

BIOMASS OF FIFTY CONIFER FORESTS AND NUTRIENT EXPORTS ASSOCIATED WITH THEIR HARVEST¹

T. Weaver² and F. Forcella²

ABSTRACT.— Biomasses of climax Rocky Mountain forests studied ranged from less than 50 to more than 300 tons/ha. Total biomass was approximately 1.5 times the biomass of normally merchantable boles. When compared with conventional bole harvest, the nutrient exports associated with harvest of all aboveground parts in these stands would apparently be at least three times higher for nitrogen, six times higher for phosphorus, four times higher for potassium, and three times higher for calcium.

The volume or biomass of a tree can be predicted from its diameter or from its diameter and height. Foresters routinely estimate the volume of logs using these dimensions and tables calculated on the assumption that tree trunks are truncated cones or parabolas (Forbes and Meyer 1961). Weights can then be estimated by multiplying their volumes by the density of the wood. In most organisms the size of one organ system is directly related to the size of other organ systems (allometry, Sinnott 1960), so one can predict the volumes or weights of whole organisms from simple measurements. This has been demonstrated for a wide variety of trees including those of the conifer genera *Abies*, *Pinus*, and *Pseudotsuga* (Ovington 1957, Ovington and Madgwick 1959, Kimura 1963, Baskerville 1965, Whittaker and Woodwell 1968, Moir 1972, Odegard 1974, Whittaker et al. 1974, and Long and Turner 1975).

This paper presents a single equation which predicts total aboveground biomass of a tree, from its diameter, for any of the seven most common tree species of the northern Rocky Mountains. A comparison of this equation with others reported in the literature emphasizes the similarity of diameter biomass relationships among conifers in general. Various shrubs may also have similar size-weight relationships (Weaver 1977). An equation predicting weight from mea-

sures of both height and diameter is similar to published conifer D²H-weight relationships but less accurate than the diameter-weight relationship. Similar relationships are presented for weights of boles, branches, twigs, and leaves.

The biomass-DBH relationship found was applied to the stand tables of Daubenmire and Daubenmire (1968) to estimate the aboveground arboreal standing crops of fifty forest stands representing the following climax associations: *Pinus ponderosa*-*Festuca idahoensis*, *P. ponderosa*-*Symphoricarpos albus*, *P. ponderosa*-*Physocarpus malvaceus*, *Pseudotsuga menziesii*-*Symphoricarpos albus*, *P. menziesii*-*Physocarpus malvaceus*, *P. menziesii*-*Calamagrostis rubescens*, and *Abies lasiocarpa*-*Vaccinium scoparium*.

The nutrient content of the boles and of all aboveground parts was estimated so the nutrient export associated with conventional logging and complete tree utilization could be compared.

METHODS

Thirty-nine trees of six coniferous species and one broadleaf species were felled in southcentral Montana. The trees were sectioned into shoot material greater than 10 cm diameter, shoots between one and 10 cm basal diameter, shoots less than 1 cm basal diameter, and leaves. Each class was

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²Department of Biology, Montana State University, Bozeman, Montana 59715.

weighed wet. Wet weights were converted to dry weights by multiplying by a conversion factor determined for each component of each tree. The conversion factor was computed as follows: dry weight (60 C to constant weight)/wet weight. The tree species and the numbers of trees per species sampled were *Abies lasiocarpa* (Hook.) Nutt., 7; *Picea engelmannii* (Parry) Engelm., 3; *Pinus contorta* var *latifolia* Engelm., 4; *Pinus ponderosa* Dougl., 6; *Pinus albicaulis* Engelm., 7; *Pseudotsuga menziesii* (Mirb.) Franco., 5; and *Populus tremuloides* Michx., 7. The trees sampled ranged from 4 to 54 cm in diameter at breast height (D at 1.35 m) and from 3 to 20 m in height (H). The trees came from a wide variety of environmental conditions ranging from dry to moist sites and from open to closed stands. A list of the trees and their habitat types, sizes, weights, and ages is available from the authors.

