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WOODY BIOMASS OF FOREST STANDS

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ABSTRACT

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Published data on the total aboveground woody biomass (stems and branches), W_T, of 640 forest and woodland stands around the world (Cannell, 1982) were divided into 32 species groups. Differences between groups were examined in the relationship: $W_T = F(HG)D$, where F was a stand form factor; H was mean tree height; G was basal area at breast height; and D was mean wood basic specific gravity. W_T was linearly related to (HG); broadleaved species, owing to their greater D, had greater regression coefficients than conifers.

Regression coefficients and F factors tended to be smallest in groups having the smallest percentage biomass as branches and greatest in those having most branches. F factors of about 0.5 corresponded to groups having 5—10% branches. The shapes of the woody parts of trees in those groups would conform most closely to quadratic paraboloids as hypothesized by Dawkins (1963) and Gray (1966). But heavily branched broadleaved stands had F factors of 0.6—0.8, and the F factor of tapped *Hevea* rubber with 81% branches exceeded 1. Thus, for any given G and H, the greatest W_T was contained in those forests which had the greatest proportion of branches.

INTRODUCTION

Those interested in complete tree utilization, fuel wood and forest ecology, often wish to estimate the total aboveground woody biomass per hectare of stems and branches, including bark, of forests or woodlands. The biomass obviously depends on the age, stocking density and height of the stands, but does it also depend on the proportion of branches to stems?

Where W_T is the total, oven-dry, aboveground woody biomass per area, D is the mean wood basic specific gravity (dry weight/fresh volume), and V_T is the total overbark volume of the stems and branches per area, then $W_T = DV_T$. Clearly, D is fairly easily estimated, but V_T is not. For those species and localities where foresters have developed reliable stand volume tables or models, the merchantable or 'derbholz' volume per area (i.e. wood greater than about 7 cm diameter) can be estimated using the mean heights of dominant trees and stand basal areas at breast height. In those instances,

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Dawkins (1967) suggested that a rough estimate of V_T could be made on the assumption that the ratio of V_T/'derbholz' volume for most forests was about 1.3. But a better method of estimating V_T, is from the equation $V_T = F(HG)$, where F is a stand form factor, H is mean tree height, and G is stand, overbark, basal area at breast height. Dawkins (1961, 1963) and Gray (1956, 1966) suggested that the value of F for a wide range of forests and woodlands was in the range 0.4—0.6 (see below), and Edwards and Grubb (1977) assumed F to be 0.5 for tropical rain forests. But Gray's work suggested that F might differ among forest types having different proportions of branches to stems (see below).

In this paper I examine variation in F among the major coniferous and broadleaved forest types of the world, making use of published estimates of W_T made by ecologists and forest researchers, notably as part of the International Biological Programme. They estimated W_T directly, by felling, subsampling, oven-drying and weighing sample trees, and then estimating the biomass per area, most often by calculating so-called allometric regressions of the form: $w = a(d)^c$ or $w = a(d^2h)^c$, where w was the woody biomass per tree; d was tree diameter at breast height; h was tree height; and a and c were constants specific to each case or species (Ogawa and Kira, 1977; Gholz et al., 1979; Satoo and Madgwick, 1982). Estimates of W_T have been made for over 1000 forest and woodland stands around the world (Cannell, 1982). For this study I selected those stands for which values of H, G and D were also available, in order to derive estimates of F from the relationship:

$$W_T = F(HG)D \tag{1}$$

Thus, it was expected that W_T was linearly related to (HG) and that the slope of the relationship differed between forests which differed in D. Any remaining variation could be partly attributed to differences in F, and the crucial question was whether those differences were related to the proportion of stems to branches. Fundamentally, this question concerned hypotheses put forward by Gray and Dawkins about the basic shape of the woody parts of trees.

HYPOTHESES OF GRAY AND DAWKINS ON TREE FORM FACTORS

Gray (1956, 1966) hypothesized that the shape of the underbark stemwood of most forest trees approximated that of a quadratic paraboloid (Fig. 1A). Consequently, their cross-sectional areas decreased linearly with increase in height, so they could be represented as triangles, as in Fig. 1B and 1C, and their parabolic volumes (v_p) were given by:

$$v_p = 0.5\,(h_p s_p) \tag{2}$$

where h_p was parabolic height, and s_p was cross-sectional area at the base of the paraboloid. That is, according to this hypothesis, the basic underbark tree stemwood form factor was 0.5.

