branches from heavily foiliated browsing levels were separated into two or three size classes, and a systematic sample consisting of every third, fourth, or fifth branch was taken so that there was a total of four to six branches for each size class. Current shoots were then clipped from the sample branches. The proportions of the fresh weights of the sample branches represented by current shoots were determined and multiplied by total fresh weights for their size classes to obtain estimates of current shoot fresh weight. A test of the reliability of this sampling method on two stems, 12,0 cm and 10,2 cm in diameter, yielded a range of deviations of estimated from actual current shoot fresh weights of from +2,8% to −7,3% for all browsing levels.

Total fresh weights of all biomass components were obtained in the field using spring balances. When practical, entire components were sealed in plastic bags and transported to the laboratory for dry weight determination. Where large biomass was involved, samples were taken. Samples of trunk and branch segments > 1,0 cm in diameter consisted of 5,0 cm long discs cut off the ends, while samples of current shoot clippings and branch segments > 1,0 cm in diameter consisted of representative portions amounting to 20%–50% of the total. Samples were weighed, dried at 105° C, and reweighed in the laboratory to obtain dry weight-fresh weight ratios. These ratios were multiplied by total fresh weights of biomass components to obtain total dry weight estimates.

Regressions, based on data from the sample stems, were computed for each species using as independent variables: height, $\log_{10}$ height, diameter, or $\log_{10}$ diameter. Dependent variables were total weight, percentage of total weight at one of the four browsing levels, actual weight at one of the levels, or the logarithms of one of the above. Both simple and multiple regressions were generated for all combinations of variables. Multiple regressions were abandoned when it was demonstrated that, in all but one case, the addition of the second variable led to an increase of less than 0,01 in the correlation coefficient (r). Simple regression equations having the highest r values were then selected to be used in the estimation of standing crop for each biomass component-species combination.

"Estimates of relative error", E and e (Whittaker and Woodwell 1968), were calculated from the standard error of the estimate (SEE = $[\sum d^2/(n-1)]^{1/2}$), where d is the difference between the actual value of y and one calculated from the regression equation for a given value of x, and n is the number of pairs of measurements of x and y. E and e are measures of the expected dispersion of values derived from logarithmic and linear regressions, respectively. For a logarithmic regression, E, the antilog of SEE, is a factor by which a given value of y is divided and multiplied to obtain a range of expected error. For a linear regression, e = SEE/$\bar{y}$, is a proportion which, when added to and subtracted from a given value of y, yields a range of expected error. These error ranges include 68% of the values, assuming they have a distribution which is log normal in the case of E, or normal in the case of e, for a given value of x.

Standing crops of wood plus bark and current shoots at the 1,6 m–2,5 m level for *C. zeyheri* and of current shoots at the 2,6 m–5,5 m level for *C. apiculatum* were estimated by subtracting the sums of the estimates for other levels from total weight estimates. This procedure eliminated regressions which due to their high E values would have produced unacceptably wide error ranges.

A computer program, developed by M. Vedder of the State University College at Oneonta, New York, Computer Centre, was employed to calculate standing crop estimates based on the estimative equations in Table 1 and the measurements of stem diameter and height in the sample plots. The program rejected standing crop estimates for heights which stems had not actually attained or for heights which produced estimates less than zero, as in the case of wood and bark at the > 5,5 m level for *C. apiculatum* stems ≤ 6,0 m tall. Standing crop estimates for stems ≤ 1,5 m tall were calculated using total weight regressions.

Results and Discussion

Estimative Equations

Correlation coefficients of regression equations selected for estimation of standing crops were all greater than 0,90 indicating relatively "good fits" and all were significant (Table 1). These "fits" were in part, however, a function of the selection of wide ranges of stem sizes for the samples. Most $\underline{E}$ values for logarithmic regressions were between 1,1 and 2,0, a range which the extensive data of Whittaker and colleagues indicates is typical (Whittaker and Woodwell 1968; Whittaker, Bormann, Likens and Siccama 1974). The two logarithmic regressions employed that had $\underline{E}$ values around 2,2, those for current shoots at 0 m–1,5 m for both species, produced by far the lowest standing crop estimates, making their errors relatively less important. Error ranges of 20%–40% are indicated by the $\underline{e}$ values for linear regressions.

