

A global budget for fine root biomass, surface area, and nutrient contents

R. B. JACKSON*, H. A. MOONEY†, AND E.-D. SCHULZE‡

*Department of Botany, University of Texas at Austin, Austin, TX 78713; †Department of Biological Sciences, Stanford University, Stanford, CA 94305; and ‡Lehrstuhl Pflanzenökologie, Universität Bayreuth, Postfach 101251, D-95440, Bayreuth, Germany

Contributed by H. A. Mooney, May 9, 1997

ABSTRACT Global biogeochemical models have improved dramatically in the last decade in their representation of the biosphere. Although leaf area data are an important input to such models and are readily available globally, global root distributions for modeling water and nutrient uptake and carbon cycling have not been available. This analysis provides global distributions for fine root biomass, length, and surface area with depth in the soil, and global estimates of nutrient pools in fine roots. Calculated root surface area is almost always greater than leaf area, more than an order of magnitude so in grasslands. The average C:N:P ratio in living fine roots is 450:11:1, and global fine root carbon is more than 5% of all carbon contained in the atmosphere. Assuming conservatively that fine roots turn over once per year, they represent 33% of global annual net primary productivity.

Fine roots (≤ 2 mm in diameter) are the primary pathway for water and nutrient uptake by plants, the same role that leaves play for carbon and energy uptake. Fine roots are also a prominent, possibly the prominent, sink for carbon acquired in terrestrial net primary productivity (1–4). Primary production allocated below ground is often greater than that allocated above ground, and annual carbon and nutrient inputs to the soil from fine roots frequently equal or exceed those from leaves (1–5). Despite their importance for nutrient cycling, resource capture, and global biogeochemistry, fine roots are poorly represented in global models. The lack of representation is in sharp contrast to the prevalence of canopy leaf area data as an important input (6–10). The input of leaf area, which can be estimated regionally by remote sensing (11), allows carbon and energy gain to be simulated biochemically in terrestrial models (12). Part of the cause for the discrepancy in representing roots and shoots is the difficulty in estimating root distributions (2, 13, 14). This analysis provides the first global fine root database for improving global models and estimates of carbon cycling. These data should enhance hydrological models [where fine roots control water absorption by plants and affect groundwater and atmospheric fluxes (15, 16)], improve estimates of nitrogen cycling and the consequences of nitrogen loading (17), and allow the biochemical modeling of nutrient uptake globally (18, 19).

METHODS

This research differs from a previous analysis (20) by calculating fine rather than total root distributions (those roots active in water and nutrient uptake), by estimating root biomass, length, surface area, and nutrient contents, by taking into account the proportion of live root biomass in each biome, and by calculating a global budget for each parameter. To

estimate fine root distributions by depth, a database of 253 field studies was analyzed (20). A study was included if fine roots were measured in three or more increments to at least 1-m soil depth (minimum depth for tundra was the level of permafrost). More than 40 references met these criteria and many included multiple sites per study. The selected references are listed in appendix 2 of reference 20, which also provides information on the location, precipitation, soil type, vegetation, and sampling method of each study. The depth distributions for each biome were fitted to a model of vertical root distribution (21) based on the asymptotic equation $Y = \beta^d$, where Y is the cumulative root fraction (a proportion between 0 and 1) from the soil surface to depth d (in centimeters) and β is the fitted extinction coefficient. β is the only fitted parameter and provides a simple numerical index of rooting distribution. High β values (e.g., 0.98) correspond to a greater proportion of roots at depth and low β values (e.g., 0.92) have a greater proportion of roots near the soil surface. β values were calculated for fine root data only.