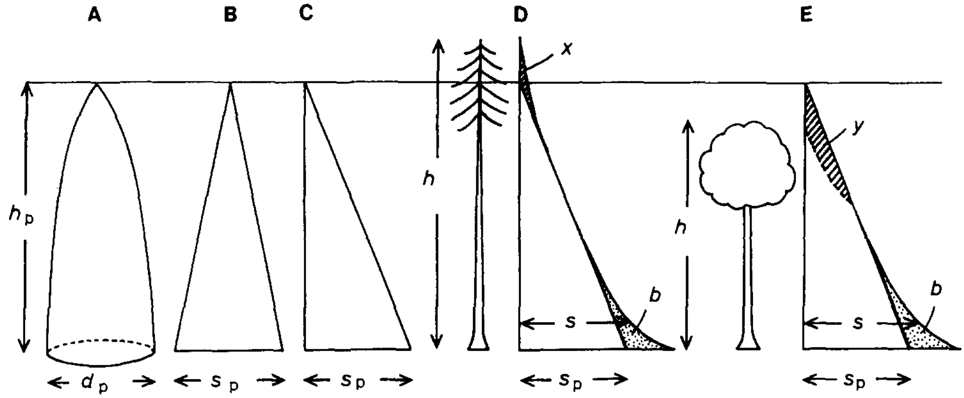

Fig. 1. The under-bark stem volume of forest trees in relation to the volume of a quadratic paraboloid: (A), (B) and (C), the dimensions of a paraboloid, where h_p = parabolic height; d_p = diameter; and s_p = sectional area at the base of the paraboloid. (D), the dimensions of a mature coniferous tree, with a small percentage of branch wood, where h = tree height; s = sectional area at breast height; b = bark plus buttswell; and x = small volume of stemwood in excess of the paraboloid volume. (E), the dimensions of a mature broadleaved tree, with a large percentage of branch wood, where y = volume of the paraboloid in excess of the stem volume. Modified from Gray (1966)

However, in reality the actual volumes of stemwood measured on trees differed from v_p in the following ways: (1) there was always some buttswell, giving volume b in Fig. 1D and 1E, additional to the theoretical parabolic volume; (2) the heights, h, of trees with small branch crowns (e.g. mature conifers) were greater than h_p, so that, for these trees, there was an additional volume, x in Fig. 1D, exceeding the parabolic volume; (3) conversely, the heights of trees with large branch crowns (e.g. broadleaved trees) were less than h_p, so that there was a volume, y in Fig. 1E, such that the volume of the paraboloid exceeded the true stemwood volume; (4) in practice, stem volume was estimated using overbark cross-sectional area at breast height, s, which was greater than s_p except on very small trees (Fig. 1D and 1E).

From measurements on several species of small-crowned trees, Gray (1966) found that the underbark stem volume was given by $0.54(h_p s_p)$, and that $h_p/h \approx 0.9$, and $s/s_p \approx 1.3$. Assuming that the ratio of overbark volume including branches to underbark stemwood volume was 1.2, then overbark total volume per tree, v_T becomes:

$$v_T \approx (0.54 \times 0.9/1.3 \times 1.2)\, hs = 0.45\, (hs)$$
$$\text{and } V_T \approx 0.45(HG) \qquad (3)$$

For heavily-crowned trees the values were approximately:

$$v_T \approx (0.54 \times 1.1/1.3 \times 1.3)\, hs = 0.59\, (hs)$$
$$\text{and } V_T \approx 0.59(HG) \qquad (4)$$

That is, according to Gray's measurements the overbark stand form factor for total aboveground wood, F, should be about 0.45 for sparsely branched conifer-type stands, and 0.59 for heavily branched broadleaved-type stands.

Dawkins (1961, 1963, personal communication) made detailed measurements of the volumes of stems and branches on individual trees of many tropical broadleaved species, and showed that v_T was linearly related to the product of h and s. Most interestingly he found that the average underbark form factor including branch wood was 0.50 (see eq. 2). He therefore suggested that, if the branches were squeezed on to the stems (as if a ring were passed up the stems) the resulting shapes would be quadratic paraboloids. This would mean that the volume y in Fig. 1E would be about equal to the underbark volume of the branches; and in Gray's equations it would mean that, for heavily-crowned trees, $h_P s_P \approx hs$.

