

Michael A. Cairns · Sandra Brown
Eileen H. Helmer · Greg A. Baumgardner

Root biomass allocation in the world's upland forests

Received: 3 July 1996 / Accepted: 23 January 1997

Abstract Because the world's forests play a major role in regulating nutrient and carbon cycles, there is much interest in estimating their biomass. Estimates of aboveground biomass based on well-established methods are relatively abundant; estimates of root biomass based on standard methods are much less common. The goal of this work was to determine if a reliable method to estimate root biomass density for forests could be developed based on existing data from the literature. The forestry literature containing root biomass measurements was reviewed and summarized and relationships between both root biomass density (Mg ha^{-1}) and root:shoot ratios (R/S) as dependent variables and various edaphic and climatic independent variables, singly and in combination, were statistically tested. None of the tested independent variables of aboveground biomass density, latitude, temperature, precipitation, temperature:precipitation ratios, tree type, soil texture, and age had important explanatory value for R/S. However, linear regression analysis showed that aboveground biomass density, age, and latitudinal category were the most important predictors of root biomass density, and together explained 84% of the variation. A comparison of root biomass density estimates based on our equations with those based on use of generalized R/S ratios for forests in the United States indicated that our method tended to produce estimates that were about 20% higher.

Key words Root biomass · Forests · Aboveground biomass · Root:shoot ratio

Introduction

There is increased interest in estimating the biomass of forests because of their role in regulating the cycling of carbon and nutrients. There are a variety of established methods for estimating the biomass in aboveground tree components, but biomass of root systems is difficult to measure in any forest ecosystem (Sanford and Cuevas 1996). Therefore, our knowledge of biomass allocation to roots lags behind that of its aboveground counterpart. A better understanding of the allocation of forest biomass, and the factors that regulate it, is needed for many applications including assessing change in forest structure, biogeochemical cycles, and various aspects of global change (Brown et al. 1993; Dixon et al. 1994; Sanford and Cuevas 1996).

Various factors are thought to determine the relative biomass allocation between roots and aboveground plant parts, commonly expressed as a root:shoot ratio (R/S) (Klepper 1991). Early studies assumed a static allometric relationship for R/S determinations (Bray 1963). More recent studies indicate that R/S varies with stand/tree age (Gerhardt and Fredriksson 1995), or is a function of tree species and differs between gymnosperms and angiosperms (Cuevas et al. 1991; Rodin and Bazilevich 1967; Sanford and Cuevas 1996). In addition to these biotic factors, several abiotic factors are thought to influence biomass allocation to roots. For example, decreasing soil moisture produces higher R/S (Axelsson 1981; Brown and Lugo 1982; Chapin 1980; Keyes and Grier 1981; Kramer and Kozlowski 1979; Murphy and Lugo 1986; Nadelhoffer et al. 1985; Nihlgård and Lindgren 1977). Soil characteristics, such as nutrient availability (Cavelier 1992; Gower 1987) and texture (Gerhardt and Fredriksson 1995; Keyes and Grier 1981; Vitousek and Sanford 1986; Vogt et al. 1995; Waring and Schlesinger 1985) are also purported to have a sig-

M.A. Cairns (✉) · S. Brown
US Environmental Protection Agency, National Health and Ecological Effects Research Laboratory, Western Ecology Division, 200 SW 35th Street, Corvallis, OR 97333, USA.
fax: (541) 754-4799; e-mail: michael@mail.cor.epa.gov

E.H. Helmer
Department of Forest Science, Forest Science Laboratory, Oregon State University, Corvallis, OR 97331, USA

G.A. Baumgardner
Anteon Corporation, US Environmental Protection Agency, National Health and Ecological Effects Research Laboratory, Western Ecology Division, 200 SW 35th Street, Corvallis, OR 97333, USA

nificant influence on root biomass. Specifically, inverse relationships between soil fertility and either root biomass density (RBD) or R/S have been reported, particularly in extremely nutrient-poor spodosols (Vitousek and Sanford 1986; Vogt et al. 1995; Waring and Schlesinger 1985). How generally applicable the conclusions reached by the above cited studies are to the world's forests is not clear because most of the studies were done over a relatively narrow range of biotic and abiotic conditions.

The objective of our study was to review data from all major biomes to determine what environmental and ecological characteristics best predict the allocation of biomass to roots. We examined the effects of latitude, tree type, temperature, precipitation, age, soil texture, and aboveground biomass density (ABD) on the allocation of biomass to tree roots. Our approach was to (1) review and summarize the literature, (2) test various statistical relationships between total RBD, including both live and dead roots, and R/S as dependent variables against the various edaphic and climatological independent variables, singly and in combination, and (3) develop equations that may be used to estimate RBD and associated uncertainty given ABD and data on one or more of the other factors. We were particularly interested in predicting RBD from ABD because of issues related to the total carbon pools in forests. Forest inventory data are useful for reliably estimating ABD, as has been done for many regions of the world (Birdsey 1992; Brown et al. 1993; Brown and Gaston 1995; Kurz et al. 1992). However, forest inventories do not provide a direct way of estimating RBD, so other means must be sought.

Methods

Building the database

We reviewed the literature to obtain sources that reported root and aboveground biomass in forest ecosystems. All data were critically reviewed using these criteria:

1. Did the methodology sufficiently indicate that all root biomass was quantified?
2. Were biomass densities reported on an oven dry weight basis?
3. Did the studies adhere to standard methods leading to comparable estimates?

In general, standard methods included spatially distributed soil cores or pits for fine to medium roots and partial to complete excavation and/or allometry for coarser roots. Most studies did not report or quantify root biomass by size classes. Further, because authors generally did not distinguish between live and dead, total RBD was reported as the sum of both live and dead roots.

Root sampling depth was either ≥ 100 cm (15%), from 40 to < 100 cm (20%), or unknown (65%). Although many sources did not specify depth, the studies were designed to quantify total root biomass. Therefore, we assumed that the investigators sampled to a depth to capture practically all the roots.

Although the sites were not randomly distributed and did not equally represent all latitudinal zones, we feel that they represent a wide range of environmental conditions. The site characteristics of the data set showed a broad range of biotic and climatic conditions,

with trees ranging in age from 2 to 350 years, mean annual precipitation from 269 to 4000 mm, and mean annual temperature from -3.4 to 28°C (Table 1). Most studies were done in the temperate zone (44%), followed by the boreal (32%) and tropical zones (24%). Information on soil texture was available for about half of the sites. Further, the data came from 25 countries on six continents.

We excluded data from forested wetlands, i.e., mangroves, bogs, and swamps. We also excluded data from sites subject to recent harvesting activities that likely reduced ABD but not RBD (e.g., coppiced stands). The resultant total number of records was 165 (Table 1) and the sample size in the various analyses ranged from 68 to 165 because some records contained certain data (e.g., temperature), but not others (e.g., age).

We also sought to determine trends and relationships between the fine:total RBD ratio and factors which may influence this ratio. Approximately 25% of the data records contained explicit estimates of fine root biomass. Sources used various definitions of fine roots, the most frequent being all roots < 5 mm diameter. We examined the 27 estimates so defined.

Based on current understanding, the major factors influencing biomass allocation to roots appear to be latitude, tree type, age, precipitation, temperature, temperature:precipitation ratio [T/P, an index of water availability (Brown and Lugo 1982)], and soil texture. In many cases latitude and longitude were not specified, but enough information was given (e.g., country) to place sampling sites in a latitudinal zone, generally defined here as: tropical forests 0 – 25° , temperate forests 26 – 50° , and boreal forests $\geq 51^{\circ}$ (Dixon et al. 1994). Tree type was coarsely categorized as either angiosperm (generally broadleaf) or gymnosperm (generally coniferous). Age (years) of the dominant trees, when given by the sources, was noted. Mean annual temperature ($^{\circ}\text{C}$) and total mean annual precipitation (mm) were used in the analyses, along with ratios of temperature to precipitation (Brown and Lugo 1982).