After a preliminary graphical analysis, all data were pooled, and simple and multiple regression analyses were made to determine which models best predicted tree biomass, independent of species. These included linear, curvilinear, and log linear regressions of 12 dependent variables (including weight and logarithms of weights of total shoot and its components) against the independent variables D, D^2 , DH, and D^2H .

D^2 -biomass relationships were used to estimate the aboveground arboreal biomasses of 50 forest stands for which Daubenmire and Daubenmire (1968) have published stand tables. Since their tables list tree numbers by 10-cm-diameter size classes, tree weights were estimated by two different methods. 1) The weight of all trees in a plot were summed. These weights were estimated by assuming that the diameter of each tree was equal to that of the midpoint of the 10-cm-diameter class in which it was recorded. 2) The weights of all trees in a plot were summed. These weights were estimated by pooling all plot data for a given habitat type on the assumption that it represented a single (abstract) forest; assigning trees in this sample to 2.5-cm-size classes from a balanced distribution of tree size vs tree number (Meyer 1953); and estimating

the weights of the trees as if their diameters were equal to the midpoint of the size classes. Regressions through logarithmically transformed data are said to underestimate biomass (Baskerville 1972); we used uncorrected values because graphical analysis suggests that the uncorrected values represent our data better than corrected values do (cf Whittaker et al. 1974).

RESULTS AND CONCLUSIONS

Linear regressions of $\log_{10}D^2$ and $\log_{10}D^2H$ against log weight generally predict biomasses of Rocky Mountain trees well (Table 1 and Fig. 1a). (1) Both independent variables predict total biomass well ($r^2 = 0.98$ and 0.96 , respectively). $\log_{10}D^2H$ may be the safer predictor if our regressions are used in habitat types where taller trees than ours may be found. (2) $\log_{10}D^2H$ vs $\log_{10}$ weight is the best predictor for woody material with diameters greater than 1 cm or greater than 10 cm ($r^2 = 0.98$ and 0.95 , respectively). This is likely so because the conic or parabolic models of stem volume are good, weights are strongly correlated with volumes, most of the weight is in the larger classes, and branch volume is both correlated with and overridden by stem volume. (3) $\log_{10}D^2$ vs $\log_{10}$ weight is the best predictor for leaves and branches with diameters less than 1 cm ($r^2 = 0.84$ and 0.79 , respectively). This may be so because the capacities of current transporting tissues is highly correlated with diameter (cf Shinozaki et al. 1964). A graphical analysis of the leaf weight-diameter relationship suggests that the relatively low r^2 is partly due to between-species differences. (4) A regression of untransformed weights against $D + D^2$ was our best predictor of branch weights (1 to 10 cm, $r^2 = 0.97$). This curve, not shown, is J-shaped because in small trees the bole is in the branch-size class. (5) Regressions of untransformed variables (D, D^2 , DH, D^2H) vs untransformed biomass were not linear, were not used, and are not presented.

Our regressions of $\log_{10}D^2$ or $\log_{10}D^2H$ against $\log_{10}$ weight are remarkably similar to, but not identical with, those determined

in other regions (Fig. 1b); predictions of weights from such relationships apparently become poorer as one considers species and environments increasingly different from those for which the relationships were developed. The differences may be due to differences in form factor, wood density, branching patterns, and height-diameter

relationships. For example, the tendency of deciduous trees (Monk 1970, Whittaker and Woodwell 1968) to outweigh conifers of similar diameters could be due to the greater wood densities and branchiness of the deciduous trees.