According to Dawkins, the overbark tree form factor, with which we are concerned here, would be about 0.6 for tropical broadleaved trees, although his measurements showed that it differed between individuals in the range 0.55 to 0.68.

SOURCES OF DATA

Published data on stem biomass (W_S), branch biomass (W_B), stand overbark basal area at breast height (G), and mean tree height per stand (H) were used for a total of 640 forest and woodland stands, divided into 32 species or species groups (Table I). The data had been abstracted from 171 studies conducted during the period 1930—1981 in a total of 23 countries around the world. Four points should be noted about this data set: (1) the studies almost certainly differed in the accuracy with which W_S and W_B had been estimated, owing to differences in the number of trees felled, the goodness-of-fit of regressions, sampling procedures, and so on; (2) the height values used were probably slight overestimates of H, because some authors seemed to have reported dominant rather than mean tree heights, although this was known to be the case in only 34 of the 640 stands (not exceeding 5% within any of the 32 groups); (3) the mean values of D and F reported here for individual species should not be regarded as wholly representative of the species, because the locations, ages, stocking densities, growth rates and number of stands for which data were available differed greatly between species (Table I); (4) *Alnus* spp. and *Populus* spp. were omitted, because the data produced insignificant regressions of W_T on (HG), and *Acacia* spp. were not included because of insufficient data on D of the sample stands.

The mean percentage branches ($100 \times W_B/W_T$) in each of the 32 groups was calculated using the sum of stem and branch biomass of all stands within each group. Mean D values were based on measurements obtained for at least 65% of the stands within each group (491 stands in all) from data in the original publications (see Cannell, 1982), from Kingsdon and Risdon (1961), HMSO (1969) and by correspondence with the original authors.

TABLE I

Forest tree species and species groups, numbers of stands (or plots), and page numbers in Cannell (1982) which give the original biomass data and source references

	Species	Number of stands or plots	Page numbers
Abies spp.	*Abies alba*	16	87—89
	Other *Abies* spp.	45	40, 123—133, 199, 289, 290, 292
	Chamaecyparis obtusa	50	134—144
	Cryptomeria japonica	114	146—150, 152—166
Picea spp.	*Picea abies*	29	29, 62, 73, 169, 170, 361—364
	Other *Picea* spp.	11	41, 43, 85, 242, 296, 297
Pinus spp.	*Pinus banksiana*	17	48, 49, 299
	Pinus densiflora	10	171, 173, 174
	Pinus elliottii	9	175, 304
	Pinus nigra	25	69, 246, 247 and ref. cited
	Pinus ponderosa	5	310, 311
	Pinus radiata	13	21, 205, 206
	Pinus resinosa	10	312, 314, 315
	Pinus sylvestris	31	63, 225—228, 232, 244, 245
	Pinus taeda	28	178, 179, 321—327
	Pinus thunbergii	11	181, 182
	Other *Pinus* spp.	15	50, 177, 303, 316, 317, 319, 328
	Pseudotsuga menziesii	22	29, 71, 329—332, 334—337, 341
	Tsuga spp.	6	185, 186, 200, 349
	Thujopsis dolobrata	9	183, 184
	Sequoia spp.	10	168, 345, 346
	Hevea braziliensis	7	192, 193
	Betula spp.	15	61, 96—98, 222, 238
Japanese evergreens	*Camellia japonica*	10	99, 101
	Castanopsis cuspidata	14	102—105
	Cyclobalanopsis myrsinaefolia	5	107
	Eucalyptus spp.	14	8, 9, 12—15
Fagus spp.	*Fagus crenata*	18	111, 114—117
	Fagus sylvatica	11	24, 31, 59, 72, 86, 224
	Quercus spp.	28	27, 67, 77, 117, 197, 201, 213, 219, 222, 223, 229, 230, 240, 276, 278—280, 282, 283, 356, 358
Tropical plantations	*Shorea robusta*	12	79, 80
	Tectona grandis	7	82, 83
Tropical rainforest	*Micranda spruceana* et al	13	370, 371

RELATIONSHIP BETWEEN WOODY BIOMASS (W_T) AND HEIGHT × BASAL AREA (HG)

Least squares linear regressions were calculated between (1) W_S or W_T (t/ha) and (2) HG (m × m^2/ha) for all 640 stands together, for each of the 32 groups, and for combinations between them.