Soils were classified into three texture classes: coarse, medium, and fine, based on FAO (1971–1981). These were assigned by using descriptions in the data sources and a standard soil texture chart. This was accomplished using either the percent composition of sand, silt, and clay (if reported) or by aggregation of subclasses.

Statistical analysis

For practical purposes of this global synthesis, we assumed that all field observations were random and independent. In some cases where allometric regression equations were used for estimating ABD and coarse RBD based on tree diameter alone, this may not be strictly the case. As part of the process of developing predictive regression equations, we tested the standard assumptions of linear regression (Neter et al. 1989) as applied to these data. Histograms and scatterplots of the variables used in our analysis revealed that transformations were required for ABD, RBD, age and R/S. A natural log transformation was used to help stabilize the non-constant variance of ABD and RBD and to help correct skewness of the age and R/S distributions (Ramsey and Schafer 1996). Temperature, precipitation, and their ratios did not require transformation.

Both R/S (a variable derived from total RBD and total ABD) and RBD were tested for statistical relationships with a series of biotic and abiotic site characteristics. General descriptive statistics and the Student-Newman-Kuehl multiple comparison procedure (Kuehl 1994) were applied to the discrete, or categorical, site characteristics (latitudinal zone, soil texture index, and tree type) with R/S as the response variable at an $\alpha = 0.05$ level of significance. Both the continuous and discrete independent variables were then separately fit to R/S using simple linear least squares regression (Myers 1990).

Following the examination of R/S predictability, we tested our ability to estimate RBD directly from ABD and other climatic and edaphic factors with a forward stepwise least squares regression algorithm (Myers 1990). A set of *a priori* two-way interactions was included in this analysis with the stipulation that no two-way in-

Table 1 Site descriptions and data sources. Each source represents one or more data points (electronic version of complete data base available from authors). *ABD* aboveground biomass density, *RBD* root biomass density (values in parentheses are the ratio of fine root (< 5 mm diameter) biomass density to total *RBD*), *MAT* mean annual temperature, *MAP* mean annual precipitation, *M* mature forest, but specific age not reported, Soil texture *C* coarse, *ME* medium, *FI* fine, *N/A* data not reported

Country	ABD (Mg/ha)	RBD (Mg/ha)	MAT (°C)	MAP (mm)	Age (year)	Texture	Forest type ^a	Source
Tropical – ≤ 25° lat.								
Malaysia	431	43	25	1810	M	ME	Lowland rain	Bandhu 1973; Kira 1990
Zaire	121	32	24.5	1700	18	N/A	Moist	Bartholomew et al. 1953
Venezuela	182	128	26	3600	M	CO	Tall bana woodlands	Bongers et al. 1985
Brazil	406	69 (0.58)	27.2	1771	M	ME	Lowland rain	Bruing and Klinge 1976; Fittkau and Klinge 1973; Klinge 1973, 1976; Klinge et al. 1975; Klinge ^b
Brazil	5–88	1–9	25	1750	3–8	FI	Evergreen rain	Buschbacher et al. 1988; Uhl et al. 1988
Mexico	74	31	23.5	707	M	ME	Dry deciduous	Castellanos et al. 1991
Panama	13	2	25	2000	2–5	N/A	Moist secondary	Ewel 1971
Puerto Rico	223	69	19.7	3725	M	N/A	Lower montane rain	Frangi and Lugo 1985
Ghana	233	54	25	1650	40	N/A	Moist semideciduous	Greenland and Kowal 1960
Venezuela	348	56 (0.44)	12.6	1500	M	N/A	Montane humid	Grimm and Fassbender 1981
Jamaica	229	55	15.5	2500	M	N/A	Upper montane	Grubb and Tanner 1976; Tanner 1980
French Guyana	323	42	N/A	N/A	M	N/A	Lowland rain	Humbel 1978; Lescure et al. 1983
Ivory Coast	513	51 (0.56)	26.2	2095	M	CO	Lowland rain	Huttel 1975; Lemece ^b
Malaysia	81	6	25.8	4000	12.5	ME	Evergreen wet, secondary	Koopmans and Andriess 1982
Sri Lanka	32	17	28	1050	32	ME	Mixed evergreen and dry deciduous	Koopman and Andriess 1982
Puerto Rico	32–125	6–22 (0.25–0.71)	22.3	2330–3920	5.5–60	FI	Lowland wet secondary and paired plantations	Lugo 1992
Surinam	415	66	25	2250	M	N/A	Lowland rain	Ohler 1980, cited in Klinge and Herrera 1983
Puerto Rico	198	65	22.3	3920	M	N/A	Lower montane rain	Ovington and Olson 1970
Brazil	97–394	32–60	25	2300	8.5–M	CO	Lowland wet mature and plantation	Russell 1983
Venezuela	58–255	10–59	25	3500	11.5–M	N/A	Lowland moist mature and secondary	Saldarriaga et al. 1988
Puerto Rico	226	75 (0.03)	22.3	3500	M	FI	Wet tabonuco	Scatena et al. 1993
Venezuela	20–34	3–4	25	3500	3–5	ME	Lowland young successional rain	Uhl 1987
Temperate – 26–50° lat.								
United States	12	3	1.5	1000	350	CO	Subalpine	Arthur and Fahey 1992
Australia	312	75	11.2	982	51	N/A	Eucalyptus	Attwill ^b
Czechoslovakia	161	76	10	570	60	N/A	Fageto- Quercetum	Biskupsky ^b
Spain	160	62	9.5	870	75	ME	Montane Mediterranean sclerophyllous	Canadell and Roda 1991
Canada	117–313	37–78 (0.08–0.17)	N/A	N/A	70–78	CO-N/A	Subalpine coniferous	Comeau and Kimmins 1989
United States	130	36 (0.23)	14.5	1390	43	ME	Mesic deciduous hardwood	Cox et al. 1978
Belgium	121	35	8.5	952	80	N/A	Mixed oak	Duvigneaud and Galoux ^b
United States	386–430	93–99 (0.01–0.06)	9.4	1440	45	N/A	Coniferous lowland	Edmonds 1980, 1987; Vogt 1991; Vogt et al. 1983, 1987

Table 1 (continued)