The database was supplemented with more than 100 additional field studies for estimating global fine root biomass, length, surface area, and nutrient contents. There are a number of excellent compilations for fine root biomass in some biomes (22–26), due in part to the efforts of the International Biological Programme. Such information is unavailable for other biomes and there has been no attempt at a global synthesis. A study was included in the biomass compilation if it included live or total fine roots to at least 25 cm depth in the soil (most studies went substantially deeper). Many excellent studies were excluded due to an inability to separate fine root biomass from total root or total underground biomass (roots, tubers, rhizomes, etc.) or because more than one reference supplied duplicate information for the same site. Relevant studies by biome were: boreal forest (27–32), deserts (33–37), sclerophyllous shrublands and forests (38–45), temperate coniferous forest (46–56), temperate deciduous forest (46, 47, 49, 50, 52, 57–67), temperate grasslands (36, 68–77), tropical deciduous forest (22, 78–83), tropical evergreen forest (22, 84–93), tropical grassland/savanna (94–98), and tundra (99–103). Some studies provided data for multiple times and locations within a site and these data were averaged for the particular site. The biomass estimates in all studies were averaged by biome and functional type to provide a value for total fine root biomass. To estimate the proportion of total root stocks active in resource uptake, the estimates of total fine root biomass were then adjusted for the fraction of living roots in each biome based on results of field studies that measured both. The average proportion of live and dead roots for each biome were (percent live): boreal forest (28–30) (42%), desert (50%), sclerophyllous shrubland and forest (40–43) (48%), temperate coniferous forest (46, 48, 50, 52, 54, 56) (56%), temperate deciduous forest (50, 54, 58, 59, 65) (56%), temperate grasslands (71, 76, 77) (63%), tropical deciduous forest

The publication costs of this article were defrayed in part by page charge payment. This article must therefore be hereby marked "advertisement" in accordance with 18 U.S.C. §1734 solely to indicate this fact.

© 1997 by The National Academy of Sciences 0027-8424/97/947362-5\$2.00/0 PNAS is available online at <http://www.pnas.org>.

Abbreviations: LAI, leaf area index; RAI, root area index.

(81) (50%), tropical evergreen forest (84, 86, 92) (57%), tropical grassland/savanna (94) (52%), and tundra (99) (35%).

To convert live fine root biomass to surface area (where models of enzymatic uptake can be applied), morphological parameters including fine root diameter and specific root length were derived and then extrapolated to other sites that provided root mass only. The morphological data were compiled from field data for fine roots of grasses, shrubs, and trees as functional types, since insufficient field data existed for a biome-based approach. Relevant studies were those in appendix 1 of reference 20 and additional references for grasses (4, 68, 103–106), shrubs (39, 40, 42, 45), and trees (52, 59, 85, 88, 107–113). The data for mean fine root diameter (in millimeters) and specific root length ($\text{m}\cdot\text{g}^{-1}$), respectively, were as follows [SEM and number (n) in parentheses]: grasses, 0.22 mm (0.036, 5) and $118 \text{ m}\cdot\text{g}^{-1}$ (38.9, 4); shrubs, 0.44 mm (0.055, 7) and $30.0 \text{ m}\cdot\text{g}^{-1}$ (11.0, 3); and trees, 0.58 mm (0.11, 10) and $12.2 \text{ m}\cdot\text{g}^{-1}$ (1.7, 10). The respective β values for fine roots of the functional groups were 0.954 ($r^2 = 0.88$) for grasses, 0.975 ($r^2 = 0.93$) for shrubs, and 0.976 ($r^2 = 0.92$) for trees. Finally, the global budget for nutrient concentrations in fine roots was calculated from the global estimate of fine root biomass in this analysis and average tissue concentrations compiled from field studies. The global estimates of C, N, P, K, Ca, Mg, and S in living fine roots came from studies in appendix 1 of reference 20, previous studies in the bibliography of this current analysis, and additional references (114–125).

RESULTS

Total fine root biomass ranged from $0.27 \text{ kg}\cdot\text{m}^{-2}$ in deserts to $1.5 \text{ kg}\cdot\text{m}^{-2}$ in temperate grasslands, and live fine root biomass was $0.13 \text{ kg}\cdot\text{m}^{-2}$ and $0.95 \text{ kg}\cdot\text{m}^{-2}$ in the same biomes (Table 1). Average live fine root biomass in all other biomes was between 0.1 and $0.5 \text{ kg}\cdot\text{m}^{-2}$. Live fine root length was an order of magnitude greater in grasslands than elsewhere, with more than $100 \text{ km}\cdot\text{m}^{-2}$ of temperate grassland and $60 \text{ km}\cdot\text{m}^{-2}$ for tropical grasslands (Table 1). Root area index (RAI, $\text{m}^2\cdot\text{m}^{-2}$) showed a pattern similar to root length (Table 1). RAI was approximately 43 and $80 \text{ m}^2\cdot\text{m}^{-2}$ for tropical and temperate grasslands and less than $12 \text{ m}^2\cdot\text{m}^{-2}$ for all other systems. Calculated depth distributions showed that tundra had the shallowest fine root distributions of any biome, with 94% of roots in the upper 30 cm of soil (Table 1). Boreal forest and temperate grasslands also showed relatively shallow profiles ($\beta = 0.943$ for both). The deepest profiles were in tropical deciduous forests, temperate coniferous forests, tropical evergreen forests, tropical grasslands/savannas, and deserts ($0.970 < \beta < 0.982$).