Because W_T differed by three orders of magnitude among stands, regressions using all 640 stands were calculated after $\log_e$ transformation, giving the following highly significant relationships:

$$\log_e W_T = -0.37 + 0.84 \log_e(HG) \qquad r^2 = 0.91 \text{ (Fig. 2)} \qquad (5)$$

$$\log_e W_S = -0.90 + 0.90 \log_e(HG) \qquad r^2 = 0.94$$

Both of these regression coefficients were significantly less than 1.0, the value which would be expected if W_T or W_S were proportional to a constant fraction of (HG). Stands with small (HG) values tended to have larger biomasses than expected relative to stands with large (HG) values, particularly when branches were included. The main reason for this was that the small stands included a high proportion of broadleaved species which had larger values of D and F than conifer species (see below).

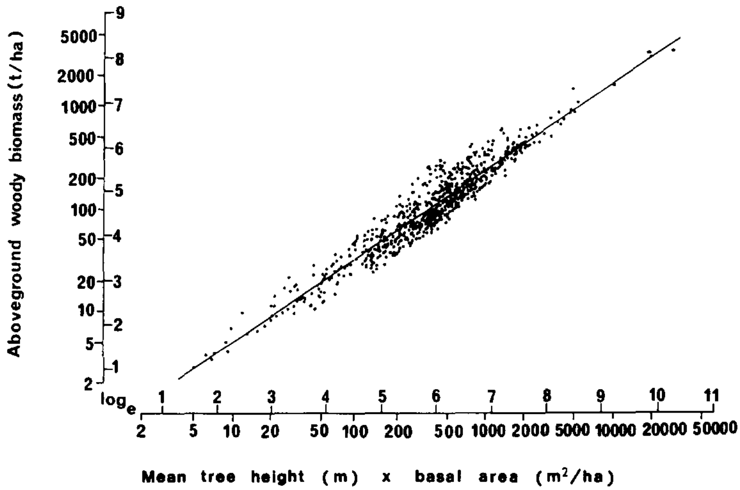

Fig. 2. Relationship, for 640 stands of all kinds of forests and woodlands around the world, between: (1) the measured aboveground dry weight of stems and branches (W_T); and (2) the product of mean tree height and stand basal area (HG). The smallest values are for young or stunted forests, the largest values are for stands of *Sequoia sempervirens* in northern California. See regression equation 5 in the text.

The relationships between W_T and (HG) were visually linear for all 32 species groups, based on 5 to 114 stands per group (Table 1). Linear regressions accounted for over 70% of the variation within all groups, and over 90% of the variation within 25 groups.

However, the regression coefficients differed significantly between groups, with or without $\log_e$ transformation (untransformed values, b, are given in Table II and Fig. 3). Broadleaved species, because of their greater D, had larger coefficients than conifers. The greatest coefficients were given by *Hevea braziliensis* (0.64), followed by *Micranda spruceana* dominated tropical forests (0.43), *Fagus sylvatica* (0.40), Japanese evergreen broad-

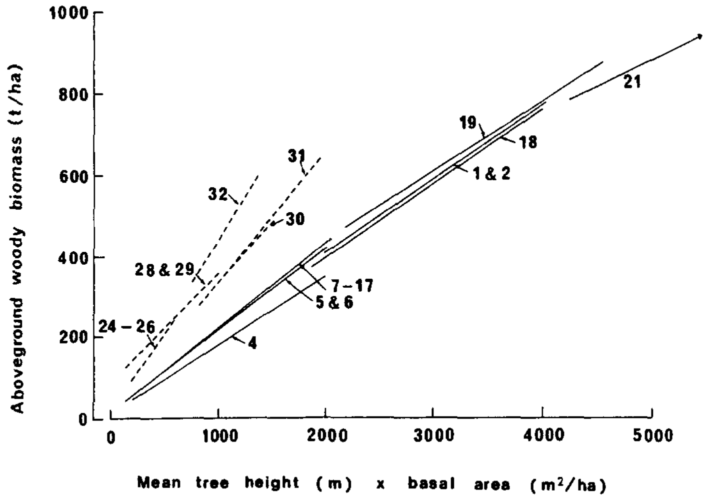

Fig. 3. Relationships between: (1) the measured aboveground dry weight of stems and branches (W_T); and (2) the product of mean tree height and stand basal area (HG), for different species and species groups given in Table I. Solid lines: conifers; broken lines: broadleaved species. The numbers on the graph correspond with the species numbers in Table II.

leaved species (0.37) and Indian plantations of *Shorea robusta* and *Tectona grandis* (0.33). Among the conifers, the smallest coefficients were given by *Sequoia* spp. (0.13) and plantations of *Cryptomeria japonica* and *Pinus radiata* (0.17).