Country	ABD (Mg/ha)	RBD (Mg/ha)	MAT (°C)	MAP (mm)	Age (year)	Texture	Forest type ^a	Source
India	27–241	14–67	8.0–12.1	2170	N/A	ME-CO	Deciduous timberline	Garkoti and Singh 1995
United States	174	31	9.8	1360	36	N/A	Douglas fir plantation	Gessel and Sollins 1981 ^b
Canada	122–462	28–106	4	1242	84–212	N/A	Spruce	Gordon ^b
United States	500–982	105–206 (0.05–0.09)	8	2300	M	ME	Douglas fir	Grier and Logan 1977; Santantonio et al. 1977; Sollins et al. 1980
United States	53–447	23–139 (0.09–0.40)	5.4	2700	23–180	ME	Cold, wet subalpine	Grier et al. 1981; Vogt et al. 1982
United States	90	22 (0.14)	15.5	1160	N/A	N/A	Pacific silver fir	Harris et al. 1977
United States	109–138	33–34	13.3	1400	30–55	N/A	Warm coniferous loblolly pine plantation	Harris and Henderson ^b
Hungary	222	36	9.9	582	66.5	N/A	Oak-hickory, pine, chestnut oak, yellow poplar	Jakucs ^b
United States	248–467	57–89 (0.05–0.18)	10.2	1000	40	ME-CO	Oak woodland	Keyes and Grier 1981
United States	93	22	15.6	1150	15	ME	Lowland coniferous	Kinerson et al. 1977; Ralston et al. ^b
Japan	192	64	4.2	1455	290	N/A	Pine plantation	Kitazawa ^b
France	262	50	12.4	987	150	N/A	Sub-alpine coniferous	Lossaint ^b
United States	266	66	6.9	777	130	N/A	Mediterranean evergreen oak	Loucks and Lawson ^b
Poland	243	49	7.8	729	100	N/A	Oak-prairie border	Medwecka-Kornas and Bandolo-Ciolczyk ^b
Former USSR	446	67	17.3	1856	20–40	N/A	Oak-hornbeam	Molotovskiy ^b
United States	276	28	N/A	N/A	N/A	N/A	Taiga	Mulholland 1979, cited in Brinson 1990
United States	– ^c	–	N/A	N/A	110	N/A	Deciduous riverine	Pearson et al. 1984
Spain	204	53	8	802	90	N/A	<i>Pinus contorta</i>	Puigdefabregas ^b
Japan	93–169	23–37	10.2–11.3	1467–1806	20–39	N/A	Pine-holly	Satoo ^b
Japan	292	44	11.3	2788	150	N/A	Pine & larch plantations	Shidei ^b
India	92–640	21–146	9.3–23	800–3500	52-M	ME-FI	Beech	Singh et al. 1994
United States	175	35	9.8	1370	34	CO	Monsoon mixed deciduous evergreen	Turner et al. 1976; Zavitovski and Stevens 1972
Czechoslovakia	314	47	N/A	N/A	N/A	N/A	<i>Alnus rubra</i>	Vyskot 1976
United States	26	8	11.6	970	N/A	ME	Deciduous riverine	Westman and Whittaker 1975
Canada	75	24	0.5	384	N/A	N/A	Mediterranean climate	Wilson 1993
United States	147–210	32–42	N/A	N/A	20–50	FI	pygmy forest	Zavitovski and Stevens 1972
Boreal – ≥ 51° lat.	– ^c	–	N/A	N/A	N/A	N/A	Aspen	Alexeyev and Birdsey 1994
Former USSR	201	34 (0.24)	7.5	644	158	FI	Rain deciduous	Andersson 1971
Sweden	218	63	6.1	1063	70	N/A	Taiga	Dylis 1971
Former USSR	275	36	N/A	N/A	122	N/A	Mixed deciduous woodland	Ellenberg ^b
Germany	251–307	65–126	6	537	80–250	ME	Luzulo-gagetum	Goryshina ^b
Former USSR	102	38	0	500	260	N/A	<i>Fagus sylvatica</i>	
Finland							Quercetum Pilosicariosum & Tilleto-quercetum	
							Aegopodiosum	
							Hylocomium-myrtillus	Havas ^b

Table 1 (continued)

Country	ABD (Mg/ha)	RBD (Mg/ha)	MAT (°C)	MAP (mm)	Age (year)	Texture	Forest type ^a	Source
Former USSR	206	74	3.4	640	110	ME	Taiga, Piceum-myrttilosa Oxalidosum	Karpov ^b
Former USSR	25–209	6–48	2.2	650	22–138	N/A	Myrttilosum	Kazimirov and Morozova ^b
Sweden	226–315	36–44	6–7	650–900	90–100	N/A	Beech, Deschampsia type	Lindgren and Nihlgard ^b
Sweden	308–324	52–58	7	800	60–87.5	N/A	Beech, Stellaria-larmitium & planted spruce	Nihlgard ^b
UK	62–164	17–49	7.7–N/A	762–N/A	23–55	FI-N/A	Coniferous plantations & deciduous	Ovington 1962
Former USSR	133	41	-1.2	499	125	N/A	Northern taiga, Piceum Hylocomiosum	Rudneva et al ^b
UK	128	76	7.8	1115	80	N/A	Mixed deciduous	Satchell ^b
Former USSR	61–207	19–43	N/A	N/A	20–67	N/A	Deciduous	Smirnova and Gorodentseva 1958
Denmark	221	44	7.1	660	87.5	N/A	Beech	Thamdrup ^b
United States	231	51	-3.4	269	130	N/A	Conifer	Van Cleve ^b
Netherlands	273	41	8.6	780	140	N/A	Oak	Van Der Drift ^b

^a As reported by the source authors^b Cited in DeAngelis et al. 1981; names of International Biological Programme investigators^c Only R/S ratio reported

teraction would be included in a model without also including both main effects. We computed an adjusted R^2 , which can either increase or decrease when additional predictor variables are added to the model because normal R^2 increases simply by adding more variables to an equation even if those variables add no real predictive power. Normal R^2 is thus a poor measure for comparing models and evaluating goodness of fit (Neter et al. 1989). Possible multicollinearity was checked by looking for fluctuations in estimated model parameters and their associated standard errors as each additional explanatory variable was added to the model. Regression model adequacy was examined by performing residual analyses to check for constant variance and normally distributed errors. For the simple linear and log-linear regression equations, a scatterplot of the response variable, its expected mean regression line, and prediction bands helped to validate the linearity assumption and the practical error associated with the predicted RBD. Examination of diagnostic plots (Studentized residuals, Cook's Distance, and HAT diagonals) revealed that none of the observations exhibited undue influence or leverage on the fitted regression equations.

Practical significance of the RBD prediction equations was examined by running each equation with hypothetical values for single explanatory variables and observing the effects on the estimated results. This provided a quantitative comparison of statistical and practical significance. Finally, we applied our equations to published estimates of aboveground forest biomass and compared our RBD predictions to those calculated with simple R/S ratios.

Results and discussion

Root:shoot ratios

The range in ABD ($4.7\text{--}982.5\text{ Mg ha}^{-1}$), RBD ($1.2\text{--}206.3\text{ Mg ha}^{-1}$), and R/S ($0.05\text{--}0.70$) varied by orders of magnitude. Examination of the basic descriptive statistics for the discrete predictive variables showed that the overall mean R/S was approximately 0.26 and the tendency was for values to be between 0.20 and 0.30, independent of latitude, soil texture, or tree type (Table 2). Aside from the slight difference in mean R/S for tropical sites, none of the three discrete predictive variables (latitudinal zone, soil texture, tree type) showed differ-

Table 2 Root:shoot biomass ratios (R/S) by latitudinal zone, soil texture, and tree type. Mean, standard deviation (SD), coefficients of variation (% CV), median, lower (LQ, 25%) and upper (UQ, 75%) quartiles, and sample size (n) are also given. The sample size varies by characteristic because of the lack of data for that characteristic in the original source. Significant differences in means are shown by different *lower case letters* (Student-Newman-Kuehl test; $\alpha = 0.05$)

	Mean (SD)	% CV	Median	LQ	UQ	n
LATITUDINAL ZONE						
Tropical	0.24 (0.14) a	58	0.21	0.14	0.31	39
Temperate	0.26 (0.07) b	27	0.24	0.22	0.28	73
Boreal	0.27 (0.10) b	37	0.25	0.22	0.30	53
SOIL TEXTURE						
Coarse	0.29 (0.17) a	58	0.26	0.20	0.33	10
Medium	0.27 (0.11) a	41	0.25	0.21	0.36	34
Fine	0.24 (0.11) a	46	0.23	0.20	0.27	24
TREE TYPE						
Angiosperm	0.25 (0.12) a	48	0.24	0.17	0.31	102
Gymnosperm	0.26 (0.07) a	27	0.24	0.22	0.29	63