Based on this analysis, a previous synthesis of total root biomass (20), and the biome classification scheme of Whitaker (126), we calculated global estimates of total root

biomass, fine root biomass, and live fine root biomass, length, and surface area (Table 2) and a global budget for nutrient concentrations in fine roots (Table 3). Tropical grasslands/savannas, temperate grasslands, and tropical rainforests had the greatest total fine root biomass ($\approx 1 \times 10^{16} \text{ g}$ for each), and there were $7.8 \times 10^{16} \text{ g}$ of fine roots globally (Table 2). The carbon in this global fine root pool was approximately 5% of the size of the atmospheric carbon pool (Table 3; $720 \times 10^{15} \text{ g}$ atmospheric C from ref. 128). Living fine roots made up more than half of total fine roots ($4.1 \times 10^{16} \text{ g}$) and 2.4% of the atmospheric pool (Tables 2 and 3). The global pool of N in living fine roots was $4.8 \times 10^8 \text{ Mg}$, approximately one-seventh of the estimate for all terrestrial vegetation (128), and the average C:N ratio of live fine roots globally was 42 (Table 3). Live fine root surface area was $2.0 \times 10^9 \text{ km}^2$ globally (Table 2), four times the surface area of earth and approximately 14 times the total land surface area. There were $2.5 \times 10^{15} \text{ km}$ of live fine root length globally (Table 2). Given the difficulty in harvesting fine roots and the potential underestimation of deep roots in some systems (91, 129, 130), the global estimates of mass, surface area, and nutrient contents are almost certainly conservative.

DISCUSSION

Global estimates of leaf area index (LAI, m^2 leaf surface area m^{-2} soil surface) are known with much greater precision than the global RAI values generated here for the first time. Based on the results in Table 1, RAI is at least comparable to LAI in all terrestrial systems, and in most systems is substantially larger. Grassland LAI rarely is greater than $10 \text{ m}^2\cdot\text{m}^{-2}$ [usually much less so (131)] and on average the absorptive surface area below ground in grasslands is at least an order of magnitude greater than that above ground (Table 1).

The number of studies measuring RAI for nonagricultural systems is small. Shalyt (74, 132) estimated an average RAI of $149 \text{ m}^2\cdot\text{m}^{-2}$ for four Russian grasslands. Adjusting the value for the proportion of live roots leads to an RAI of $99 \text{ m}^2\cdot\text{m}^{-2}$, similar to our independently derived estimate of $79 \text{ m}^2\cdot\text{m}^{-2}$ (Table 1). Kummerow and Mangan (42) studied a *Quercus dumosa* chaparral and estimated RAI to be $7.7 \text{ m}^2\cdot\text{m}^{-2}$ for live roots $< 1 \text{ mm}$ in diameter. Incorporating the surface area of roots 1–2 mm in diameter (assuming equivalent tissue densities and a mean root size of 1.5 mm for the interval) leads to a total fine root RAI of $10.4 \text{ m}^2\cdot\text{m}^{-2}$, close to the calculated value of $11.6 \text{ m}^2\cdot\text{m}^{-2}$ for all sclerophyllous vegetation (Table 1). Estimates in another CA chaparral were slightly smaller (39). For forest systems, Berish (85) estimated RAI at $4.1 \text{ m}^2\cdot\text{m}^{-2}$ for a 70-year successional forest in Costa Rica (total fine roots, $< 2 \text{ mm}$ diameter to 0.85 m depth), compared with the global estimate of $7.4 \text{ m}^2\cdot\text{m}^{-2}$ calculated here. The estimates of Farrish (60) for temperate coniferous and deciduous sites in