Regressions were also calculated forcing the intercepts through the origins (b_l in Table II). This was done to remove intercept differences as a source of variation when comparing species values of F (see below), although the true intercepts must have been greater than 0, because G was measured at breast height. Forcing the intercepts through 0 generally decreased the percentage of variation accounted for, and increased the regression coefficients by an average of 0.03.

WOOD SPECIFIC GRAVITY AND PERCENTAGE BRANCHES

The mean wood basic specific gravity (D) of the broadleaved species was 0.61 g/cm^3 compared with 0.41 g/cm^3 for the conifer species. As mentioned, this difference accounted for much of the difference *between* the two groups in the regressions between W_T and (HG). However, variation in regression coefficients *among* either broadleaved species or conifers were not related to variation in D (Fig. 4).

By contrast, species differences in the mean percentage of branches explained 35% and 42% of the variation in regression coefficients among the broadleaved and conifer species, respectively (Fig. 5) — those species

TABLE II

Forest stand biomass relationships

Numbers in Figures 3 to 6	Species	Intercept	Regression coefficients		Specific gravity	Percentage branches	Stand form factors		
		(a)	(b)	(b_l)	(D)	(%B)	(F)	(F_l)	(F_s)
1	*Abies alba*	37	0.20 ± 0.001	0.23 ± 0.003	0.37	10.5	0.62	0.61	0.56
2	Other *Abies* spp.	39	0.18 ± 0.005	0.21 ± 0.005	0.39	15.2	0.57	0.53	0.49
3	*Chamaecyparis obtusa*	21	0.20 ± 0.007	0.23 ± 0.004	0.43	10.9	0.55	0.54	0.49
4	*Cryptomeria japonica*	12	0.17 ± 0.004	0.19 ± 0.003	0.35	9.7	0.53	0.53	0.48
5	*Picea abies*	28	0.19 ± 0.008	0.22 ± 0.007	0.47	12.4	0.52	0.47	0.45
6	Other *Picea* spp.	−11	0.25 ± 0.028	0.24 ± 0.015	0.38	16.3	0.61	0.64	0.52
7	*Pinus banksiana*	5	0.22 ± 0.004	0.23 ± 0.003	0.40	15.5	0.60	0.57	0.49
8	*Pinus densiflora*	17	0.22 ± 0.010	0.24 ± 0.009	0.42	11.5	0.63	0.58	0.54
9	*Pinus elliottii*	−1	0.26 ± 0.011	0.25 ± 0.003	0.37	16.7	0.68	0.68	0.56
10	*Pinus nigra*	15	0.23 ± 0.013	0.25 ± 0.006	0.39	14.5	0.66	0.65	0.56
11	*Pinus ponderosa*	74	0.18 ± 0.030	0.29 ± 0.004	0.42	17.6	0.82	0.69	0.68
12	*Pinus radiata*	11	0.17 ± 0.005	0.18 ± 0.005	0.39	13.6	0.49	0.46	0.43
13	*Pinus resinosa*	11	0.19 ± 0.008	0.21 ± 0.005	0.36	14.9	0.61	0.58	0.51
14	*Pinus sylvestris*	8	0.21 ± 0.004	0.22 ± 0.004	0.41	15.1	0.59	0.55	0.49
15	*Pinus taeda*	12	0.18 ± 0.010	0.21 ± 0.007	0.45	18.8	0.49	0.46	0.40
16	*Pinus thunbergii*	10	0.32 ± 0.033	0.39 ± 0.026	0.51	20.0	0.84	0.77	0.55
17	Other *Pinus* spp.	12	0.25 ± 0.014	0.27 ± 0.014	0.46	19.9	0.69	0.59	0.54
18	*Pseudotsuga menziensii*	22	0.19 ± 0.010	0.19 ± 0.007	0.45	9.2	0.46	0.43	0.40