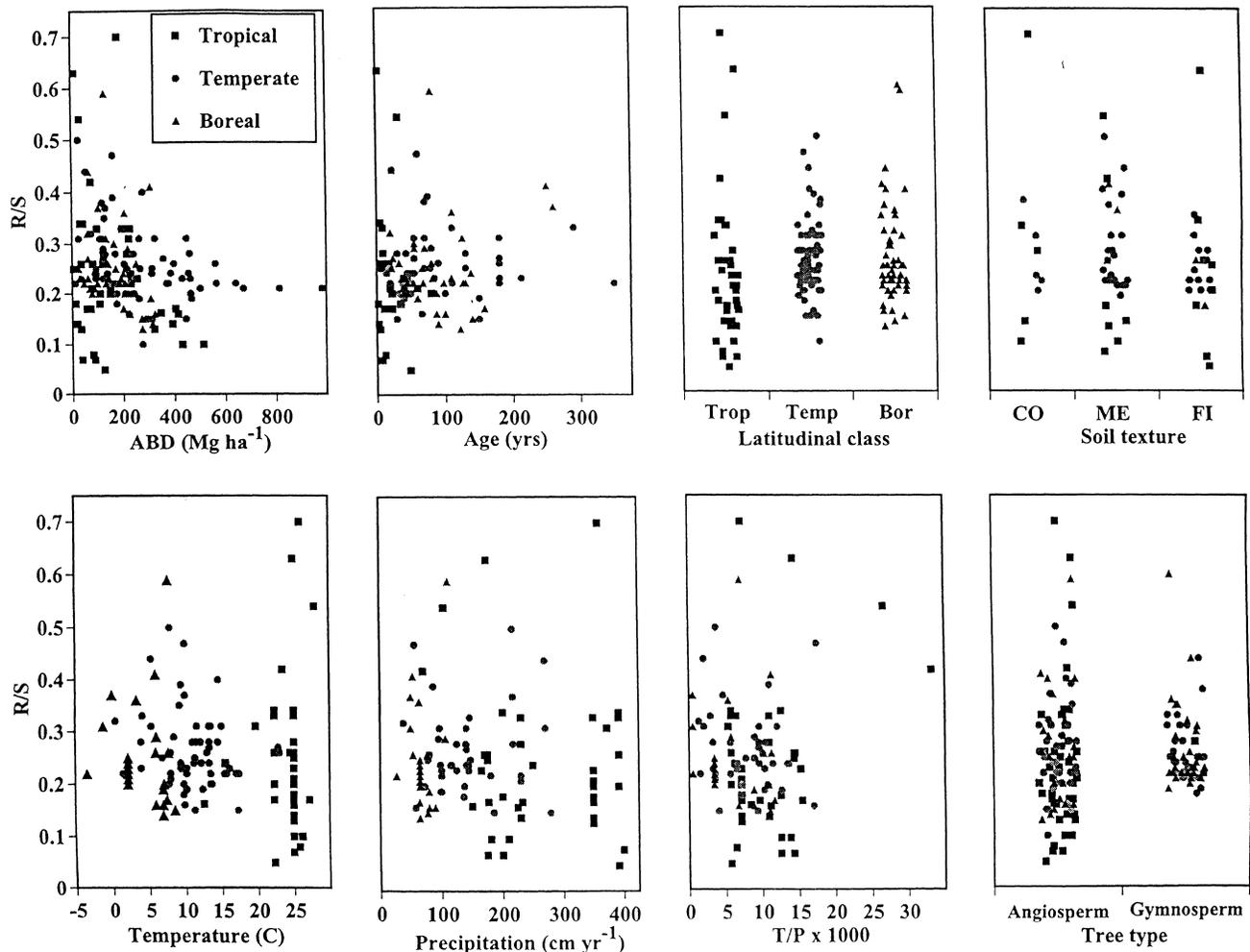


Fig. 1 Scatterplots of root:shoot ratios (R/S) versus aboveground biomass density (ABD), age, latitude, soil texture, mean annual temperature (T), mean annual precipitation (P), T/P ($^{\circ}C/mm$) ratios, and tree type. The discrete variables (latitudinal zone, soil texture, and tree type) are plotted in a staggered manner for clarity

ences in mean R/S with a change in parameter values. A multiple comparison test indicated that the R/S in tropical sites was significantly lower than in the other latitudinal zones. As might be expected, the R/S was higher in coarse soils than in the other soil texture classes, although this trend was not statistically significant. The coefficient of variation was higher in the tropics than in the other two zones, reflecting a greater heterogeneity of forest types. Similarly, the higher coefficient of variation for angiosperm R/S , despite the larger sample size (Table 2) reflects the greater heterogeneity of these tree types compared to gymnosperms.

Scatterplots of R/S versus eight possible predictive variables showed no apparent relationships with any of the independent variables tested (Fig. 1). Simple linear regressions of transformed and untransformed data revealed that none of the independent variables alone exhibited predictive value for R/S . Natural log trans-

formations aided in meeting standard assumptions of linear regression and were thus used in such analyses. Although the model parameters for ABD , latitudinal zone, and mean annual temperature were statistically significant ($\alpha = 0.05$) in explaining the variation in R/S , the highest coefficient of determination was an adjusted R^2 of 0.05 for latitudinal zone, indicating little practical significance. Age, soil texture index, tree type, temperature:precipitation ratio, and mean annual precipitation, alone or in combination, were not statistically significant ($\alpha = 0.05$) in explaining variation in R/S .

Root:shoot ratios are routinely used to partition plant biomass into aboveground and root component (e.g., Klepper 1991; Russell 1977). Our lack of a predictive relationship between R/S and eight biotic and abiotic factors (Fig. 1) was in contrast to previous conclusions (e.g., Rodin and Bazilevich 1967). Our results also contrast with those of Körner (1994) who reviewed 73 studies on biomass partitioning in temperate and boreal zone forests. He reported R/S for conifers of 0.24, which is higher than the 0.19 he reported for deciduous trees. By comparison, Cannell (1982) reported R/S of 0.26, 0.25, and 0.31 for coniferous, deciduous, and tropical forests, respectively.

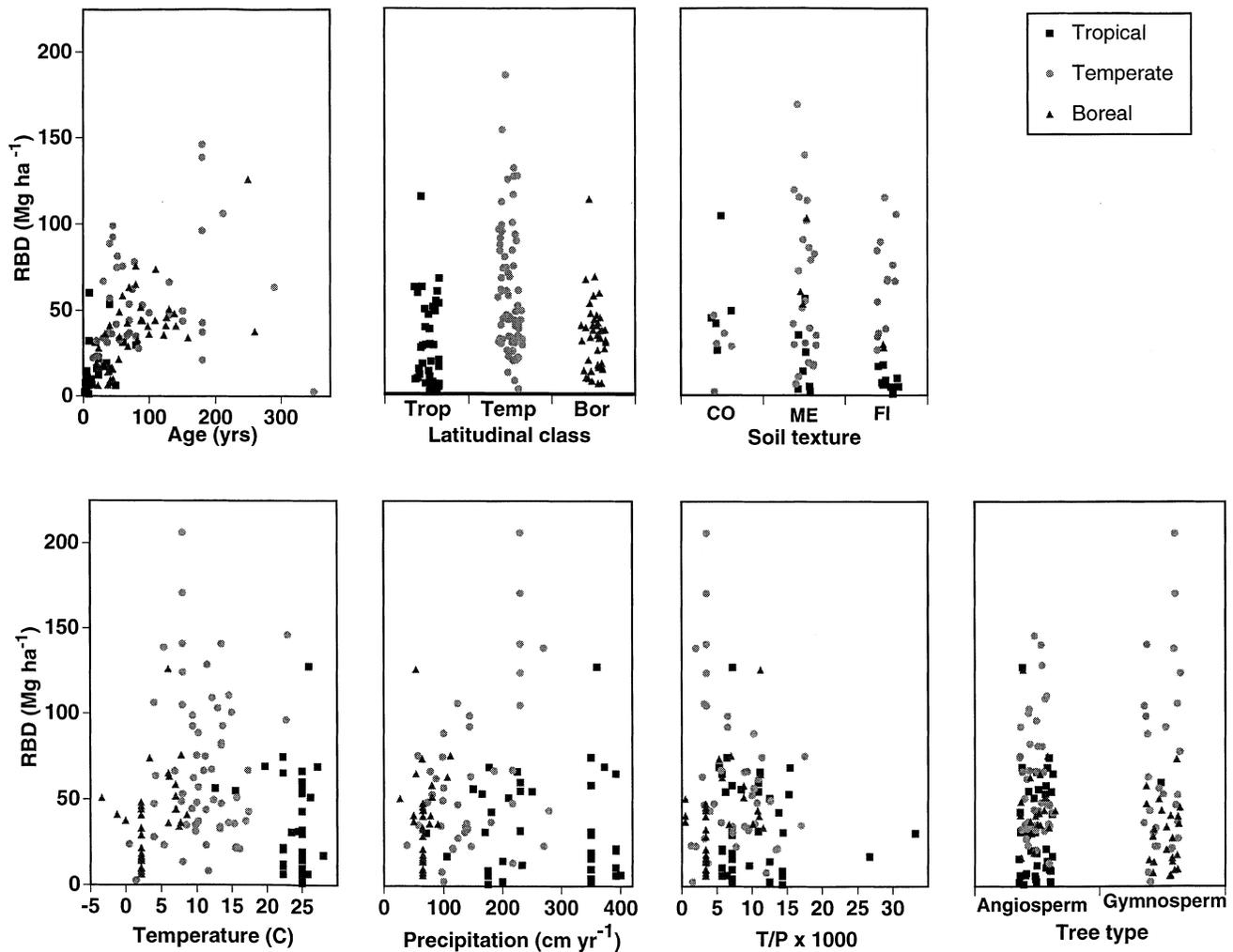


Fig. 2 Scatterplots of root biomass density (*RBD*) versus age, latitude, soil texture, mean annual temperature (*T*), mean annual precipitation (*P*) *T/P* ($^{\circ}\text{C}/\text{mm}$) ratios, and tree type. The discrete variables (latitudinal zone, soil texture, and tree type) are plotted in a staggered manner for clarity