A criticism of the use of logarithmic regressions to estimate standing crop of trees has been that they tend to produce overestimates for large trees (Whittaker and Woodwell 1968). This results from the regressions being overly influenced by the smaller trees in the sample, which show relatively greater increases in biomass with increases in diameter or height than do large trees. Plots of actual biomass of our sample trees compared with plots of biomass derived from regression equations for the same trees, indicate that there was a tendency to over-estimate, up to approximately 50%, standing crops at all browsing levels for *C. apiculatum* stems > 20 cm in diameter. Stems in this category, represented 35% of the estimated total standing crop of current shoots in the sample plots. No other trends of overestimation or underestimation were indicated by the plotting. It is recommened that, in future investigations, care be taken not to under-represent large stems in samples used to generate regression equations.

In most cases regressions with diameter as the independent variable, produced higher $\underline{r}$ values than regressions with height as the independent variable. Exceptions to this were those based on the relatively small amounts of *C. apiculatum* current shoots projecting down into the 0 m–1,5 m and 1,6 m–2,5 m levels, or the somewhat greater of amounts of either wood plus bark or current shoots projecting up into the > 5,5 m level. *Combretum apiculatum,* unlike *C. zeyheri* produces well-formed crowns, the bulk of which are in the 2,6 m–5,5 m level. It seems reasonable that the biomass of branches or shoots projecting upward or downward from these crowns would be more closely correlated with height of the crowns above ground rather than with stem diameter. The indication is that estimates of browse production at different height levels should be based on measurements of both height and diameter.

Logarithmic equations, in general, had "better fits" than linear regressions. Exceptions were equations for the > 5,5 m level of *C. apiculatum* which demonstrated linear relationships between standing crops and stem diameter or height. These relationships probably are a result

Table 1

Equations used in Combretum *standing crop estimates where:* W_x = *biomass (g dry wt.) at browsing level* x; W_T = *total biomass;* h = *stem height (m);* d = *basal diameter (cm);* E *and* e = *estimates of relative error for logarithmic and linear regressions, respectively* r = *coefficient of correlation; and* N = *sample size.*

Species + Component	*Level (m)*	*N*	*Equation (s)*	*r*	*E or e*
C. apiculatum current shoots	0–1,5	4	$W_{0-1,5} = W_T \left(\frac{W_{0-1,5}}{W_T}\right)$; $\log_{10}\left(\frac{W_{0-1,5}}{W_T}\right) = 3{,}4115 - 8{,}6821 \log_{10} h$	0,940*	E=2,220
	1,6–2,5	6	$W_{1,6-2,5} = W_T \left(\frac{W_{1,5-2,5}}{W_T}\right)$; $\log_{10}\left(\frac{W_{1,5-2,5}}{W_T}\right) = 1{,}8851 - 4{,}5291 \log_{10} h$	0,977**	E=1,443
	2,6–5,5	–	$W_{2,6-5,5} = W_T - (W_{0-1,5} + W_{1,5-2,5} + W_{>5,5})$	—	—
	>5,5	8	$W_{>5,5} = -3692{,}1 + 371{,}2d$	0,953**	e=0,195
	Total	14	$\log_{10} W_T = 0{,}7424 + 2{,}4354 \log_{10} d$	0,972**	E=1,338
C. apiculatum wood & bark	0–1,5	14	$\log_{10} W_{0-1,5} = 1{,}7360 + 2{,}0851 \log_{10} d$	0,994**	E=1,119
	1,6–2,5	14	$\log_{10} W_{1,6-2,5} = 1{,}0113 + 2{,}5157 \log_{10} d$	0,962**	E=1,424
	2,6–5,5	13	$\log_{10} W_{2,6-5,5} = 0{,}0660 + 3{,}5401 \log_{10} d$	0,976**	E=1,109
	>5,5	8	$W_{>5,5} = 37299{,}6 + 5871{,}3\, h$	0,920**	e=0,413
	Total	–	$W_T = W_{0-1,5} + W_{1,5-2,5} + W_{2,5-5,5} + W_{>5,5}$		

Species + *Component*	*Level (m)*	*N*	*Equation (s)*	*r*	*E or e*
C. zeyheri current shoots	0–1,5	16	$W_{0-1,5} = W_T \left(\frac{W_{0-1,5}}{W_T}\right)$; $\log_{10}\left(\frac{W_{0-1,5}}{W_T}\right) = 0{,}3001 - 0{,}2681d$	0,915**	E=2,172
	1,6–2,5	–	$W_{1,6-2,5} = W_T - (W_{0-1,5} + W_{2,5-5,5})$	—	—
	2,6–5,5	13	$\log_{10} W_{2,6-5,5} = 0{,}0516 + 3{,}1402 \log_{10} d$	0,925**	E=1,782
	Total	23	$\log_{10} W_T = 1{,}2664 + 1{,}8082 \log_{10} d$	0,922**	E=1,599
C. zeyheri wood & bark	0–1,5	22	$\log_{10} W_{0-1,5} = 1{,}4315 + 2{,}3634 \log_{10} d$	0,989**	E=1,243
	1,6–2,5	–	$W_{1,6-2,5} = W_T - (W_{0-1,5} + W_{2,5-5,5})$	—	—
	2,6–5,5	10	$\log_{10} W_{2,6-5,5} = -1{,}2039 + 4{,}7096 \log_{10} d$	0,973**	E=1,626
	Total	23	$\log_{10} W_T = 1{,}3013 + 2{,}7710 \log_{10} d$	0,989**	E=1,293

* P = 0,05
** P = 0.01

Table 2

Summary of measurements and standing crop estimates for stems of Combretum *species based on two 0,25 ha sample plots in red bushwillow veld, Kruger National Park*

A. Mean density (stems/ha), basal diameter (cm), and height (m)

Species	*Density*			*Mean Diameter*			*Mean Height*		
	Plot 1	*Plot 2*	*Both*	*Plot 1*	*Plot 2*	*Both*	*Plot 1*	*Plot 2*	*Both*
C. apiculatum	204	288	246	15,0	13,6	14,2	5,8	5,8	5,8
C. zeyheri	1 766	811	1 288	4,5	5,3	4,7	2,4	3,0	2,6

B. Estimated mean standing crops (kg/ha)

Species	*Component*	*Browsing Levels (m)*				
		0–1,5	*1,6–2,5*	*2,6–5,5*	> 5,5	*Total*
C. apiculatum	Current Shoots	2,0	28,5	620,0	370,6	1 021,2
	Wood & Bark	3 488,0	2 379,6	5 088,4	292,9	11 248,9
C. zeyheri	Current Shoots	55,9	49,5	400,0	0,0	505,8
	Wood & Bark	2 335,1	517,8	1 280,3	0,0	4 133,2
Both Species	Current Shoots	57,9	78,3	1 020,1	370,6	1 527,0
	Wood & Bark	5 823,1	2 987,4	6 368,7	292,9	15 382,0
	Grand Total	5 881,0	2 975,7	7 388,8	663,5	16 909,0

of the tendency of crown diameters of that species to diminish with increasing height above 5,5 metres.

At the lower browsing levels, 0 m–2,5 m for *C. apiculatum* and 0 m–1,5 m for *C. zeyheri*, there were high negative correlations between the proportion of total current shoot weight and stem diameter or height; while other relationships evidenced low correlations. Barnes, Lloyd and McNeill (1976) also found a high negative correlation between the logarithm of the proportion of leaf biomass below 2,0 m and stem height for *Colophospernum mopane* in Rhodesia. In the middle browsing levels, 2,6 m – 5,5 m for *C. apiculatum* and 1,6 m – 2,5 m for *C. zeyheri*, all correlations involving current shoot biomass had r values below 0,90. Large stems have lower proportions of their current shoot biomass at lower browsing levels than small stems, while the actual biomass be either greater or smaller on large stems depending on available light, browsing pressure, etc. At mid-levels there is a shift from this relationship to one of increasing biomass with increasing size, with this shift occurring at different heights on different stems. The shift in relationships makes high correlations unlikely. It is probable that similar shifts in the relationships between current shoot biomass and stem size with increasing height hold for virtually all tree and shrub species.

The safest generalization that can be made is that when generating equations for the estimation of standing crop of woody plant biomass at different browsing levels, one must expect that each species will produce a unique set of equations.

Standing Crop Estimates

The mean standing crop of both species, 16 909 kg ha^{-1} (Table 2), approaches the mean standing crop estimate for all trees and shrubs, 19 940 kg ha^{-1}, on *Colophospermum mopane* veld in southeastern Rhodesia (Kelly and Walker 1976). The mean standing crop of current shoots, 1 527 kg ha^{-1}, also corresponds closely to that of Rhodesian mopane veld trees and shrubs, 1 506 kg ha^{-1}.

Nine per cent of the total standing crop was current shoots, biomass that might be consumed by impala, kudu or giraffe. Of this potentially edible tissue, only 3,8% was within reach of impala and only 5,1% was within reach of kudu, while 67,0% was within reach of giraffe and 24,0% was out of reach of browsers.

Combretum apiculatum, the preferred browse species, comprised 67,0% of the total current shoot standing crop, but its contribution varied between browsing levels. All of the current shoot biomass above 5,5 m consisted of *C. apiculatum,* but the proportion declined to 61,0% at 2,6 m–5,5 m, 36,0% at 1,6 m–2,5 m and 3,4% at 0 m–1,5 metres. A very small proportion of the 1976–77 total *Combretum* current shoot biomass consisted of preferred browse within reach of impala or kudu. The percentages of the total were 0,13 at 0 m–1,5 m, 1,9 at 1,6 m–2,5 m, 41 at 2,6 m–5,5 m and 24 at more than 5,5 metres. It may be argued that current shoots on lower branches or sprout growth were already browsed before the harvest of stems used in the regression sample. Little sprout growth was noted in the sample plots when diameters were measured in February, however, and what was noted did not become browsed until the dry season. Browsing damage was not observed on lower branches of sample trees when current shoots were clipped.

It seems that prolonged intensive browsing on *C. apiculatum* within the study area had reduced shoot growth below 2,5 m and made the species essentially unavailable to impala and kudu.

The scarcity of current shoots below 2,5 m height did not represent a kudu browse line, but resulted from a predominance (116 out of 123) of stems $\geq$ 4,0 m tall in the sample plots, caused by prolonged browsing back of seedlings and sprouts by impala. The growth form of the remaining tall stems did not provide for significant growth of current shoots below 2,5 m. Visual inspection of areas of red bushwillow veld away from permanent water supplies and not subject to heavy browsing, indicated no lack of smaller *C. apiculatum* shoots. The following questions arise: (1) Is the recent decline in impala density in the KNP (Diederichs 1977) due to reduced browse availability adjacent to permaenent water supplies? (2) Will continued browsing pressure on *C. apiculatum* and other preferred species in these areas cause a long-term reduction in the carrying capacity of the KNP for browsing ungulates?

Acknowledgements

This study was made possible by National Geographic Society Research Grant No. 1707. The National Parks Board of Trustees and its Division of Nature Conservation is thanked for providing facilities, assistance and advice.

REFERENCES

BARNES, D. L., B. V. LLOYD and L. McNEILL. 1976. The use of shoot dimensions to estimate the leaf mass or leaf area of certain indigenous trees in Rhodesia. *Proc. Grassld Soc. Sth Afr.* 11: 47–50.

BRYNARD, A. M. 1964. The influence of veld burning on the vegetation and game of the Kruger National Park. *In:* DAVIS, D. H. S. (ed.): *Ecological Studies in Southern Africa.* The Hague: W. Junk.

COETZEE, B. J. and W. P. D. GERTENBACH. 1977. Technique for describing woody vegetation composition and structure in inventory type classification, ordination and animal habitat surveys. *Koedoe* 20:67–75.

DIEDERICHS, P. 1977. Lion-cropping: the balance is rectified. *Custos* 6(10): 6–9, 11–15.

KELLY, R. D. and B. H. WALKER. 1976. The effects of different forms of land use on the ecology of a semi-arid region in south-eastern Rhodesia, *J. Ecol.* 64: 553–576.

PIENAAR, U. de V. 1972. The culling of game . . . why? *Custos* 1(2): 3–5, 7, 11.

VAN DYNE, G. M. 1968. Measurement of quantity and quality of the diet of large herbivores. *In:* GOLLEY F. B. and H. K. BUECHNER, (eds): *A practical guide to the study of the productivity of large herbivores.* IBP Handbook No. 7. Oxford and Edinburg: Blackwell.

VAN WYK, P. 1974. Trees of the Kruger National Park. Johannesburg: Purnell.

WHITTAKER, R. H. and G. M. WOODWELL. 1968. Dimension and production relations of trees and shrubs in the Brookhaven Forest, New York. *J. Ecol.* 56: 1–25.

WHITTAKER, R. H., F. H. BORMANN, G. E. LIKENS, and T. G. SICCAMA. 1974. The Hubbard Brook ecosystem study: forest biomass and production. *Ecol. Monogr.* 44: 233–254.