19	*Tsuga* spp.	93	0.17 ± 0.015	0.20 ± 0.012	0.42	13.7	0.51	0.48	0.44
20	*Thujopsis dolobrata*	46	0.16 ± 0.033	0.24 ± 0.012	0.43	13.9	0.56	0.55	0.49
21	*Sequoia* spp.	209	0.13 ± 0.012	0.15 ± 0.008	0.39	4.1	0.36	0.37	0.36
22	*Hevea braziliensis*	—4	0.64 ± 0.068	0.63 ± 0.041	0.51	81.3	1.23	1.26	0.23
23	*Betula* spp.	10	0.29 ± 0.032	0.32 ± 0.015	0.55	15.0	0.60	0.58	0.51
24	*Camellia japonica*	51	0.34 ± 0.038	0.47 ± 0.002	0.73	25.1	0.67	0.64	0.50
25	*Castanopsis cuspidata*	6	0.37 ± 0.011	0.38 ± 0.006	0.51	19.7	0.76	0.75	0.61
26	*Cyclobalanopsis myrsinaefolia*	3	0.40 ± 0.021	0.42 ± 0.005	0.71	23.2	0.58	0.59	0.45
27	*Eucalyptus* spp.	19	0.21 ± 0.022	0.23 ± 0.013	0.69	9.3	0.33	0.34	0.31
28	*Fagus crenata*	104	0.24 ± 0.034	0.39 ± 0.023	0.56	20.6	0.75	0.69	0.60
29	*Fagus sylvatica*	–27	0.40 ± 0.054	0.37 ± 0.015	0.65	19.3	0.56	0.56	0.45
30	*Quercus* spp.	30	0.29 ± 0.024	0.33 ± 0.018	0.60	23.2	0.58	0.55	0.45
31	*Shorea and Tectona*	0	0.33 ± 0.011	0.33 ± 0.007	0.59	13.7	0.56	0.55	0.48
32	*Micranda spruceana*	6	0.43 ± 0.053	0.44 ± 0.024	0.61	38.8	0.72	0.72	0.44

Units: W_T and W_S: t/ha, H: m, G: m²/ha,

(a) Intercept of regression between total aboveground woody biomass, W_T, and height times basal area (HG), (t/ha).
(b) Regression coefficient (± *S.E.*) between W_T and (HG).
(b_l) As above, with the intercept forced through the origin.
(D) Mean wood basic specific gravity (oven-dry weight/green volume) of the sampled stands (g/cm³).
($\%B$) Mean percentage branches (branch biomass/total aboveground biomass).
(F) Stand form factor for total woody biomass, where $F = (a/HGD) + (b/D)$ using mean values of (HG) in each species group.
(F_l) As above, where $F_l = b_l/D$.
(F_s) Stand form factor for the stems only, where $F_s = (a_s/HGD) + (b_s/D)$ where a_s and b_s are the intercepts and coefficients of regressions of stem biomass (W_s) against (HG).

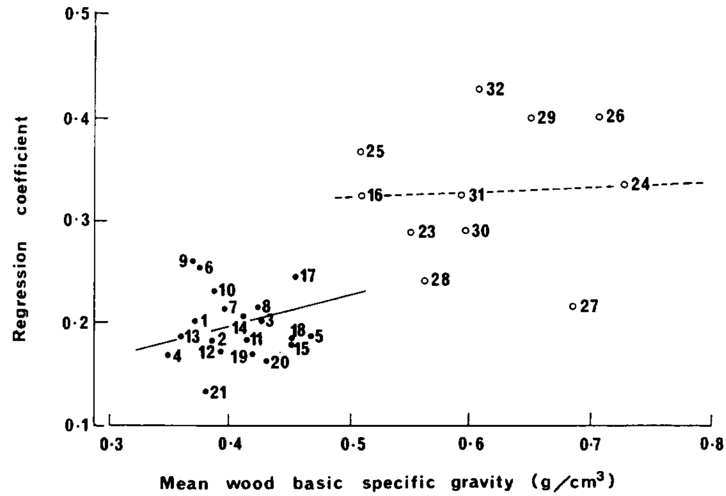

Fig. 4. Relationship between: (1) the regression coefficients (b in Table II) between aboveground woody biomass and height times basal area: and (2) mean wood basic specific gracity (D in Table II). Values are numbered as in Table II. *Hevea braziliensis* is not included. •, conifers; ○ broadleaved species.