Root biomass density

Scatterplots of *RBD* versus seven possible predictive variables showed a possible relationship with age and no apparent relationships with any other independent variables (Fig. 2). Forward stepwise least squares linear regression of the various site characteristics revealed that *ABD* alone accounted for 83% of the variation in *RBD* (Fig. 3). After accounting for *ABD*, age and latitudinal zone also significantly improved the predictive utility of *RBD* (Table 3). When age was included along with *ABD*, the adjusted R^2 increased slightly, to 0.84. The combination of *ABD* and latitude also resulted in a slightly increased adjusted R^2 value (Table 3). No other combinations were significant. Examination of six interactions, chosen *a priori* (*ABD* \times age, *ABD* \times latitudinal zone, *ABD* \times mean annual temperature, age \times mean annual temperature, *ABD* \times mean annual precipitation,

and age \times mean annual precipitation) revealed no significant effects.

While highly significant, variability was large around *RBD* estimates calculated from *ABD*, producing wide 95% prediction bands (Fig. 3). For example, mean estimates of *RBD* from Eq. 1 (Table 3) at *ABDs* of 200 and 400 Mg ha^{-1} are 46 and 87 Mg ha^{-1} , respectively. The corresponding upper and lower 95% prediction bands are 24 and 87 and 45 and 165 Mg ha^{-1} , respectively. Another way of looking at this variability is that the true *RBD* may be up to 91% higher or 47% lower than the mean estimate. This variability is likely the result of not only differences in sampling methodology, but also the natural variability of biological systems. Additionally, our equation was developed from the data available in the literature, not from a systematically, statistically rigorous experimental design executed with the same sampling methods. We expect that if data points were proportionally derived in the same manner from all conditions of latitude, soil texture, age, *ABD*, tree type and climatic factors, the prediction bands would be narrower. We would, however, also expect the prediction bands to deviate from the mean more at older ages (= larger *ABDs*) because of the inherent hetero-

Fig. 3 The relationship between aboveground biomass density (*ABD*) and root biomass density (*RBD*), showing 95% prediction bands. Data are plotted using Eq. 1 from Table 3

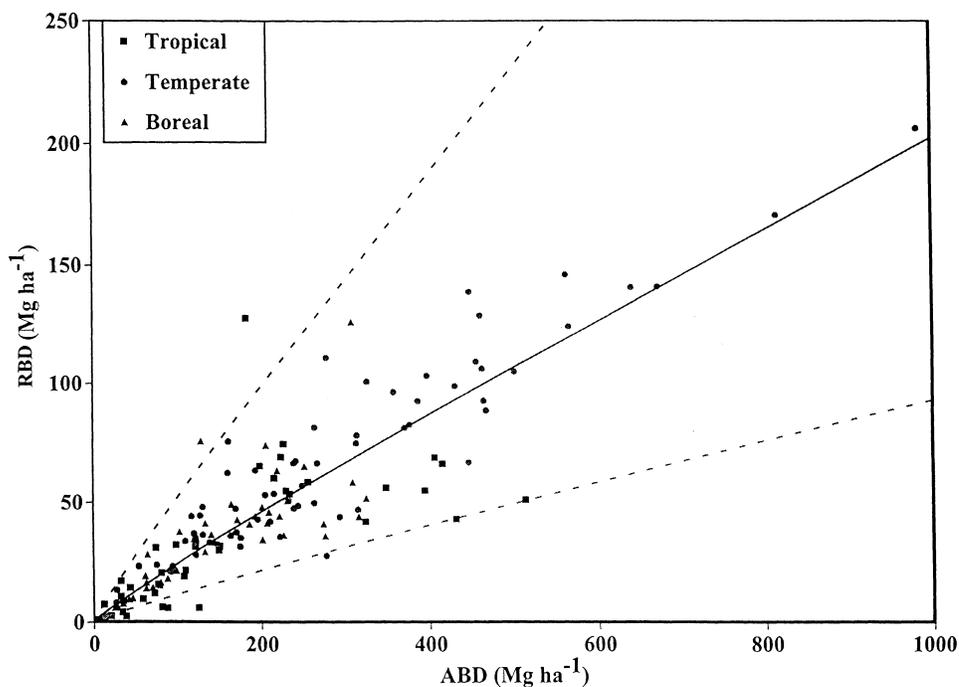


Table 3 Regression equations for predicting root biomass density (*RBD*). All equations are of the form Y (*RBD*, Mg/ha) = exp [intercept + $a(\ln A)$ + $b(\ln B)$ + $c(C)$ + $d(D)$]. (A *ABD* (Mg/ha), B age (year), C 1 in temperate sites and 0 in boreal sites, D 1 in boreal sites and 0 in temperate sites, both C and D 0 in tropical sites). Equation 1 estimates *RBD* based on aboveground biomass density (*ABD*) only, Equation 2 adds age, and Equation 3 includes *ABD* and latitudinal zone. The standard errors of regression coefficients (SE) are in parentheses. All model parameters were statistically significant ($\alpha = 0.05$) in accounting for variation in *RBD*

Equation	Intercept	a	b	c	d	n	Adjusted R^2
Equation 1	-1.0850 (0.177)	0.9256 (0.035)	N/A	N/A	N/A	151	0.83
Equation 2	-1.3267 (0.203)	0.8877 (0.053)	0.1045 (0.044)	N/A	N/A	109	0.84
Equation 3	-1.0587 (0.175)	0.8836 (0.036)	N/A	0.2840 (0.079)	0.1874 (0.084)	151	0.84

geneity of larger and older stands. It should also be noted that estimates from our equations have measures of variability and most reported *RBD* estimates from *R/S* ratios do not.

As a test of practical significance, we ran the three equations (Table 3) with hypothetical values of the predictive variables. We found that for each doubling of *ABD*, the estimated mean *RBD* increased by a factor of 1.9 in Eq. 1. When we maintained a fixed level of *ABD* and doubled age in Eq. 2, the mean *RBD* increased by 8%. Although Eq. 2 only marginally increased the adjusted R^2 over Eq. 1 (Table 3), the effect of adding tree age was of both practical and statistical significance. Holding *ABD* constant, the estimated mean *RBD* from

Eq. 3 was 33% higher in the temperate latitudes than in the tropics, 10% higher in the temperate latitudes than in the boreal latitudes, and 21% higher in the boreal latitudes than in the tropics.

Multicollinearity appeared not to be a problem in Eq. 2 and 3, as evidenced by the relative stability of both parameter estimates and their associated standard errors (Table 3). For example, the three parameter estimates for *ABD* were similar, as were their standard errors.