Table 1. Average total and live fine root biomass ($\text{kg}\cdot\text{m}^{-2}$), live fine root length ($\text{km}\cdot\text{m}^{-2}$), live fine root surface area ($\text{m}^2\cdot\text{m}^{-2}$), β values (and associated r^2 values) for fine roots, and the percentage of fine roots in the upper 30 cm of soil for 10 terrestrial biomes

| Biome | Total fine root biomass ($\text{kg}\cdot\text{m}^{-2}$) | Live fine root biomass ($\text{kg}\cdot\text{m}^{-2}$) | Live fine root length ($\text{km}\cdot\text{m}^{-2}$) | Live fine root area index ($\text{m}^2\cdot\text{m}^{-2}$) | β | r^2 | % fine root biomass in upper 30 cm |
|---------------------------------|---|--|---|--|---------|-------|------------------------------------|
| Boreal forest | 0.60 (0.13, 5) | 0.23 (0.034, 5) | 2.6 | 4.6 | 0.943 | 0.89 | 83 |
| Desert | 0.27 (0.10, 4) | 0.13 (0.051, 4) | 4.0 | 5.5 | 0.970 | 0.99 | 60 |
| Sclerophyllous shrubs and trees | 0.52 (0.13, 6) | 0.28 (0.096, 6) | 8.4 | 11.6 | 0.950 | 0.84 | 79 |
| Temperate coniferous forest | 0.82 (0.14, 10) | 0.50 (0.10, 10) | 6.1 | 11.0 | 0.980 | 0.96 | 45 |
| Temperate deciduous forest | 0.78 (0.092, 14) | 0.44 (0.053, 14) | 5.4 | 9.8 | 0.967 | 0.96 | 63 |
| Temperate grassland | 1.51 (0.12, 21) | 0.95 (0.078, 21) | 112 | 79.1 | 0.943 | 0.88 | 83 |
| Tropical deciduous forest | 0.57 (0.098, 6) | 0.28 (0.049, 6) | 3.5 | 6.3 | 0.982 | 0.99 | 42 |
| Tropical evergreen forest | 0.57 (0.069, 12) | 0.33 (0.050, 12) | 4.1 | 7.4 | 0.972 | 0.91 | 57 |
| Tropical grassland/savanna | 0.99 (0.24, 5) | 0.51 (0.13, 5) | 60.4 | 42.5 | 0.972 | 0.97 | 57 |
| Tundra | 0.96 (0.22, 5) | 0.34 (0.078, 5) | 7.4 | 5.2 | 0.909 | 0.90 | 94 |

Fine roots are defined as those $\leq 2 \text{ mm}$ in diameter. See text for a description of the model (20, 21); larger values of β imply deeper rooting profiles.

Table 2. Global land area (10^6 km²), total root biomass (10^9 Mg) (calculated from data in ref. 20), total fine root biomass (10^9 Mg), live fine root biomass (10^9 Mg), live fine root length, and live fine root surface area for the global classification scheme of Whittaker

| Biome | Land area (10^6 km ²) | Total root biomass (10^9 Mg) | Total fine root biomass (10^9 Mg) | Live fine root biomass (10^9 Mg) | Global fine root length (10^{15} km, live) | Global fine root surface area (10^7 km ² , live) |
|----------------------------|---|------------------------------------|--|---|---|--|
| Tropical rainforest | 17.0 | 83 | 9.7 | 5.7 | 0.069 | 12.6 |
| Tropical seasonal forest | 7.5 | 31 | 4.3 | 2.1 | 0.026 | 4.7 |
| Temperate evergreen forest | 5.0 | 22 | 4.1 | 2.5 | 0.031 | 5.5 |
| Temperate deciduous forest | 7.0 | 29 | 5.6 | 3.1 | 0.038 | 6.9 |
| Boreal forest | 12.0 | 35 | 7.2 | 2.8 | 0.031 | 5.5 |
| Woodland and shrubland | 8.5 | 41 | 4.4 | 2.4 | 0.099 | 9.9 |
| Savanna | 15.0 | 21 | 14.9 | 7.7 | 0.91 | 63.8 |
| Temperate grassland | 9.0 | 14 | 13.6 | 8.5 | 1.01 | 71.2 |
| Tundra/alpine | 8.0 | 10 | 7.7 | 2.7 | 0.059 | 4.2 |
| Desert | 18.0 | 6.6 | 4.9 | 2.3 | 0.072 | 9.9 |
| Cultivated | 14.0 | 2.1 | 2.1 | 1.1 | 0.13 | 5.0 |
| Totals | 121 | 292 | 78.2 | 40.8 | 2.47 | 199 |