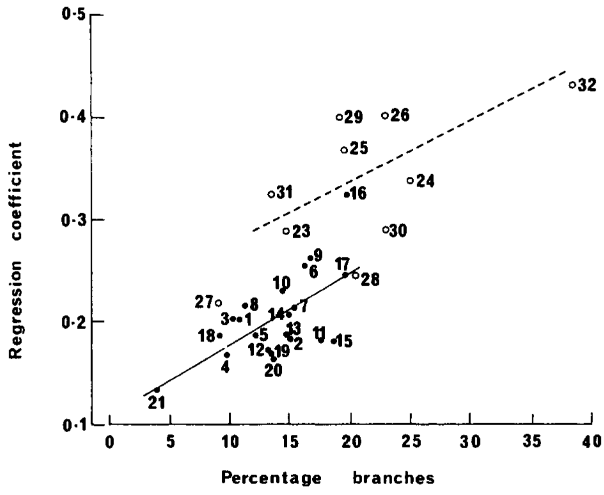

Fig. 5. Relationship between: (1) the regression coefficients (b in Table II) between aboveground woody biomass and height times basal area; and (2) branches as a percentage of the total aboveground woody biomass (%B in Table II). (See legend to Fig. 4.)

with most branches had the greatest woody biomass (W_T) for a given (HG).

Multiple linear regressions were calculated using (HG), D and percentage branches as regressor variables on W_T. Using 491 stands for which all variables were known, (HG) and D together accounted for 94% of the variation, (HG) and percentage branches accounted for 92%, and all three regressor variables accounted for 95%. When the 32 individual groups of species were considered separately, there were ten conifer and five broadleaved groups for which the addition of percentage branches significantly improved the regression of W_T on (HG).

STAND FORM FACTORS

Since $W_T = a + b\ (HG)$, it follows from equation 1 that the stand form factor derived from total aboveground woody biomass is $F = (a/HGD) + (b/D)$. Thus, F values tended to be greatest in those species groups with the greatest intercept values, a, and in all groups, F decreased slightly with increase in (HG). Values of F are given in Table II calculated using the mean values of (HG) for each group. To remove potential bias owing to species differences in intercept and in mean (HG), alternative stand form factors were calculated as $F_l = b_l/D$ (see Table II).

The very large regression coefficients b and b_l given by *Hevea braziliensis*, combined with its wood specific gravity of 0.51 g/cm^3 (Ng, personal communication), gave F and F_l values of 1.23 and 1.26, respectively, suggesting that the trees were 'top heavy'. This could well have been the case, because the trees had been tapped for latex, which decreases stem radial growth, and the branches formed 81% of the total aboveground woody biomass.

The mean F value of the other broadleaved species was 0.72, compared with 0.59 for the conifers. (Equivalent F_l values were 0.60 and 0.56). Most importantly, the variation among species in F was positively correlated with percentage branches (%B) with no significant curvilinearity or difference in slope between conifer and broadleaved species (Fig. 6). Excluding

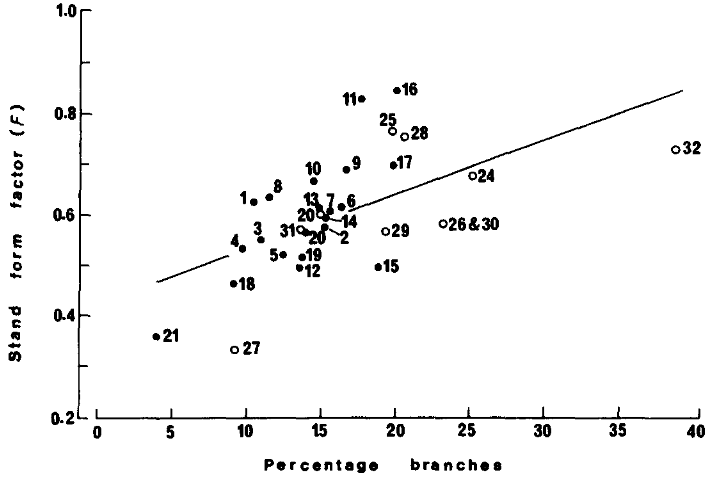

Fig. 6. Relationship between the stand form factor (F) and the percentage branches, for each of the species groups in Table II. (See legend to Fig. 4.)