Our results generally agree with Bray (1963) who suggested that biomass allocation to roots can be estimated based on *ABD* allometries. Our finding that soil texture had no predictive value for *RBD* contrasted with others (Sanford and Cuevas 1996; Vitousek and Sanford 1986) who indicated that coarse tropical soils produce greater *RBD*. Our larger data base may be more representative of global forests than those of either Sanford and Cuevas (1996) or Vitousek and Sanford (1986). Our analysis also contrasts with other studies indicating that available soil moisture is strongly correlated with root biomass allocation, with water stress causing greater biomass allocation to roots (Kramer and Kozlowski 1979; Murphy and Lugo 1986; Sanford and Cuevas 1996). This is consistent with the theory that trees should allocate more resources to roots on infertile sites to optimize nutrient uptake (Bloom et al. 1985). Allocation of biomass to roots versus shoots on fertile sites has not been well documented (Vitousek and Sanford 1986).

The ratios of fine:total *RBD* among the 27 data records ranged from 0.01 to 0.71, with a mean of 0.23 (Fig. 4). Angiosperm fine root ratios were generally greater than 0.2, while those for gymnosperms were less than 0.2, with one exception. Fine root ratios also appear to be high at low *RBD*s, decrease rapidly as *RBD* increases, and then level at *RBD*s greater than 75 Mg

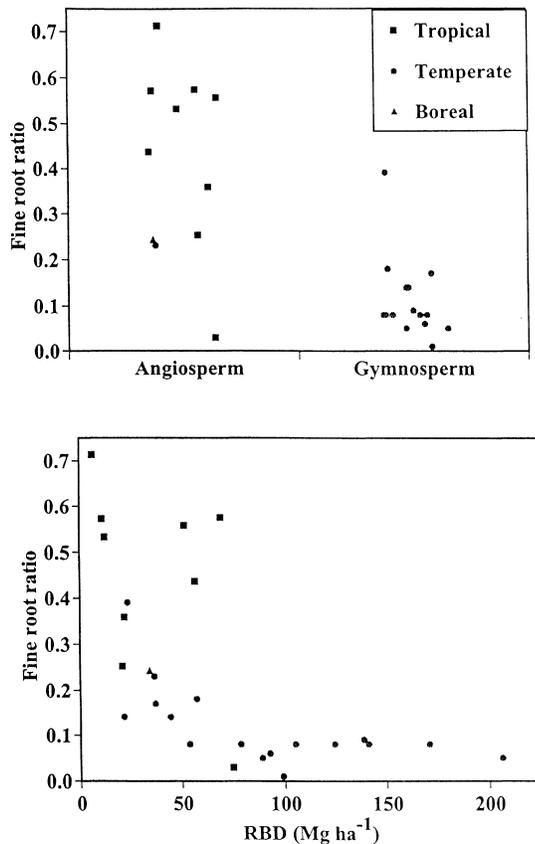


Fig. 4 Scatterplots of fine root ratios (biomass density of roots < 5 mm diameter to total RBD) versus tree type and root biomass density. Tree type, a discrete variable, is plotted in a staggered manner for clarity

ha^{-1} (Fig. 4), a trend in close agreement with Kurz et al. (1996).

Most of the sites with high fine root ratios were in tropical latitudes. This may be due to the continual growing season, tree architecture, water stress, or soil nutrient status (e.g., exchangeable and total nutrient concentrations, pH, organic matter content, trace nutrient concentrations, and cation exchange capacity). Thus, although total RBD may not relate to soil moisture, texture, or nutrients, fine roots, which are purported to be active in nutrient and water uptake, may.

Implications for estimates of carbon storage in the world's forests

Estimates of RBD are fundamental to understanding carbon storage and the biogeochemical dynamics of forest ecosystems. At the stand level, combinations of soil cores or pits and species-specific regression equations are often developed to estimate fine and coarse RBD, respectively. At larger spatial scales, average R/S ratios are commonly developed from the literature to quantify RBD at regional scales when only ABD is known (e.g., Birdsey 1992; Brown et al. 1993; Schroeder and Winjum

1995). Here we compare RBD estimates for U.S. forests using our equations with those based on the use of regional average R/S. Birdsey's estimation (Birdsey 1992) of the carbon budget of United States forests used R/S for hardwood forests ranging from 0.18 to 0.24 and for softwood forests ranging from 0.19 to 0.20. Using Birdsey's estimates of the ABD for eastern (45–127 Mg ha^{-1}) and western (48–144 Mg ha^{-1}) forests and Eq. 1 (Table 3), we produced estimates of RBD of 12–30 Mg ha^{-1} in eastern and 12–34 Mg ha^{-1} in western forests. This resulted in corresponding R/S values of 0.24–0.26 for eastern and 0.23–0.25 for western forests. These are somewhat higher than those used by Birdsey (1992), particularly for softwood stands. We believe that these differences are large enough to urge the adoption of the statistically stronger regression equations developed in the present paper.

A recent report focused on boreal and temperate forest RBD estimation from ABD alone, without considering edaphic and climatic variables, and reported separate regression equations for hardwood and softwood species (Kurz et al. 1996). Although our analysis showed no differences between tree types, and our Eq. 1 had a higher R^2 value [0.83 for ours versus 0.71 and 0.77 for softwood and hardwood species, respectively, in Kurz et al. (1996)], results were similar to each other. Kurz et al. (1996), while not reporting prediction bands, estimated 42 and 46 Mg ha^{-1} RBD for hardwoods and softwoods, respectively, at an ABD of 200 Mg ha^{-1} . The corresponding estimate from our Eq. 1 is 46 Mg ha^{-1} . At the same ABD of 200 Mg ha^{-1} , our Eq. 3 estimates a temperate latitude RBD of 50 Mg ha^{-1} and a boreal latitude RBD of 45 Mg ha^{-1} .

The equations presented here can be used to make point and interval estimates of root biomass allocation in the world's upland forests based on knowledge of aboveground biomass, age, and latitude. Use of these equations in unique forest ecosystems, such as wetland forests, may not be appropriate because of additional overriding site or climatic characteristics. However, this analysis clearly indicated that RBD could be estimated directly, rather than by using R/S ratios.

Acknowledgements We thank Ronald Shea and Patricia Haggerty for help with data collection, and Ariel Lugo, Whendee Silver, and two anonymous referees for technical reviews of a previous draft of this manuscript. The information in this document has been wholly funded by the U.S. Environmental Protection Agency, partially through National Network for Environmental Management Studies fellowship U-914602-01-0 (EHH) and Interagency Agreement DW47936459 with the General Services Administration (GAB). It has been subjected to the Agency's peer and administrative review and approved for publication as an EPA document. Mention of trade names or commercial products does not constitute endorsement or recommendation for use.

References

- Alexeyev VA, Birdsey RA (1994) Carbon in ecosystems of forests and peatlands of Russia. Sukachev Institute for Forest Research, Siberian Division of Russian Academy of Sciences and