The aboveground arboreal biomasses of 50 stands are summarized in Fig. 2; the val-

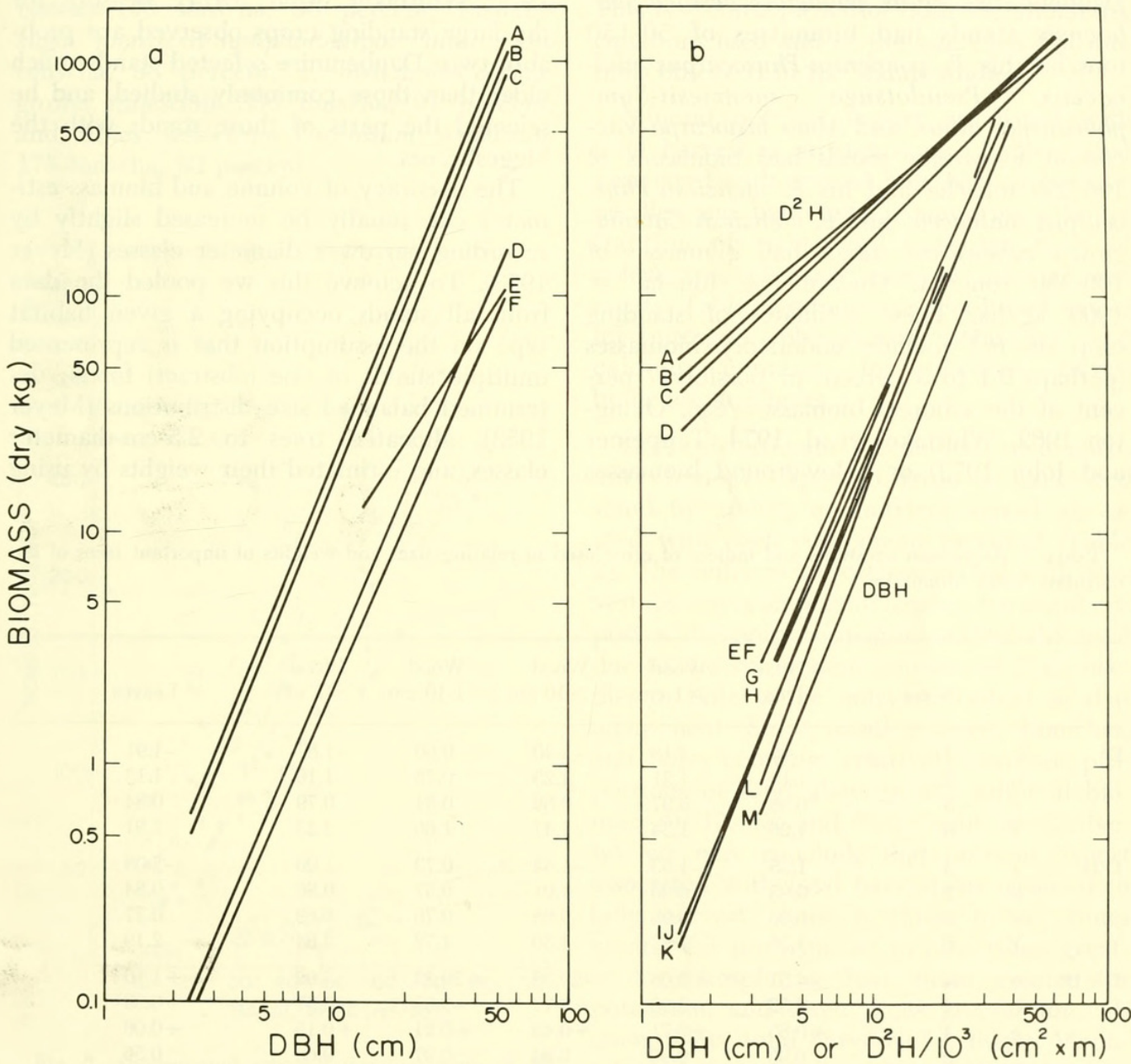


Fig. 1. Biomass-dimension relationships for coniferous species. (A) Diameter-biomass relations for seven species of the northern Rocky Mountains: a = total biomass, b = stem biomass (diameters greater than 1 cm), c = bole biomass (diameters greater than 10 cm), d = twig biomass (diameters less than 1 cm), e = branch biomass (diameters 1-10 cm), and f = leaf biomass. (B) Published DBH-biomass and D^2H -biomass relationships: a = *Picea rubens* (Whittaker et al. 1974), b = *Pinus rigida* (Whittaker and Woodwell 1968), c = seven species (Fig. 1a), d = *Pinus contorta* (Odegard 1974), e = *Picea rubens* (Whittaker et al. 1974), f = *Pseudotsuga menziesii* (Long and Turner 1975), g = *Pinus contorta* (Moir 1972), h = *Pinus sylvestris* (Ovington and Madgwick 1959), i = *Pinus rigida* (Whittaker and Woodwell 1968), j = seven species (Fig. 1a), k = *Abies balsamea* (Baskerville 1965), l = *Abies veitchii* (Kimura 1963), and m = *Pinus sylvestris* (Ovington 1957).

ues presented were calculated by assuming that tree diameters were equal to the mid-points of their 10-cm-size classes, i.e., by method 1. One may conclude (1) that total arboreal biomasses of climax conifer stands of the northern Rocky Mountains are generally in the 50-300 tons/ha range and (2) that those of specific forest series or associations generally have a narrower range: Daubenmire's *Pinus ponderosa-Festuca idahoensis* stands had biomasses of 50-150 tons/ha; his *P. ponderosa-Physocarpus malvaceus*, *Pseudotsuga menziesii-Symphoricarpos albus*, and *Abies lasiocarpa-Vaccinium scoparium* stands had biomasses of 100-250 tons/ha and his *P. menziesii-Physocarpus malvaceus* and *P. menziesii-Calamagrostis rubenscens* stands had biomasses of 100-350 tons/ha. One metric ton/ha = 1000 kg/ha. These estimates of standing crop do not include understory biomasses (perhaps 0.1 to 3 percent or possibly 7 percent of the arboreal biomasses: e.g., Ovington 1962, Whittaker et al. 1974, Tappeiner and John 1973) or belowground biomasses