H. braziliensis, the regression was:

$$F = 0.42 + 0.0107\ (\%B) \qquad r^2 = 0.34\ \text{(Fig. 6)} \qquad (6)$$

The equivalent equation using F_l was very similar, namely, $F_l = 0.41 + 0.0101\ (\%B)$, with $r^2 = 0.38$.

Stand form factors were also calculated for the stems only, from the equation $F_s = (a_s/HGD) + (b_s/D)$ where a_s and b_s were the intercepts and coefficients of regressions of W_s against (HG). The mean F_s value for broadleaved species excluding *H. braziliensis* was 0.48, and for conifer species was 0.50 (Table II). There was no significant relationship between F_s and percentage branches.

The reality of the relationship in Fig. 6 was reinforced by the fact that the predicted value of F (from equation 6) for *H. braziliensis* was 1.29, which was very similar to the actual value of 1.23.

DISCUSSION

Clearly, the woody biomass of any tree stand can be estimated from the product of its basal area, mean tree height, basic wood specific gravity, and a form factor (eq. 1). This study supports Gray's (1966) finding that the form factor is smaller for sparsely-branched conifers than for heavily-branched broadleaved trees (equations 3 and 4). However the form factor seems to be the same function of percentage branches (100 × branch biomass/total aboveground woody biomass) irrespective of whether the trees are coniferous or broadleaved (Fig. 6). For any tree stand, the overbark, total, aboveground, wood form factor seems to be 0.4—0.5, 0.5—0.6, 0.6—0.7 and 0.7—0.8 for stands having about 5%, 15%, 25% and 35% branches, respectively. These values are somewhat greater than suggested by Gray's work (equations 3 and 4, 0.45 for conifers, 0.59 for broadleaved species). The majority of coniferous forest stands have 10—20% branches, and so have form factors of 0.60 ± 0.05, while tropical broadleaved stands can have over 35% branches; and *Hevea* rubber can have over 80% branches, corresponding to a form factor exceeding 1. It follows that the shapes of the overbark total aboveground woody parts of trees (compressed as if by a ring passed upwards from the base of the stems) conform to the shapes of quadratic paraboloids only when 5—10% of the wood is branches. Only then will the volume of stems and branches be about half the product of basal area and tree height (eq. 2). An interpretation is that very sparsely branched trees taper more than paraboloids, whereas heavily branched trees are probably bulged at the level of the branches, as in Fig. 7. It may be concluded that for any given basal area and mean tree height, the greatest woody biomass will be contained in those stands with a large proportion of branch wood.

By contrast, the volumes of the stems alone seem to conform more closely to those of paraboloids. Most stand form factors calculated for stems alone

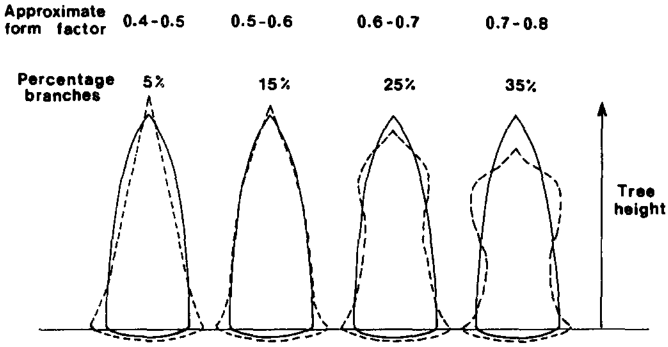

Fig. 7. Hypothetical profiles of the woody parts of trees (stems and branches with bark) having different percentages of branches, shown relative to the shape of a quadratic paraboloid. Solid lines: paraboloids. Dashed lines: shapes of woody tree parts, i.e. of stems and branches as if a ring had been passed up the stems from the base.

(F_S) were in the range 0.5 ± 0.05 (Table II), although much lower values were given by *Sequoia* and *Eucalyptus*, which had a small proportion of branches, and by *Hevea* which had a large proportion of branches.

Although these points are supported by trends in the world biomass data, it should be stressed that there was considerable scatter in the data, especially in the relationship between stand form factors and percentage branches (Fig. 6). Some of this scatter will have been due to differences in the accuracy with which biomass, basal areas and heights were estimated in different studies, but it is also likely that species, site and other factors influence the shapes of trees, and hence the form factors, as well as the percentage branches.

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