- Northeastern Forest Experiment Station, U.S.D.A. Forest Service. Krasnoyarsk, Russia
- Andersson F (1971) Methods and preliminary results of estimation of biomass and primary production in a south Swedish mixed deciduous woodland. In: Duvigneaud P (ed) Productivity of forest ecosystems. Proceedings of the Brussels symposium, 1969, ecology and conservation 4. UNESCO, Paris, pp 282–288
- Arthur MA, Fahey TJ (1992) Biomass and nutrients in an Englemann spruce-subalpine fir forest in north central Colorado: pools, annual production, and internal cycling. *Can J For Res* 22:315–325
- Axelsson B (1981) Site differences in yield-differences in biological production or in redistribution of carbon within trees. *Swed Univ Agric Sci Dep Ecol Environ Res Rep* 9:1–11
- Bandhu D (1973) Chakia project. Tropical deciduous forest ecosystem. In: Kern L (ed) Modeling forest ecosystems (EDFB-TBP-737). Oak Ridge National Laboratory, Oak Ridge, pp 39–61
- Bartholomew W, Meyer J, Laudelout H (1953) Mineral nutrient immobilization under forest and grass fallow in the Yangambi (Belgian Congo) region. *Publ Inst Nat Etude Agron Congo Belge Ser Sci* 57:1–27
- Birdsey RA (1992) Carbon storage and accumulation in United States forest ecosystems (Gen Tech Rep WO-59). USDA Forest Service, Washington DC
- Bloom AJ, Chapin FS, Mooney HA (1985) Resource limitation in plants—an economic analogy. *Annu Rev Ecol Syst* 16:363–393
- Bongers F, Engelen D, Klinge H (1985) Phytomass structure of natural plant communities on spodosols in southern Venezuela: the Bana woodland. *Vegetatio* 63:13–34
- Bray JR (1963) Root production and the estimation of net productivity. *Can J Bot* 41:65–72
- Brinson MM (1990) Riverine forests. In: Lugo AE, Brinson M, Brown S (eds) Forested wetlands (Ecosystems of the World vol 15) Elsevier, New York, pp 87–141
- Brown S, Gaston G (1995) Use of forest inventories and geographic information systems to estimate biomass density of tropical forests: application to tropical Africa. *Environ Monit Assess* 38:157–168
- Brown S, Lugo AE (1982) The storage and production of organic matter in tropical forests and their role in the global carbon cycle. *Biotropica* 14:161–187
- Brown S, Iverson LR, Prada A, Liu D (1993) Geographical distributions of carbon in biomass and soils of tropical Asian forests. *Geocarto Int* 8:45–59
- Brunig EF, Klinge H (1976) Comparison of the phytomass structure of equatorial “rainforest” in central Amazonas, Brazil, and in Sarawak, Borneo. *Gard Bull Singapore* 29:81–101
- Buschbacher R, Uhl C, Serrão EAS (1988) Abandoned pastures in eastern Amazonia. II. Nutrient stocks in the soil and vegetation. *J Ecol* 75:682–701
- Canadell J, Roda F (1991) Root biomass of *Quercus ilex* in a montane Mediterranean forest. *Can J For Res* 21:1771–1778
- Cannell MGR (1982) World forest biomass and primary production data. Academic Press, London
- Castellanos J, Maass M, Kummerow J (1991) Root biomass of a dry deciduous tropical forest in Mexico. *Plant Soil* 131:225–228
- Cavelier J (1992) Fine-root biomass and soil properties in a semi-deciduous and a lower montane rain forest in Panama. *Plant Soil* 142:187–201
- Chapin FS III (1980) The mineral nutrition of wild plants. *Annu Rev Ecol Syst* 11:233–260
- Comeau PG, Kimmins JP (1989) Above- and below-ground biomass and production of lodgepole pine on sites with differing soil moisture regimes. *Can J For Res* 19:447–454
- Cox TL, Harris WF, Ausmus BS, Edwards NT (1978) The role of roots in biogeochemical cycles in an eastern deciduous forest. *Pedobiologica* 18:264–271
- Cuevas E, Brown S, Lugo AE (1991) Above- and belowground organic matter storage and production in a tropical pine plantation and a paired broadleaf secondary forest. *Plant Soil* 135:257–268
- DeAngelis DL, Gardner RH, Shugart HH (1981) Productivity of forest ecosystems studied during the IBP: the woodlands data set. In: Reichle D (ed) Dynamic properties of forest ecosystems. Cambridge University Press, Cambridge, pp 567–672
- Dixon RK, Brown S, Houghton RA, Solomon AM, Trexler MC, Wisniewski J (1994) Carbon pools and flux of global forest ecosystems. *Science* 263:185–190
- Dylis N (1971) Primary production of mixed forests. In: Duvigneaud P (ed) Productivity of forest ecosystems. Proceedings of the Brussels symposium, 1969, ecology and conservation 4. UNESCO, Paris, pp 227–232
- Edmonds RL (1980) Litter decomposition and nutrient release in Douglas-fir, red alder, western hemlock, and Pacific silver fir ecosystems in western Washington. *Can J For Res* 10:327–337
- Edmonds RL (1987) Decomposition rates and nutrient dynamics in small-diameter woody litter in four forest ecosystems in Washington, U.S.A. *Can J For Res* 17:499–509
- Ewel J (1971) Biomass changes in early tropical succession. *Turrialba* 21:110–112
- FAO (1971–1981) Soil map of the world 1:5,000,000. Food and Agricultural Organization of the United Nations-UNESCO, Rome
- Fittkau EJ, Klinge NH (1973) On biomass and trophic structure of the central Amazonian rain forest ecosystem. *Biotropica* 5:2–14
- Frangi JL, Lugo AE (1985) Ecosystem dynamics of a subtropical floodplain forest. *Ecol Monogr* 55:351–369
- Garkoti SC, Singh SP (1995) Variation in net primary productivity and biomass of forests in the high mountains of Central Himalaya. *J Veg Sci* 6:23–28
- Gerhardt K, Fredriksson D (1995) Biomass allocation by broadleaf mahogany seedlings, *Swietenia macrophylla* (King), in abandoned pasture and secondary dry forest in Guanacaste, Costa Rica. *Biotropica* 27:174–182
- Gower ST (1987) Relations between mineral nutrient availability and fine root biomass in two Costa Rican tropical wet forests: a hypothesis. *Biotropica* 19:171–175
- Greenland DJ, Kowal JML (1960) Nutrient content of the moist tropical forest of Ghana. *Plant Soil* 12:154–173
- Grier CC, Logan RS (1977) Old-growth *Pseudotsuga menziesii* communities of a western Oregon watershed: biomass distribution and production budgets. *Can J For Res* 47:373–400
- Grier CC, Vogt KA, Keyes MR, Edmonds RL (1981) Biomass distribution and above- and below-ground production in young and mature *Abies amabilis* zone ecosystems of the Washington Cascades. *Can J For Res* 11:155–167
- Grimm U, Fassbender HW (1981) Ciclos bioquímicos en un ecosistema forestal de los Andes Occidentales de Venezuela I. Inventario de las reservas orgánicas y minerales (N, P, K, Ca, Mg, Mn, Fe, Al, Na). *Turrialba* 31:27–37
- Grubb PJ, Tanner EVJ (1976) The montane forest and soils of Jamaica: a reassessment. *J Arnold Arbor* 57:313–368
- Harris WF, Kinerson RS, Edwards NT (1977) Comparison of belowground biomass of natural deciduous forest and loblolly pine plantations. *Pedobiologia* 17:369–381
- Humbel F-X (1978) Caracterisation, par des mesures physiques, hydriques et d’ enracinement, de sols de Guyane française a dynamique de l’eau superficielle. *Bull Assoc Fr Etude Sol* 2:83–94
- Huttel C (1975) Root distribution and biomass in three Ivory Coast rain forest plots. In: Golley FB, Medina E (eds) Tropical ecological systems (Ecological Studies 11). Springer, Berlin Heidelberg New York pp 123–130
- Keyes MR, Grier CC (1981) Above- and belowground net production in 40-year-old Douglas-fir stands on low and high productivity sites. *Can J For Res* 11:599–605
- Kinerson RS, Ralston CW, Wells CG (1977) Carbon cycling in a loblolly pine plantation. *Oecologia* 29:1–10
- Kira T (1990) Community architecture and organic matter dynamics in tropical lowland rain forests of southeast Asia with special reference to Pasoh Forest, West Malaysia. In: Tomlinson PB, Zimmermann MH (eds) Tropical trees as living systems. Cambridge University Press, Cambridge, pp 561–590

- Klepper B (1991) Root-shoot relationships. In: Waisel Y, Eshel A, Kafkafi U (eds) Plant roots: the hidden half. Marcel Dekker, New York, pp 265–286
- Klinge H (1973) Root mass estimation in lowland tropical rain forests of central Amazonia, Brazil. II. Coarse root mass of trees and palms in different height classes. *Ann Acad Bras Cien* 45:595–609
- Klinge H (1976) Root mass estimation in lowland tropical rain forests of central Amazonia, Brazil. *Trop Ecol* 17:79–83
- Klinge H, Herrera R (1983) Phytomass structure of natural plant communities on spodosols in southern Venezuela: the tall Amazon caatinga forest. *Vegetatio* 53:65–84
- Klinge H, Rodrigues WA, Brung E, Fittkau EJ (1975) Biomass and structure in a central Amazonia rainforest. In: Golley FB, Medina E (eds) Tropical ecological systems (Ecological Studies 11). Springer, Berlin Heidelberg New York, pp 115–122
- Koopmans TTh, Andriess JP (1982) Baseline study, monitoring project of nutrient cycling in shifting cultivation, Vanathavillu, Sri Lanka, Semongok (Sarawak), Malaysia. Department of Agricultural Research, Koninklijk Instituut Voor De Tropen, Amsterdam
- Körner C (1994) Biomass fractionation in plants: a reconsideration of definitions based on plant functions. In: Roy J, Garnier E (eds) A whole plant perspective on carbon-nitrogen interactions. SPB Academic, The Hague, pp 173–185
- Kramer PJ, Kozlowski TT (1979) Physiology of woody plants. Academic Press, New York
- Kuehl RO (1994) Statistical principles of research design and analysis. Duxbury, Belmont
- Kurz WA, Apps MJ, Webb TM, McNamee PJ (1992) The carbon budget of the Canadian forest sector: phase 1 (Information Report NOR-X-326). Forestry Canada, Northwest Region, Northern Forestry Center, Edmonton, Alberta
- Kurz WA, Beukema SJ, Apps MJ (1996) Estimation of root biomass and dynamics for the carbon budget model of the Canadian forest sector. *Can J For Res* 26:1973–1979
- Lescure JP, Puig H, Riera B, Leclerc D, Beekman F (1983) La phytomasse épigée d'une forêt dense en Guyane française. *Acta Oecol* 4:237–251
- Lugo AE (1992) Comparison of tropical tree plantations with secondary forests of similar age. *Ecol Monogr* 62:1–41
- Mulholland PJ (1979) Organic carbon cycling in a swamp-stream ecosystem and export by streams in eastern North Carolina. PhD Dissertation, University of North Carolina, Chapel Hill
- Murphy PG, Lugo AE (1986) Structure and biomass of a subtropical dry forest in Puerto Rico. *Biotropica* 18:89–96
- Myers RH (1990) Classical and modern regression with applications, 2nd edn. Duxbury, Belmont
- Nadelhoffer KJ, Aber JD, Melillo JM (1985) Fine roots, net primary production, and soil nitrogen availability: a new hypothesis. *Ecology* 66:1377–1390
- Neter J, Wasserman W, Kutner MH (1989) Applied linear regression models, 2nd edn. Richard D. Irwin, Homewood
- Nihlgård B, Lindgren L (1977) Plant biomass, primary production and bioelements of three mature beech forests in South Sweden. *Oikos* 28:95–104
- Ohler FMJ (1980) Phytomass and mineral content in untouched forests (CELOS report). University of Surinam, Paramaribo
- Ovington JD (1962) Quantitative ecology and the woodland ecosystem concept. *Adv Ecol Res* 1:103–192
- Ovington JD, Olson JS (1970) Biomass and chemical content of El Verde lower montane rain forest plants. In: Odum HT, Pigeon RF (eds) A tropical rain forest. A study of irradiation and ecology at El Verde, Puerto Rico (Division of Technical Information TID 24270). US Atomic Energy Commission, Washington DC, pp 53–77
- Pearson JA, Fahey TJ, Knight DH (1984) Biomass and leaf area in contrasting lodgepole pine forests. *Can J For Res* 14:259–265
- Ramsey FL, Schafer DW (1996) The statistical sleuth, a second course in statistical data analysis. Duxbury, Belmont
- Rodin LE, Bazilevich NI (1967) Production and mineral cycling in terrestrial vegetation. Oliver and Boyd, Edinburgh
- Russell CE (1983) Nutrient cycling and productivity of native and plantation forests at Jari Florestal, Para, Brazil. PhD thesis. University of Georgia, Athens
- Russell EW (1977) Soil conditions and plant growth, 10th edn. Longman, London
- Saldarriaga JG, West DC, Tharp ML, Uhl C (1988) Long-term chronosequence of forest succession in the upper Rio Negro of Colombia and Venezuela. *J Ecol* 76:938–958
- Sanford RL Jr, Cuevas E (1996) Root growth and rhizosphere interactions in tropical forests. In: Mulkey SS, Chazdon RL, Smith AP (eds) Tropical forest plant ecophysiology. Chapman and Hall, New York, pp 268–300
- Santantonio D, Hermann RK, Overton WS (1977) Root biomass studies in forest ecosystems. *Pedobiologia* 17:1–31
- Scatena FN, Silver W, Siccama T, Johnson A, Sanchez MJ (1993) Biomass and nutrient content of the Bisley experimental watersheds, Luquillo Experimental Forest, Puerto Rico, before and after Hurricane Hugo, 1989. *Biotropica* 25:15–27
- Schroeder PE, Winjum JK (1995) Assessing Brazil's carbon budget I. Biotic carbon pools. *For Ecol Manage* 75:77–86
- Singh SP, Adhikari BS, Zobel DB (1994) Biomass, productivity, leaf longevity, and forest structure in the central Himalaya. *Ecol Monogr* 64:401–421
- Smirnova KM, Gorodentseva GA (1958) The consumption and rotation of nutritive elements in birch woods. *Bull Nat Soc Moscow* 62:135–147
- Sollins P, Grier CC, McCorison FM, Cromack K, Fogel R, Fredriksen RL (1980) The internal element cycles of an old-growth Douglas-fir ecosystem in western Oregon. *Ecol Monogr* 50:261–285
- Tanner EV (1980) Studies on the biomass and productivity in a series of montane rain forests in Jamaica. *J Ecol* 68:573–588
- Turner J, Cole DW, Gessel SP (1976) Mineral nutrient accumulation and cycling in a stand of red alder (*Alnus rubra*). *J Ecol* 64:965–974
- Uhl C (1987) Factors controlling succession following slash-and-burn agriculture in Amazonia. *J Ecol* 75:377–407
- Uhl C, Buschbacher R, Serrão EAS (1988) Abandoned pastures in eastern Amazonia. I. Patterns of plant succession. *J Ecol* 75:663–681
- Vitousek PM, Sanford RL Jr, (1986) Nutrient cycling in moist tropical forest. *Annu Rev Ecol Syst* 17:137–167
- Vogt KA (1991) Carbon budgets of temperate forest ecosystems. *Tree Physiol* 9:69–86
- Vogt KA, Grier CC, Meier CE, Edmonds RL (1982) Mycorrhizal role in net primary production and nutrient cycling in *Abies amabilis* ecosystems in western Washington. *Ecology* 63:370–380
- Vogt KA, Moore EE, Vogt DJ, Redlin MJ, Edmonds RL (1983) Conifer fine root and mycorrhizal root biomass within the forest floors of Douglas-fir stands of different ages and site productivities. *Can J For Res* 13:429–437
- Vogt KA, Vogt DJ, Moore EE, Fatuga BA, Redlin MR, Edmonds RL (1987) Conifer and angiosperm fine-root biomass in relation to stand age and site productivity in Douglas-fir forests. *J Ecol* 75:857–870
- Vogt KA, Vogt DJ, Brown S, Tilley JP, Edmonds RL, Silver WL, Siccama TG (1995) Dynamics of forest floor and soil organic matter accumulation in boreal, temperate, and tropical forests. In: Lal R, Kimble J, Levine E, Stewart BA (eds) Soil management and greenhouse effect. CRC, Lewis Publishers, Boca Raton, FL, pp 159–178
- Vyskot M (1976) Floodplain forest biomass. In: Young HE (ed) Oslo biomass studies. University of Maine, Orono, pp 175–202
- Waring RH, Schlesinger WH (1985) Forest ecosystems: concepts and management. Academic Press, Orlando
- Westman EE, Whitaker RH (1975) The pygmy forest region of northern California: studies on biomass and primary productivity. *J Ecol* 63:493–520
- Wilson SD (1993) Belowground competition in forest and prairie. *Oikos* 68:146–150
- Zavitovski J, Stevens RD (1972) Primary productivity of red alder ecosystems. *Ecology* 53:235–242