The calculations are based on Whittaker's estimate (126) of land area for each biome and the conversion factors in Table 1. (Total continental land area in Whittaker's classification also includes 2.8×10^7 km² of extreme desert, rock, sand, ice, swamps, marshes, lakes, and streams). Where the two classification schemes are not perfectly matched, the values for temperate coniferous forests were substituted for Whittaker's temperate evergreen forest and the sclerophyllous shrublands/woodlands were used for Whittaker's woodland and shrubland category. Conversion values for cultivated land were derived from Dittmer (127).

Louisiana were 8.2 and 14.8 m²·m⁻², respectively (live roots <3 mm diameter to 90 cm depth). These also were close to the independently derived global estimates of 11.0 and 9.8 m²·m⁻² (Table 1). Independent RAI estimates for Belgian beech and spruce forests (54) were 6.8 and 5.4 m²·m⁻² for roots <5 mm in diameter, with roots <1 mm diameter comprising 85–90% of total RAI. Despite few existing datasets and issues of spatial variability, the data provide good agreement without data tuning.

A similar comparison of measured root length from field studies also shows close agreement with calculated estimates. Live root length for temperate coniferous forests ranged from 2.7 to 7.7 km·m⁻² in four field studies (49, 52, 109, 113), close to the biome estimate of 6.1 km·m⁻² (Table 1). Values for total roots <2 mm in diameter in two tropical evergreen forests (85, 88) were 2.0 and 2.3 km·m⁻² compared with the live root estimate for the biome of 4.1 km·m⁻². A 64-year-old beech stand (*Fagus sylvaticus*) studied by Hendriks and Bianchi (49) had higher than predicted fine root length (18.4 km·m⁻²) than the biome estimate of 5.4 km·m⁻². Estimates for sclerophyllous vegetation (39–42) ranged from 2.1 to 7.7 km·m⁻², slightly lower than the biome estimate of 8.4 km·m⁻², but none of the three studies included roots >1.25 mm in diameter. Clearly more estimates of fine root length and surface area are needed, particularly since no estimates were found for half the biomes. Root tissue densities calculated from the compiled morphological data are also similar to published estimates from the field. Such a check is valid because, in most cases, the estimates

of specific root length were derived from a different subset of studies than the estimates of fine root diameter. Based on the global estimates, average fine root tissue densities were 0.21, 0.22, and 0.31 g dry weight·cm⁻³ for grasses, shrubs, and trees. In comparison, average fine root tissue densities from field studies ranged from 0.15 to 0.52 g·cm⁻³ for trees (59, 108, 112).

There are a number of caveats for any analysis that averages data across such broad categories as biomes or plant functional types. Important seasonal and spatial dynamics within a biome are masked by pooling information within and across sites, as are climatic and edaphic factors (133). In savannas, for example, the relative proportion of trees and grasses can change spatially and temporally and will have large effects on the functioning of the ecosystem and the distribution of roots. At any particular site there may also be small-scale variation important to individual plants (134). To take seasonal dynamics into account, our estimates of biomass, length, and surface area can be used in models with the most appropriate root phenology described for a particular site. Surprisingly, many studies showed little seasonal variation in such parameters as root biomass or the proportion of live and dead roots, and even in deciduous systems it is clear that roots do not disappear in concert with leaves. Overall, two primary goals for our estimates are (i) to generate broad hypotheses among biomes and plant functional groups to be tested in the field and (ii) to provide a benchmark for improvement as additional data become available.

This analysis provides to the best of our knowledge the first global estimates for fine root biomass, length, surface area, and nutrient contents and their distribution with depth in the soil. There are at least three important uses for these data. First, efforts to model water and nutrient uptake globally in a biochemical or physiologically explicit manner could be improved by including the absorptive surface area of live roots and their vertical distribution in soil. Consider the importance of LAI for global models of carbon and energy gain (7–10), and the importance of RAI for nutrient and water uptake is apparent. Better representation of mycorrhizae in such models is also needed and could be accomplished by building upon the data presented here. Second, there are approximately one-quarter million species of higher plants (135), and their grouping into meaningful functional and community types is necessary for successfully predicting the consequences of global change (136). This analysis provides the basis for a number of such groupings. Third, improved estimates of total and live fine root biomass should refine estimates of terrestrial

Table 3. Nutrient concentrations in living fine roots (percent) (SEM, *n*) and global nutrient pools in living fine roots (10^9 Mg), and total fine roots (10^9 Mg, assuming the same elemental concentrations)

| Element | % concentration in living fine roots | Global nutrients in living fine roots (10^9 Mg) | Global nutrients in total fine roots (10^9 Mg) |
|---------|--|---|--|
| C | 48.8 (0.95, 4) | 19.9 | 38.1 |
| N | 1.17 (0.073, 24) | 0.48 | 0.92 |
| P | 0.11 (0.017, 14) | 0.044 | 0.085 |
| K | 0.30 (0.064, 12) | 0.12 | 0.24 |
| Ca | 0.41 (0.10, 11) | 0.17 | 0.32 |
| Mg | 0.14 (0.025, 10) | 0.054 | 0.11 |
| S | 0.088 (0.009, 5) | 0.036 | 0.069 |

Live and total fine root biomass values are from Table 2. The global C:N:P ratio for fine roots is 450:11:1.

carbon and nutrient cycling. The total fine-root C pool is 5% of the size of the atmospheric C pool, and the biomass of living fine roots is similar in magnitude to 33% of annual net primary productivity. The small diameter, relatively short lifespan, and low C:N ratio of fine roots (Table 3) result in their rapid turnover and quick decomposition compared with woody biomass (3), making them disproportionately important for estimates of annual net primary production, nutrient cycling, and carbon allocation (1–5).

We wish to thank members of the first of two workshops on root distributions and global models at the National Center for Ecological Analysis and Synthesis. Drs. M. M. Caldwell, B. A. Hungate, O. E. Sala, L. J. Anderson, J. Canadell, K. Pregitzer, and C. Field provided helpful comments on the manuscript. The research was supported by the Andrew W. Mellon Foundation, the National Center for Ecological Analysis and Synthesis, and National Institute for Global Environmental Change, U.S. Department of Energy Grant TUL-038-95/98 and contributes to the Global Change and Terrestrial Ecosystems (GCTE) Core Project of the International Geosphere Biosphere Programme (IGBP).

- Nadelhoffer, K. J. & Raich, J. W. (1992) *Ecology* **73**, 1139–1147.
- Vogt, K. A., Grier, C. C. & Vogt, D. J. (1986) *Adv. Ecol. Res.* **15**, 303–377.
- Hendrick, R. L. & Pregitzer, K. S. (1994) *Nature (London)* **361**, 59–61.
- Caldwell, M. M. & Richards, J. H. (1986) in *On the Economy of Plant Form and Function*, ed. Givnish, T. J. (Cambridge Univ. Press, Cambridge, U.K.), pp. 251–273.
- Reichle, D. E., Dinger, B. E., Edwards, N. T., Harris, W. F. & Sollins, P. (1973) in *Carbon and the Biosphere*, eds. Woodwell, G. M. & Pecan, E. V. (U.S. Atomic Energy Commission, Brookhaven, NY), pp. 345–365.
- Melillo, J. M., McGuire, A. D., Kicklighter, D. W., Moore, B., III, Vorosmarty, C. J. & Schloss, A. L. (1993) *Nature (London)* **363**, 234–240.
- Neilson, R. P. (1995) *Ecol. Appl.* **5**, 362–385.
- Potter, C. S., Randerson, J. T., Field, C. B., Matson, P. A., Vitousek, P. M., Mooney, H. A. & Klooster, S. A. (1993) *Global Biogeochem. Cycles* **7**, 811–841.
- Parton, W. J., Haxeltine, A., Thornton, P., Anne, P. & Hartman, M. (1996) *Global Planetary Change* **13**, 89–98.
- Dickinson, R. E., Bryant, R. & Graumlich, L. (1997) *J. Clim.*, in press.
- Hobbs, R. J. & Mooney, H. A., eds. (1990) *Remote Sensing of Biosphere Functioning* (Springer, Berlin).
- Farquhar, G. D., Von Caemmerer, S. & Berry, J. A. (1980) *Planta* **149**, 78–90.
- Böhm, W. (1979) *Methods of Studying Root Systems* (Springer, Berlin).
- Gower, S. T., Pongracic, S. & Landsberg, J. J. (1996) *Ecology* **77**, 1750–1755.
- Dunne, K. A. & Willmott, C. J. (1996) *Int. J. Climatol.* **16**, 841–859.
- Paruelo, J. M. & Sala, O. E., *Ecology* **76**, 510–520.
- Wedin, D. A. & Tilman, D. (1996) *Science* **274**, 1720–1723.
- Jackson, R. B., Manwaring, J. H. & Caldwell, M. M. (1990) *Nature (London)* **344**, 58–60.
- Jackson, R. B. & Caldwell, M. M. (1996) *J. Ecol.* **84**, 891–903.
- Jackson, R. B., Canadell, J., Ehleringer, J. A., Mooney, H. A., Sala, O. E. & Schulze, E.-D. (1996) *Oecologia* **108**, 389–411.
- Gale, M. R. & Grigal, D. K. (1987) *Can. J. For. Res.* **17**, 829–834.
- Cavelier, J. (1992) *Plant Soil* **142**, 187–201.
- Coupland, R. T. (1979) in *Grassland Ecosystems of the World*, ed. Coupland, R. T. (Cambridge Univ. Press, Cambridge, U.K.), pp. 335–355.
- Rodin, E. & Basilevich, N. I. (1967) *Production and Mineral Cycling in Terrestrial Vegetation* (Oliver and Boyd, Edinburgh).
- Santantonio, D., Hermann, R. K. & Overton, W. S. (1977) *Pedobiologia* **17**, 1–31.
- Vogt, K. A., Vogt, D. J., Boon, P., O'Hara, J. & Asbjornsen, H. (1996) *Plant Soil*, in press.
- Marchenko, A. I. & Karpov, E. M. (1962) *Soviet Soil Sci.* **7**, 722–734.
- Persson, H. (1980) *Oikos* **34**, 77–87.
- Persson, H. (1982) *Swedish Coniferous Forest Project* (Swedish Univ. of Agricultural Sciences, Uppsala), Rep. No. 31.
- Persson, H., von Fircks, Y., Majdi, H. & Nilsson, L. O. (1995) *Plant Soil* **168/169**, 161–165.
- Saurina, N. E. & Kameneckaja, I. V. (1969) *Bull. Mosk. Obsc. Ispyt. Prir.* **74**, 96 (abstr.).
- Vanninen, P., Ylitalo, H., Sievänen, R. & Mäkelä, A. (1996) *Trees* **10**, 231–238.
- Kumar, A. & Joshi, M. C. (1972) *J. Ecol.* **60**, 665–678.
- Moorhead, D. L., Reynolds, J. F. & Fonteyn, P. J. (1989) *Soil Sci.* **148**, 244–249.
- Sturges, D. L. (1977) *Am. Midl. Nat.* **98**, 257–274.
- Sims, P. L. & Singh, J. S. (1978) *J. Ecol.* **66**, 547–572.
- Wallace, A., Bamberg, S. A. & Cha, J. W. (1974) *Ecology* **55**, 1160–1162.
- Canadell, J. & Roda, F. (1991) *Can. J. For. Res.* **21**, 1771–1778.
- Kummerow, J., Krause, D. & Jow, W. (1977) *Oecologia* **29**, 163–177.
- Kummerow, J., Krause, D. & Jow, W. (1978) *Oecologia* **37**, 201–212.
- Kummerow, J., Kummerow, M. & Trabaud, L. (1990) *Vegetatio* **87**, 37–44.
- Kummerow, J. & Mangan, R. (1981) *Acta Oecol.* **2**, 177–188.
- Low, A. B. & Lamont, B. B. (1990) *Aust. J. Bot.* **38**, 351–359.
- Martinez-Garcia, F. & Rodriguez, J. M. (1988) *Lagascalia* **15**, 549–557.
- