COMPARISON OF TREE BASAL AREA AND CANOPY COVER IN HABITAT MODELS: SUBALPINE FOREST

BRIAN S. CADE, National Biological Service, 4512 McMurry Ave., Fort Collins, Colorado, 80525-3400, USA.

Abstract: Canopy cover and basal area are 2 common measures of tree cover used in forest wildlife habitat models and resource selection studies. When choosing between these 2 measures, it is important to recognize that they may differentially estimate relative cover of coexisting tree species due to differences in bole diameter distributions, crown overlap, and crown widths as a function of bole diameter. I found moderate agreement (multivariate $\rho = 0.62$, $P < 0.0001$) between lodgepole pine (*Pinus contorta*), Engelmann spruce (*Picea engelmannii*), and subalpine fir (*Abies lasiocarpa*) composition estimated by relative canopy cover and relative basal area in young to old-growth stands ($n = 31$) in subalpine forest of northcentral Colorado. However, differences between stand compositions estimated by relative canopy cover and relative basal area (average = 17%, range = 1–44%) were predictable based on multiple regression models of canopy cover as a function of basal area and trees/ha. I attributed most (11 of 14) above average deviations (>17%) to differences in diameter distributions among species in mature to old-growth (>200 yr) stands. Low densities of large diameter lodgepole pine or Engelmann spruce were a greater proportion of the basal area than of the canopy cover, while the converse occurred for higher densities of small and large diameter subalpine fir. Only 3 of 14 deviations >17% were attributed to species differences in crown overlap and crown width as a function of bole diameter, which occurred for young (22 yr) and intermediate-aged (48–80 yr) stands. I recommend use of basal area rather than canopy cover to estimate tree cover when it is desirable to emphasize large, uncommon trees that are resources used by the wildlife species of interest or that are indicators of important forest disturbance and successional conditions.

J. WILDL. MANAGE. 61(2):326–335

Key words: *Abies lasiocarpa,* basal area, canopy cover, habitat, habitat models, *Picea engelmannii, Pinus contorta,* resource selection, subalpine forest, tree cover

The objective of many studies of wildlife habitat is to develop relations that can be used to predict changes in wildlife abundance and fitness through time under various management alternatives (Brand et al. 1986, Bunnell 1989, Stauffer et al. 1992). Plant species composition is recognized as an important attribute of habitat for many wildlife species (Rotenberry 1985, Armleder et al. 1989, Block and Brennan 1993) and is fundamental for describing vegetation changes associated with plant succession (Mueller-Dombois and Ellenberg 1974). Depending on the wildlife species, important resources may be provided more or less directly by certain plants. For example, lodgepole pine in subalpine forests of the central Rocky Mountains provides winter food for blue grouse (*Dendragapus obscurus*), which selectively feed on pine needles rather than subalpine fir and Engelmann spruce needles (Cade and Hoffman 1990, Remington and Hoffman 1996). Subalpine fir and Engelmann spruce indirectly influence habitat suitability for marten (*Martes americana*) because older stands dominated by fir (*Abies* spp.) and spruce (*Picea* spp.) provide greater prey availability, thermal cover, and subnivean access sites (Allen 1982, Spencer et al. 1983, Buskirk 1992, Corn and Raphael 1992).

Because the specific resources provided to wildlife by plants often are unknown or difficult to quantify, estimates of plant species abundance usually are based on dimensional quantities that are easily measured. Tree cover in temperate forests often is estimated by either of 2 variables, basal area of the boles measured at breast height or canopy cover measured as the percent of the ground covered by a vertical projection of the tree canopy (Hays et al. 1981). Because plant cover incorporates an element of size in addition to number of individuals, it is more directly related to biomass than frequency or density estimates (Mueller-Dombois and Ellenberg 1974:80). Basal area is the easier, less ambiguous quantity to measure in the field. However, canopy cover may be the only feasible measure of tree cover when estimates must be made from aerial photographs, e.g., for landscape level evaluations of habitat for animals with large area requirements such as marten (Buskirk 1992).

Correlations between basal area and canopy cover for a given tree species exist because there is a positive relation between crown width and bole diameter (Alexander et al. 1967, Alexander 1971, Francis 1986, Tabush and White 1988, Farr et al. 1989, Smith et al. 1992). However, there are several reasons canopy cover and basal area may not yield comparable estimates of floristic composition in stands of coexisting tree species. Numerical relations between crown width and bole diameter may differ among species (Alexander 1971, Francis 1986, Gering and May 1995). Equivalent basal areas distributed across a different number and diameter of tree boles will have different crown areas (Godman and Tubbs 1973) when crown width is not proportional to bole diameter (e.g., a linear model with a nonzero intercept or a nonlinear model). Basal area is a measure of area covered by boles of individual trees, whereas canopy cover is a measure of area potentially covered by multiple trees due to crown overlap. Consequently, tree species composition estimated by canopy cover and by basal area may differentially emphasize species depending on differences in (1) crown width as a function of bole diameter, (2) bole diameter distributions, and (3) degree of crown overlap (e.g., due to shade tolerance).

My objective in this study was to compare tree composition and cover estimated from canopy cover and basal area across successional stages of forest, using subalpine forests in the central Rocky Mountains as an example. I examined agreement between composition estimated by relative canopy cover and relative basal area for each species across a successional gradient of stands where the 3 species coexist. Using linear regression, I explored functional relations among canopy cover, basal area, and tree density that might contribute to differences in composition estimates. Engelmann spruce and subalpine fir are shade-tolerant trees associated with later successional stages of subalpine forest development and commonly occur in multi-layered canopies; lodgepole pine is a shade-intolerant tree associated with early successional stages and commonly occurs as a single, dominant canopy layer (Aplet et al. 1988). Crown widths are narrower per bole diameter for open-grown Engelmann spruce (crown width [m] = 1.324 + 0.123 × dbh [cm], Alexander 1971) than for lodgepole pine (crown width [m] = 0.997 + 0.171 × dbh [cm], Alexander et al. 1967). I could not find a similar equation for subalpine fir in the literature but used data in Brown (1978: Table 12) to estimate (crown width [m] = 0.734 + 0.154 × dbh [cm] − 0.002 × dbh^2 [R^2 = 0.93, n = 25]), indicating smaller crown widths per bole diameter than for Engelmann spruce or lodgepole pine.

A. W. Allen, J. A. Bendykowski, J. G. Corn, P. J. Sousa, and K. L. Stone provided field assistance. C. B. Edminster and M. R. Kaufmann of the Rocky Mountain Forest and Range Experiment Station provided suggestions about study design and for locating suitable sample stands at the Fraser Experimental Forest. A. W. Allen, J. G. Corn, C. B. Edminster, J. E. Roelle, and J. W. Terrell reviewed drafts of the manuscript.

STUDY AREA

One 50- × 20-m (0.1-ha) plot was located in each of 31 stands in the Fool Creek and King Creek drainages of the Fraser Experimental Forest in northcentral Colorado (Alexander 1987). The long axes of sample plots ran north-south and were located away from stand edges. Stands were selected so that 10 had ≥67% of the basal area in lodgepole pine, 11 had 34–66% of the basal area in pine, and 10 had ≤33% of the basal area in pine. In addition, 8 stands were young (22 yr old), 9 were intermediate aged (48–80 yr old), and 14 were mature to old-growth (>200 yr old). Young stands were created during 1954–56 as a result of block cuttings for snowpack manipulation in the Fool Creek drainage and intermediate aged stands were the result of fires and logging since 1900 (Alexander 1987). Sample stands were located on western, northern, and northeastern slopes of 2–20 degrees at 2,804–3,231 m elevation and represented colonization, spruce exclusion, spruce reinitiation, and second generation phases of Engelmann spruce-subalpine fir forest development (Aplet et al. 1988), with low to high proportions of lodgepole pine.

METHODS

All live trees ≥3-cm dbh were tallied by 1-cm dbh classes by species in 1989 or 1990 to measure basal area (m^2/ha) and density (trees/ha). Canopy cover was estimated by summing intercepts on canopies from vertical sighting projections made with a modification of an instrument for measuring tree crown width (Shepperd 1973) at 100 points in each plot (25 2-m inter-

vals on the plot length by 4 parallel transects 2.5, 7.5, 12.5, and 17.5 m on the plot width). At each point canopy intercepts were recorded on species in the overstory (>5 m in height) and understory (≤5 m in height but ≥3 cm dbh), counting hits on multiple trees of the same species as a single intercept for that species. A canopy hit was recorded whenever the vertical projection occurred within the perimeter formed by connecting the outer edge of branches (Hays et al. 1981: 7). I did not use spherical densiometers to estimate canopy cover because densiometers measure a wide angle projection that is influenced both by canopy height and cover, i.e., estimates of canopy cover are biased high (Bunnell and Vales 1990, Cook et al. 1995). Canopy cover estimates in each plot had 95% confidence intervals (assuming binomial sampling distribution) that ranged from a low of ±4% for values close to 1 or 99% to a high of ±10% for values close to 50%.

To compare species composition across stands where the total cover of trees differed, canopy cover and basal area of species within a plot were re-expressed as relative measures. Relative canopy cover for a tree species in a plot was calculated as total intercepts for a species divided by the sum of intercepts of all tree species. Relative basal area for a species was total basal area for that species divided by the sum of basal areas of all species. The null hypothesis of no agreement between composition measured by relative canopy cover and by relative basal area for lodgepole pine, Engelmann spruce, and subalpine fir was tested with a chance-corrected agreement statistic, ρ, a special application of multiresponse randomized block permutation procedures (Berry and Mielke 1988). Perfect agreement occurs when $\rho = 1.0$ and deviations from perfect agreement ($\rho < 1.0$) are quantified by the average, absolute deviation (simple Euclidean distance) between relative canopy cover and relative basal area. The agreement statistic, ρ, is interpreted as the percent reduction in observed average absolute deviation (δ) over that expected under the null hypothesis of no agreement (μ_δ). Probabilities that $\rho = 0$ (no agreement) under the null hypothesis are provided by using the exact mean, variance, and skewness of δ with a Pearson type III function to approximate the discrete $n!$ permutation distribution (Berry and Mielke 1988).

Functional relations between canopy cover and basal area were modeled with linear regression. Nonlinear forms considered were quadratic polynomial ($y = aX + bX^2$) and logarithmic ($y = aX^b$), where y is canopy cover and X is basal area. Models were forced through the origin after testing that estimated intercepts did not differ from zero ($P > 0.20$), because canopy cover must be zero when basal area is zero. I added a parameter for trees/ha (Z) and retained it in the model if it was significant ($P < 0.05$) given parameters for basal area were in the model. Trees per ha and basal area together account for total cover of trees and whether that cover is distributed on many small diameter or fewer large diameter boles. Interaction terms for basal area and trees per ha (XZ) were tested for inclusion in the models. Residual plots were examined for adequacy of model fit and to detect heteroscedastic error distributions.

I used least absolute deviation (LAD) regression to estimate linear models because it estimates the conditional median of the dependent variable given the independent variables, which is a more efficient estimate for asymmetric and heavy-tailed symmetric error distributions than the conditional mean of least squares (LS) regression (Dielman and Pfaffenberger 1982, Birkes and Dodge 1993, Cade and Richards 1996). Furthermore, LAD estimates are less sensitive than LS estimates to violations of the assumption of homoscedastic error distributions due to a few outlying values of the dependent variable. The LAD regression estimates are median unbiased and remain unbiased for nonlinear (e.g., logarithmic) as well as linear, monotonic transformations, whereas LS estimates remain mean unbiased only for linear transformations (Bassett 1992). Use of LAD regression when the assumptions of LS regression are met yields comparable estimates with minor loss of efficiency (power). In my analyses, LAD and LS regression estimates were similar, but 95% confidence interval widths for LAD estimates were 68–88% of those for LS estimates for subalpine fir and lodgepole pine, and 105–124% of those for LS estimates for Engelmann spruce.

Null hypotheses that parameters equal zero in LAD regressions were tested with permutation procedures (Cade and Richards 1996). The observed test statistic, the proportionate reduction in the sum of absolute deviations between reduced (SAR) and full (SAF) parameter models, $T_o = (SAR - SAF)/SAF$, was compared to

the same statistic (T) for LAD regressions on 10,000 random permutations of residuals from the reduced model to the independent variable matrix. Probability under the null hypothesis was given by (no. $T \geq T_o$)/10,000. Power simulations indicated that this procedure maintained nominal error rates well under the null hypothesis for identical error distributions for both full and partial model tests (Cade and Richards 1996). Confidence intervals were computed for each parameter by inverting the above hypothesis testing procedure. A LAD regression coefficient of determination was computed as $R = 1 - (SAF/SAR)$, where SAR is for the reduced parameter model with only a constant term (Cade and Richards 1996). The LAD coefficient of determination has a simple interpretation as the proportionate reduction in absolute deviations about the median of the dependent variable due to including parameters in the model other than the constant. Because the LAD coefficient of determination is in the original units of measure it will be smaller than the coefficient of determination, R^2, from LS regression that is based on squared units of measure. To convert R to units comparable to R^2, let $R^{*2} = 1 - (1 - R)^2$ (McKean and Sievers 1987). Statistical analyses were conducted with routines in the BLOSSOM software available from the Midcontinent Ecological Science Center, National Biological Service.

RESULTS

Total stem density was 890–3,910/ha, total basal area (adjusted for slope) was 10.1 to 71.1 m^2/ha, quadratic mean dbh (diam for a tree of average basal area) was 7.1–24.6 cm, and total tree canopy cover was 24–81%. Engelmann spruce basal area was 0.4–29.6 m^2/ha, canopy cover was 1–30%, and density was 10–1,520/ha; subalpine fir basal area was 0.8–20.6 m^2/ha, canopy cover was 2–57%, and density was 70–2,350/ha; and lodgepole pine basal area was 2.0–46.7 m^2/ha, canopy cover was 4–62%, and density was 50–2,810/ha (Table 1). Quaking aspen (*Populus tremuloides*) occurred as a small percentage of the basal area and canopy cover in 8 plots, was included in total basal area and total canopy cover for calculating relative values for conifer species, but was not included as a variable in analyses.

Composition of Engelmann spruce, subalpine fir, and lodgepole pine estimated by relative canopy cover and relative basal area had moderate agreement ($\rho = 0.62$, $\delta = 0.168$, $P < 0.0001$) although they differed by an average of 17% in this multivariate comparison (Fig. 1). Similar results were found when canopy cover was calculated only for trees >5 m in height and basal area was calculated only for stems ≥10 cm dbh ($\rho = 0.61$, $\delta = 0.178$, $P < 0.0001$). Smallest absolute deviations occurred in young (0.006–0.170, $\bar{x} = 0.111$) and intermediate-aged stands (0.044–0.269, $\bar{x} = 0.115$), and largest absolute deviations were in mature to old-growth stands (0.043–0.443, $\bar{x} = 0.235$). Univariate agreement comparisons were made to examine species contributions to the multivariate agreement (Fig. 2). Relative canopy cover and relative basal area deviated less and had stronger agreement (all $P < 0.0001$) for Engelmann spruce ($\rho = 0.71$, $\delta = 0.047$) and lodgepole pine ($\rho = 0.69$, $\delta = 0.094$) than for subalpine fir ($\rho = 0.50$, $\delta = 0.111$).

Because canopy cover was estimated by subsampling within plots, it is possible that differences less than 0.15 could occur due to subsampling variation. This upper bound to differences due to subsampling variation was arrived at by calculating the extreme case of canopy cover estimates near 50% for 2 species differing from true values by ±10% (95% CIs) and an estimate near 1% for 1 species differing from its true value by ±4%. The absolute deviation for this case when all differences are due to canopy cover estimation error is $0.147 = (0.10^2 + 0.10^2 + 0.04^2)^{0.5}$, based on computations for the agreement statistic.

Examination of the 3-dimensional plot of differences between relative canopy cover and relative basal area (Fig. 1) and univariate comparisons (Fig. 2) indicated 3 patterns in deviations exceeding the average of 0.170. In 8 mature and old-growth plots (M and P – V), fir was a greater proportion of the canopy cover than of the basal area while the converse was true for pine. Relative cover was as much as 33% higher for subalpine fir and as much as 29% lower for lodgepole pine when estimated by canopy cover than when estimated by basal area. In 3 mature and old-growth plots (K, L, and N), fir was a greater proportion of the canopy cover than of the basal area while the converse occurred for spruce. Relative cover was as much as 29% higher for subalpine fir and 22% lower for Engelmann spruce when estimated by canopy cover than when estimated by basal area. Both patterns described above oc-

Table 1. Trees/ha, dbh range (cm), basal area (m^2/ha), and canopy cover (%) for lodgepole pine, subalpine fir, and Engelmann spruce in young (<22 yr), intermediate (48–80 yr), and mature to old-growth (>200 yr) stands in subalpine forest at Fraser Experimental Forest, Colorado

	Lodgepole pine				Subalpine fir				Engelmann spruce			
Plot	Trees /ha	dbh range	Basal area	Canopy cover	Trees/ha	dbh range	Basal area	Canopy cover	Trees	dbh range	Basal area	Canopy cover
						Young						
1	230	3–19	2.1	11	750	3–35	7.5	12	210	3–27	3.0	7
2	510	3–20	3.6	15	1,100	3–22	6.0	19	220	3–21	2.2	6
3	1,910	3–17	10.5	35	500	3–12	1.5	3	290	3–13	1.3	3
4	450	3–14	2.0	7	1,200	3–19	4.4	13	900	3–23	3.7	10
5	1,510	3–19	8.5	25	2,060	3–23	10.3	30	200	3–10	0.8	2
6	1,420	3–16	6.0	22	450	3–27	4.7	11	340	3–19	2.9	15
7	690	3–20	2.5	4	1,700	3–18	7.7	13	270	3–16	1.9	7
8	1,550	3–15	6.8	24	600	3–20	2.9	10	320	3–17	1.5	8
						Intermediate						
A	1,440	7–36	44.4	61	470	3–24	3.9	10	90	4–27	2.7	4
B	870	6–35	34.6	49	100	3–21	1.4	2	180	4–36	5.5	4
C[1]	1,330	3–30	23.5	39	860	3–34	12.0	23	430	3–36	7.9	13
D[1]	1,100	3–36	17.8	34	2,170	3–34	16.5	37	410	3–42	4.7	7
E[1]	2,810	3–26	36.2	62	580	3–22	8.0	23	40	3–24	0.8	1
F[1]	2,800	3–32	37.7	62	70	3–23	0.8	2	40	10–20	0.7	1
G[1]	2,070	3–28	33.2	57	110	6–31	5.3	6	10	22–22	0.4	1
H[1]	310	3–33	8.9	26	1,010	3–36	18.7	30	120	5–24	2.1	10
I[1]	760	3–17	3.9	24	1,510	3–29	20.0	43	90	3–19	1.2	3
						Mature to old-growth						
J	570	3–43	35.7	40	160	3–30	2.9	5	500	3–34	8.4	8
K	90	19–34	5.2	2	2,350	3–28	20.6	51	430	5–66	29.6	24
L	50	29–45	4.4	2	2,080	3–25	14.9	36	720	3–45	25.9	30
M	920	10–46	46.7	58	880	3–18	4.7	14	290	3–30	5.1	14
N	110	12–39	6.6	3	1,020	3–40	20.3	39	260	9–48	28.2	19
O	690	7–49	32.7	43	1,050	3–33	10.5	21	720	3–39	8.8	13
P	470	7–50	27.5	30	560	3–35	8.7	20	1,520	3–33	15.4	30
Q	540	10–47	29.4	21	910	3–48	16.9	26	730	3–45	24.8	25
R	600	3–42	19.2	25	1,990	3–43	17.6	52	400	3–32	4.5	13
S	840	3–39	23.7	30	600	3–36	4.7	27	370	3–36	6.0	15
T[1]	460	3–37	14.6	12	460	3–34	7.2	26	820	3–36	13.4	30
U	310	5–54	25.3	26	2,230	3–24	11.8	57	260	3–57	8.1	13
V	200	7–40	13.4	10	1,310	3–30	13.0	32	350	4–45	18.5	29
W	790	3–50	37.3	40	70	13–33	3.1	6	30	4–42	1.7	1

[1] Plots with quaking aspen.

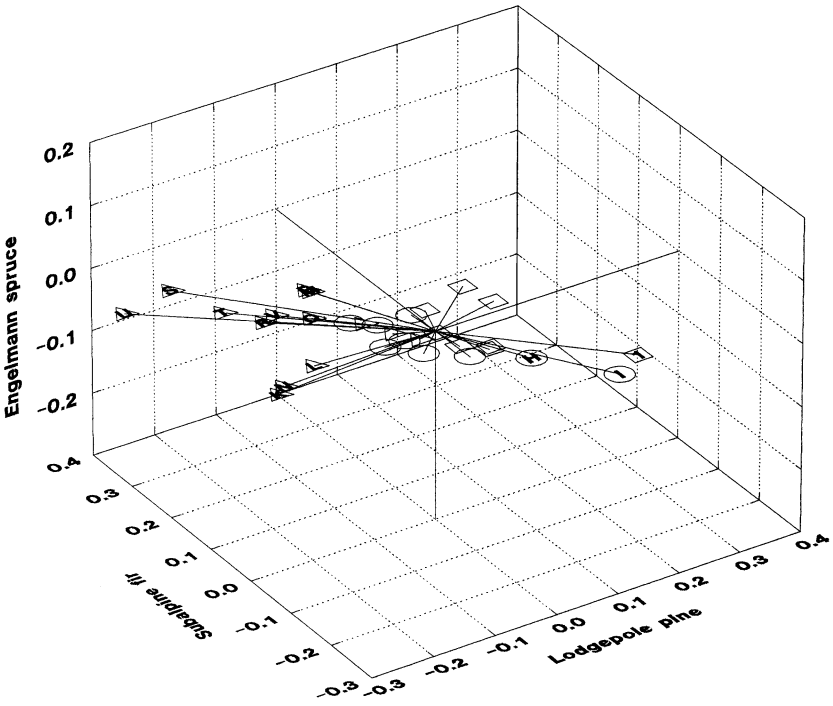

Fig. 1. Deviations between relative canopy cover and relative basal area for subalpine fir, Engelmann spruce, and lodgepole pine for 31 plots in subalpine forest at the Fraser Experimental Forest in northcentral Colorado. Positive numbers indicate relative canopy cover exceeded relative basal area and negative numbers indicate the converse. Squares are for young (<22 yr), circles are for intermediate-aged (48–80 yr), and triangles are for mature to old-growth (>200 yr) stands. Symbol numbers and letters correspond to plots in Table 1 with absolute deviations ≥0.170. Vectors connect to zero difference point (0,0,0) and range in length from 0.006 for the shortest to 0.443 for the longest.

curred where there were high densities (460–2,350/ha) of small and large dbh fir (3–48 cm) and lower densities (200–920/ha) of larger dbh pine (20–54 cm) or spruce (20–66 cm), i.e., larger quadratic mean dbh. The third pattern of differences occurred in young (1) and intermediate-aged stands (H and I) where fir was a smaller proportion of the canopy cover than of the basal area and conversely for pine (1 and I) or aspen (H). This pattern occurred where there were low densities of pine or aspen (230–760/ha) comparable in dbh (3–33 cm) to the higher densities of fir (750–1,510/ha).

Differences between composition estimated by relative canopy cover and relative basal area were consistent with the different functional relations between canopy cover and basal area for the tree species. Regression models included significant estimates for trees/ha for all 3 species, indicating the dependence of canopy cover on the dbh and density of the boles (Table 2, Fig. 3). Change in canopy cover as a function of basal area at a given density was 40% lower for lodgepole pine than for fir and there was no overlap between 95% confidence intervals for these regression estimates (Table 2). Subalpine fir canopy cover was on a mix of small and large dbh boles as basal area increased, whereas lodgepole pine canopy cover was on larger boles of similar dbh. Smaller dbh boles had disproportionately more crown area per unit of basal area than larger dbh boles because crown width was not proportional to bole diameter. Canopy cover of Engelmann spruce changed at a rate similar to that for subalpine fir at basal areas <10 m^2/ha but at a reduced rate at larger basal areas, as evident from inclusion of the quadratic term for basal area (Table 2, Fig. 3). Largest basal areas of Engelmann spruce were associated with low densities of large dbh boles. Change in canopy cover as a function of trees/ha at a given basal area was 50% greater for lodgepole pine than for fir and spruce, but there was overlap in 95% confidence intervals for these regression estimates for the 3 conifers (Table 2). Canopy cover was on greater densities of smaller dbh boles as trees/ha increased at a given basal area, and small dbh lodgepole pine

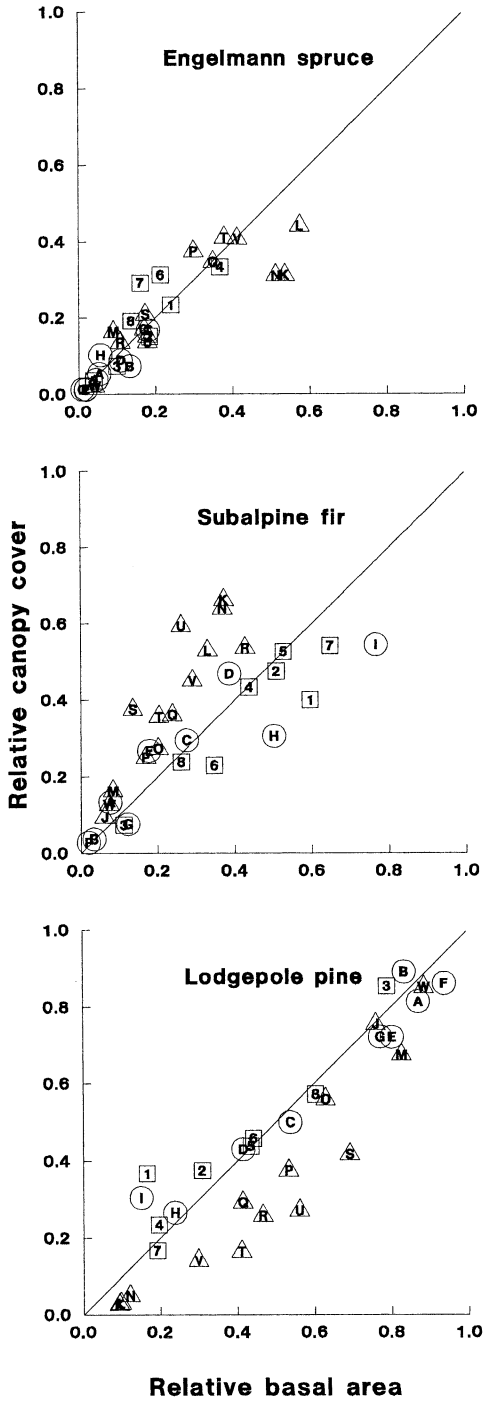

Fig. 2. Relative canopy cover and relative basal area of Engelmann spruce, subalpine fir, and lodgepole pine in young to old-growth stands (n = 31) in subalpine forests at Fraser Experimental Forest in northcentral Colorado. Solid lines indicate where values would fall if univariate agreement was perfect (ρ = 1). Squares are for young (<22 yr), circles are for intermediate-aged (48–80 yr), and triangles are for mature to oldgrowth (>200 yr) stands. Symbol numbers and letters correspond to plots in Table 1.

had greater crown widths per bole diameter and less crown overlap than subalpine fir and Engelmann spruce. Basal area and trees/ha were more strongly correlated for subalpine fir (r = 0.70) than for lodgepole pine (r = 0.40) or Engelmann spruce (r = 0.47). Basal area of spruce ≤15 m^2/ha was related to trees/ha similar to subalpine fir, but larger basal areas of spruce occurred on fewer large diameter trees, resulting in a weak linear correlation.

DISCUSSION

Choosing between canopy cover and basal area to estimate tree cover and composition depends on logistical constraints on sampling and on perceptions about the functional importance of trees as wildlife habitat. Compared to canopy cover, basal area emphasized the uncommon (lower trees/ha), large diameter Engelmann spruce and lodgepole pine more than the abundant (higher trees/ha) mix of small and large diameter subalpine fir. Cover of large diameter lodgepole pine and Engelmann spruce in the absence of small diameter regeneration was indicative of important disturbance and successional patterns in subalpine forests. Shade-tolerant subalpine fir readily regenerates beneath its own canopy and, thus, fir basal area occurred on numerous small and large diameter boles. Lodgepole pine is shade-intolerant and regenerates poorly under canopies in older stands. Therefore, pine basal area occurred on fewer, larger diameter boles, providing less canopy cover per unit of basal area than for fir. Stands with large basal areas of large diameter lodgepole pines and large basal areas of smaller diameter subalpine fir and Engelmann spruce were indicative of more xeric sites, with greater frequency of fires that reduced longevity of the spruce-fir forest (Romme and Knight 1981). Stands with large basal areas of large diameter Engelmann spruce (>15 m^2/ha and <800 trees/ha) and large basal areas of subalpine fir were indicative of the spruce exclusion phase of subalpine forest development, where a few large Engelmann spruce (that are less shade-tolerant but have greater longevity than subalpine fir) from the initial colonization remained in the overstory, but little regeneration occurred in the understory (Aplet et al. 1988). Mortality of older fir eventually will allow spruce regeneration to occur (spruce reinitiation phase).

Basal area and canopy cover estimates differentially emphasized conifers in only 3 of 17

Table 2. Parameter estimates, 95% confidence intervals, and *P* for least absolute deviation (LAD) regressions of percent canopy cover as a function of m^2/ha basal area and trees/ha for Engelmann spruce, subalpine fir, and lodgepole pine in subalpine forest stands (n = 31) at Fraser Experimental Forest in northcentral Colorado. *P* for all tests and confidence intervals were based on 10,000 random permutations of residuals from reduced model to the independent variables. *P* for coefficient of determination tests the null hypothesis that all parameters equal zero for the full model.

	Engelmann spruce			Subalpine fir			Lodgepole pine		
Variable	Estimate	95% CI	*P*	Estimate	95% CI	*P*	Estimate	95% CI	*P*
Basal area	1.582	0.95–2.74	0.0001	1.537	1.15–1.85	0.0001	0.935	0.81–1.05	0.0001
Trees/ha	0.008	0.001–0.014	0.0326	0.008	0.004–0.011	0.0001	0.012	0.009–0.014	0.0001
Basal area^2	−0.030	−0.066–−0.011	0.0080						
Coefficient of determination	0.627		0.0001	0.662		0.0001	0.722		0.0001

young and intermediate-aged stands. There are 2 possible reasons lodgepole pine (and quaking aspen) was a greater proportion of the canopy cover than of the basal area compared to subalpine fir and Engelmann spruce. Shade-intolerant lodgepole pine (aspen) had less crown overlap (crown disengagement) than shade-tolerant fir and spruce (crown engagement; Jack and Long 1991). Thus, subalpine fir and Engelmann spruce crowns overlapped more and covered less surface area than lodgepole pine (aspen) per unit of basal area at a given density. Crown widths, and thus crown area, also were greater for pine than for fir and spruce at equivalent dbh (basal areas). However, differences between the 2 cover measures were small in most young and intermediate-aged stands. Any increase in canopy cover of pine per unit of basal area due to less crown overlap and greater crown widths was offset by increased canopy cover of fir and spruce per unit of basal area due to higher densities of smaller diameter trees. Species differences in crown widths per bole diameter, crown overlap, and bole diameter distributions can interact in complex ways to reduce species differences in canopy cover per unit of basal area.

Differences among crown width to bole diameter relations for Engelmann spruce, subalpine fir, and lodgepole pine in subalpine forests were small compared to differences that may occur among species in other forest ecosystems. For example, wide canopy oaks (*Quercus* spp.) and hickories (*Carya* spp.) have 1.5 × crown width per bole diameter compared to narrow canopy loblolly (*Pinus taeda*) and shortleaf (*P. echinata*) pines in southeastern forests (Gering and May 1995). A working hypothesis for other forest ecosystems is that shade-intolerant, early successional species that have greater crown widths per bole diameter will provide greater canopy cover per unit of basal area in stands where they are numerous. Shade-tolerant species will provide greater canopy cover per unit of basal area in later successional stands where they are more numerous. If shade-intolerant, early successional species have narrower crown widths per bole diameter, differences in canopy cover per unit of basal area will be reduced or reversed.

Using basal area as an estimate of tree cover may be advantageous when the resources important to wildlife species of interest are directly linked to tree biomass, e.g., lodgepole pine needles as winter food for blue grouse, because basal area measures the contribution of individual trees. When the resources important to wildlife species of interest are less directly linked to tree biomass, e.g., spruce/fir forests providing increased prey and thermal cover for marten, either basal area or canopy cover may serve as a reasonable estimate, depending on the logistical constraints on sampling. However, basal area will give greater emphasis to the cover of large diameter, uncommon trees than will canopy cover. This is desirable if these large diameter, uncommon trees are important resources for the wildlife species of interest or identify important disturbance and successional pathways. Another advantage of estimating tree cover and composition by basal area is that tree and stand projection models are available (Edminster 1987) for predicting changes in boles per unit area (stem density or basal area) over time under different management alternatives. This is an important consideration in applications of habitat models for resource planning purposes (Brand et al. 1986, Stauffer et al. 1992). Canopy cover projections are more involved but have been made from relations between bole characteristics (dbh and ht) and crown diameter, coupled with adjustments for crown overlap (Moeur 1985, 1986).

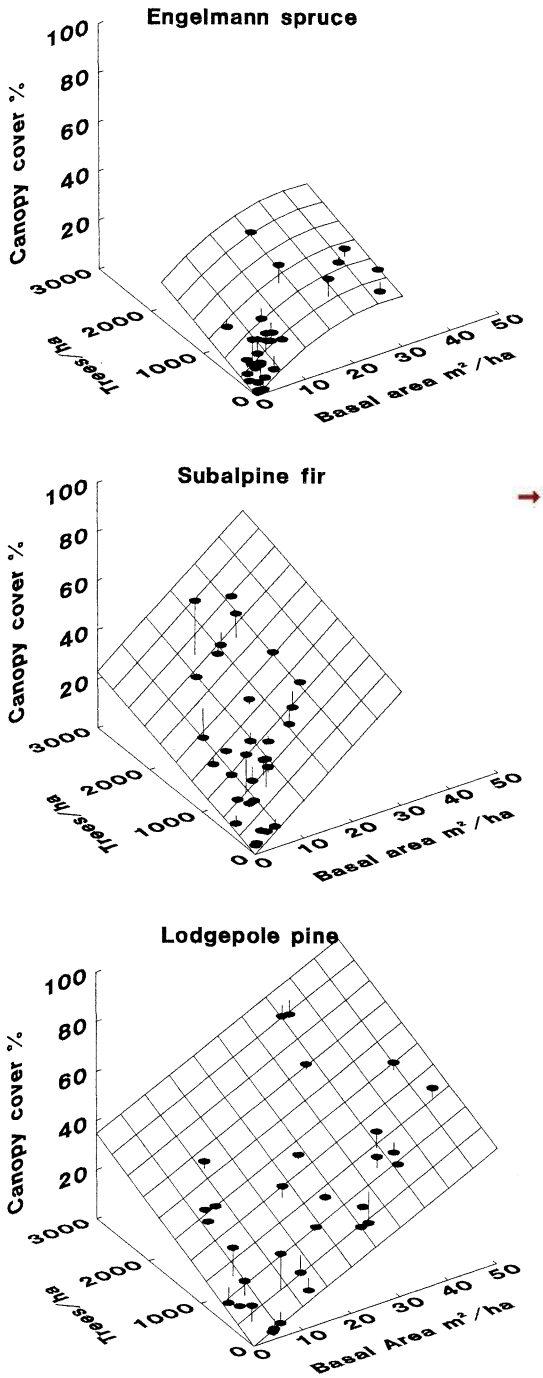

Fig. 3. Canopy cover (%) of Engelmann spruce, subalpine fir, and lodgepole pine as a function of basal area (m^2/ha) and trees/ha in young to old-growth stands (n = 31) in subalpine forests at Fraser Experimental Forest in northcentral Colorado. Surfaces plotted are least absolute deviation regressions from Table 2 and vertical spikes are residuals.

LITERATURE CITED

ALEXANDER, R. R. 1971. Crown competition factor (CCF) for Engelmann spruce in the central Rocky Mountains. U.S. For. Serv. Res. Note RM-188. 4pp.

———. 1987. Early history of St. Louis Creek and the Fraser Experimental Forest: a narrative. Pages 1–11 *in* C. A. Troendle, M. R. Kaufmann, R. H. Hamre, and R. P. Winokur, tech. coords. Management of subalpine forests: building on 50 years of research. U.S. For. Serv. Gen. Tech. Rep. RM-149. 253pp.

———, D. TACKLE, AND W. G. DAHMS. 1967. Site indices for lodgepole pine, with corrections for stand density: Methodology. U.S. For. Serv. Res. Pap. RM-29. 18pp.

ALLEN, A. W. 1982. Habitat suitability index models: marten. U.S. Fish Wildl. Serv. Biol. Rep. 82(10.11). 9pp.

APLET, G. H., R. D. LAVEN, AND F. W. SMITH. 1988. Patterns of community dynamics in Colorado Engelmann spruce-subalpine forests. Ecology 69:312–319.

ARMLEDER, H. M., D. A. LECKENBY, D. J. FREDDY, AND L. L. HICKS. 1989. Integrated management of timber and deer: interior forests of western North America. U.S. For. Serv. Gen. Tech. Rep. PNW-227. 23pp.

BASSETT, G. 1992. The Gauss Markov property for the median. Pages 23–31 *in* Y. Dodge, ed. L_1 statistical analyses and related methods. North Holland, New York, N.Y.

BERRY, K. J., AND P. W. MIELKE, JR. 1988. A generalization of Cohen's Kappa agreement measure to interval measurement and multiple raters. Educ. and Psychol. Meas. 48:921–933.

BIRKES, D., AND Y. DODGE. 1993. Alternative methods of regression. John Wiley and Sons, New York, N.Y. 228pp.

BLOCK, W. M., AND L. A. BRENNAN. 1993. The habitat concept in ornithology: theory and applications. Current Ornithol. 11:35–91.

BRAND, G. J., S. R. SHIFLEY, AND L. F. OHMANN. 1986. Linking wildlife and vegetation models to forecast the effects of management. Pages 383–387 *in* J. Verner, M. L . Morrison, and C. J. Ralph, eds. Wildlife 2000: modeling habitat relationships of terrestrial vertebrates. Univ. Wisconsin Press, Madison.

BROWN, J. K. 1978. Weight and density of crowns of Rocky Mountain conifers. U.S. For. Serv. Res. Pap. INT-197. 56pp.

BUNNELL, F. L. 1989. Alchemy and uncertainty: what good are models? U.S. For. Serv. Gen. Tech. Rep. PNW-232. 27pp.

———, AND D. J. VALES. 1990. Comparison of methods for estimating forest overstory cover: differences among techniques. Can. J. For. Res. 20:101–107.

BUSKIRK, S. W. 1992. Conserving circumboreal forests for martens and fishers. Conserv. Biol. 6:318–320.

CADE, B. S., AND R. W. HOFFMAN. 1990. Winter use of Douglas-fir forests by blue grouse in Colorado. J. Wildl. Manage. 54:471–479.

———, AND J. D. RICHARDS. 1996. Permutation tests for least absolute deviation regression. Biometrics 52:886–902.

COOK, J. G., T. W. STUTZMAN, C. W. BOWERS, K. A. BRENNER, AND L. L. IRWIN. 1995. Spherical densiometers produce biased estimates of forest canopy cover. Wildl. Soc. Bull. 23:711–717.

CORN, J. G., AND M. G. RAPHAEL. 1992. Habitat characteristics at marten subnivean access sites. J. Wildl. Manage. 56:442–448.

DIELMAN, T., AND R. PFAFFENBERGER. 1982. LAV (least absolute value) estimation in linear regression: a review. TIMS Studies in Manage. Sci. 19:31–52.

EDMINSTER, C. B. 1987. Growth and yield of subalpine conifer stands in the central Rocky Mountains. Pages 33–40 *in* C. A. Troendle, M. R. Kaufmann, R. H. Hamre, and R. P. Winokur, tech. coords., Management of subalpine forests: building on 50 years of research. U.S. For. Serv. Gen. Tech. Rep. RM-149. 253pp.

FARR, W. A., D. L. DEMARS, AND J. E. DEALY. 1989. Height and crown width related to diameter for open-grown western hemlock and Sitka spruce. Can. J. For. Res. 19:1203–1207.

FRANCIS, J. K. 1986. The relationship of bole diameters and crown widths of seven bottomland hardwood species. U.S. For. Serv. Res. Note SO-328. 3pp.

GERING, L. R., AND D. M. MAY. 1995. The relationship of diameter at breast height and crown diameter for four species groups in Hardin County, Tennessee. South. J. Appl. For. 19:177–181.

GODMAN, R. M., AND C. H. TUBBS. 1973. Establishing even-age northern hardwood regeneration by the shelterwood method—a preliminary guide. U.S. For. Serv. Res. Pap. NC-99. 9pp.

HAYS, R. L., C. SUMMERS, AND W. SEITZ. 1981. Estimating wildlife habitat variables. U.S. Fish and Wildl. Serv. FWS/OBS-81/47. 111pp.

JACK, S. B., AND J. N. LONG. 1991. Analysis of stand density effects on canopy structure: a conceptual approach. Trees 5:44–49.

MCKEAN, J. W., AND G. L. SIEVERS. 1987. Coefficients of determination for least absolute deviation analysis. Stat. Probability Letters 5:49–54.

MOEUR, M. 1985. COVER: a user's guide to the CANOPY and SHRUBS extension of the stand Prognosis model. U.S. For. Serv. Gen. Tech. Rep. INT-190. 49pp.

———. 1986. Predicting canopy cover and shrub cover with the Prognosis— COVER model. Pages 339–346 *in* J. Verner, M. L. Morrison, and C. J. Ralph, eds. Wildlife 2000: modeling habitat relationships of terrestrial vertebrates. Univ. Wisconsin Press, Madison.

MUELLER-DOMBOIS, D., AND H. ELLENBERG. 1974. Aims and methods of vegetation ecology. John Wiley and Sons, New York, N.Y. 547pp.

REMINGTON, T. E., AND R. W. HOFFMAN. 1996. Food habits and preferences of blue grouse during winter. J. Wildl. Manage. 60:808–817.

ROMME, W. H., AND D. H. KNIGHT. 1981. Fire frequency and subalpine forest succession along a topographic gradient in Wyoming. Ecology 62:319–326.

ROTENBERRY, J. T. 1985. The role of habitat in avian community composition: physiognomy or floristics. Oecologia 67:213–217.

SHEPPERD, W. D. 1973. An instrument for measuring tree crown width. U.S. For. Serv. Res. Note RM-229. 3pp.

SMITH, W. R., R. M. FARRAR, JR., P. A. MURPHY, J. L. YEISER, R. S. MELDAHL, AND J. S. KUSH. 1992. Crown and basal area relationships of open-grown southern pines for modeling competition and growth. Can. J. For. Res. 22:341–347.

SPENCER, W. D., R. H. BARRETT, AND W. J. ZIELINSKI. 1983. Marten habitat preferences in the northern Sierra Nevada. J. Wildl. Manage. 47:1181–1186.

STAUFFER, D. F., A. H. FARMER, AND B. S. CADE. 1992. Use of wildlife habitat models for habitat management planning. Pages 609–616 *in* Proc. resource technology 90. Am. Soc. Photogrammetry and Remote Sensing, Bethesda, Md.

TABUSH, P. M., AND I. M. S. WHITE. 1988. Canopy closure in Sitka spruce—the relationship between crown width and stem diameter for open grown trees. Forestry 61:23–27.

Received 24 July 1996.
Accepted 21 November 1996.
Associate Editor: McDonald.