(perhaps 20-30 percent or possibly 7-50 percent of the arboreal biomasses: e.g., Ovington 1962, Rodin and Bazilevich 1965, Whittaker and Woodwell 1968).

Despite the exclusion of understory and underground biomasses, the standing crops reported are larger than most of those reported in the literature (30-70 tons/ha; Rodin and Bazilevich 1965, Art and Marks 1971, Whittaker et al. 1974). Reasons for the large standing crops observed are probably two: Daubenmire selected stands much older than those commonly studied, and he selected the parts of those stands with the biggest trees.

The accuracy of volume and biomass estimates can usually be increased slightly by recording narrower diameter classes (Meyer 1953). To achieve this we pooled the data from all stands occupying a given habitat type on the assumption that it represented multiple stands of one (abstract) forest; determined balanced size distributions (Meyer 1953), allocated trees to 2.5-cm-diameter classes, and estimated their weights by using

TABLE 1. Regression constants and indices of error used in relating sizes and weights of important trees of the northern Rocky Mountains.

Notes ¹			Total Tree	Wood >1 cm	Wood >10 cm	Wood 1-10 cm	Wood <1 cm	Leaves
D ²	a	2	-1.05	-1.18	-1.40	0.60	-1.87	-1.91
	b	2	1.19	1.21	1.25	0.75	1.16	1.13
	r ²	5	0.98	0.97	0.89	0.81	0.79	0.84
	E	6	1.26	1.34	1.47	1.60	2.23	1.91
D ² H	a	3	1.35	-1.53	-1.84	-0.73	-1.99	-2.08
	b	3	0.93	0.96	1.01	0.57	0.86	0.84
	r ²	5	0.96	0.98	0.95	0.76	0.69	0.77
	E	6	1.36	1.27	1.30	1.72	2.64	2.19
D + D ²	a	4	-4.51	+0.08	-29.36	+29.37	-3.02	+1.16
	b	4	-3.32	-2.96	+0.71	-3.69	-0.57	+0.39
	c	4	+0.85	+0.71	+0.49	+0.21	+0.15	+0.06
	r ²	5	0.96	0.96	0.94	0.97	0.63	0.56
	e	6	0.29	0.38	0.25	1.14	0.28	1.00

¹Identification of symbols to the left.

²Log₁₀ WT = a + b log₁₀ D² with weight in kg and diameter in cm.

Log₁₀ WT = a + b log₁₀ D²H with weight in kg, diameter in cm, and height in m.

WT = a + b D + c D² with weight in kg and diameter in cm.

r is the correlation coefficient, r² is the fraction of the variation explained by the regression.

E is the antilog of the standard error of a logarithmic regression; expected errors lie between the predicted value x E and the predicted value/E. An estimate of relative error (e) is the standard error of a linear regression divided by the average weight (y) used (Whittaker and Woodwell 1968).

the midpoints of those classes as diameters (method 2). Forest weights estimated by method 2 ranged from 80 to 98 percent of the mean of stand weights determined with 10-cm-diameter classes (i.e., by method 1). They were: *Pinus ponderosa*-*Festuca idahoensis* 75 tons/ha, 80 percent; *P. ponderosa*-*Symphoricarpos albus* 155 tons/ha, 82 percent; *P. ponderosa*-*Physocarpus malvaceus* 140 tons/ha, 98 percent; *Pseudotsuga menziesii*-*Symphoricarpos albus* 180 tons/ha, 98 percent, *P. menziesii*-*Calamagrostis rubescens* 336 tons/ha, 91 percent; and *Abies lasiocarpa*-*Vaccinium scoparium* 178 tons/ha, 93 percent.

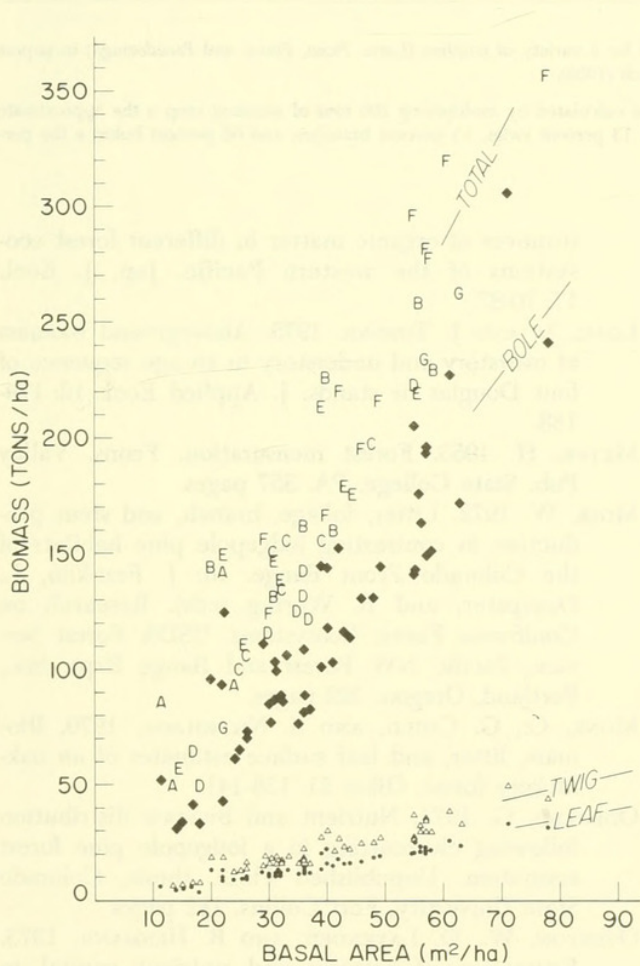


Fig. 2. Aboveground arboreal standing crops of 50 forest stands representing 7 habitat types: *Pinus ponderosa*-*Festuca idahoensis* (A), *P. ponderosa*-*Symphoricarpos alba* (B), *P. ponderosa*-*Physocarpus malvaceus* (C), *Pseudotsuga menziesii*-*Symphoricarpos alba* (D), *P. menziesii*-*Physocarpus malvaceus* (E), *P. menziesii*-*Calamagrostis rubescens* (F), and *Abies lasiocarpa*-*Vaccinium scoparium* (G). Calculations include all trees with DBH's greater than 5 cm; basal areas of stands 66, 101, 149, 173, 174, and 179 were recalculated from stand table data.

Biomasses in the leaf, twig, branch, and bole compartments are very nearly (SE $\pm$ 1 percent) 9 percent, 13 percent, 13 percent, and 66 percent of the arboreal biomass in the mature forests studied. Total harvest in most Rocky Mountain forests should therefore equal approximately 1.5 times the normal (10 cm +) stem harvest (Fig. 2). Whittaker et al. (1974) give similar values. This is a consequence of both the allometric equations used and of the size class distributions observed in the stands studied.

Mineral nutrient export associated with total harvest is greater than 1.5 times that associated with normal bole harvest because needles and bark (which comprise a larger fraction of twigs and branches than of boles) are relatively rich in mineral elements. Table 2 summarizes published values for nitrogen, phosphorus, potassium, and calcium contents for needles, twigs, branches, and boles.

One can estimate the amount of a nutrient element exported from a harvested stand by adding up nutrient export associated with each component exported (Table 2). The nutrient export associated with harvest of any component equals the total export x the proportion (percent) of the total due to the component considered (e.g., needles or bole) x the nutrient content of that component. Since needles, twigs, branches, and boles comprise relatively constant proportions of total aboveground arboreal biomass (9, 13, 13, and 66 percent, respectively), we may conclude that nutrient export associated with total harvest—as opposed to bole harvest alone—is three to six times greater for nitrogen, six to nine times greater for phosphorus, four times greater for potassium, and three times greater for calcium. Thus, total harvest of a Rocky Mountain conifer stand with a relatively low aboveground arboreal biomass of 100 tons/ha might remove 160-460 kg/ha of nitrogen, 20-40 kg/ha of phosphorus, 80-180 kg/ha of potassium, and 120-500 kg/ha of calcium. Bole harvest alone would remove only 25-160 kg/ha of nitrogen, 2-6 kg/ha of phosphorus, 20-40 kg/ha of potassium, and 40-200 kg/ha of calcium. Exports from for-

TABLE 2. Typical nutrient contents of conifers.^{1,2}

		Nitrogen		Phosphorus		Potassium		Calcium	
		%	kg/ 100t	%	kg/ 100t	%	kg/ 100t	%	kg/ 100t
Needles	max	1.34	121	0.22	20	0.78	70	1.05	95
	min	0.84	76	0.08	7	0.28	25	0.15	14
Twigs	max	0.60	78	0.07	9	0.30	39	1.10	143
	min	0.31	40	0.05	7	0.14	18	0.27	35
Branches	max	0.77	100	0.06	8	0.25	32	0.54	70
	min	0.15	20	0.02	3	0.12	16	0.28	36
Bole	max	0.24	158	0.01	7	0.06	40	0.30	198
	min	0.04	26	0.00	2	0.03	20	0.06	40
Total	max		457		43		181		506
	min		162		18		79		125

¹Percentage compositions reported are the highest and lowest values reported for a variety of conifers (*Larix*, *Picea*, *Pinus*, and *Pseudotsuga*) in papers by Odegard (1974), Overton et al. (1974), Stark (1973), and Rodin and Bazilevich (1965).

²Kg/100t contents refer to 100 tons of aboveground standing crop. They were calculated by multiplying 100 tons of standing crop x the approximate percentage of the standing crop contributed by the organ (9 percent needles, 13 percent twigs, 13 percent branches, and 66 percent boles) x the percentage of the organ contributed by the nutrient considered (N, P, K, or Ca).

est twice to three times as productive would be twice to three times as great.

One wonders whether the forest product value of 'slash' will exceed its fertilizer value. If inputs from nitrogen fixation processes or from decomposition of rocky substrates are small, the fertilizer value of branch material with diameters less than 10 cm might exceed its forest product value.

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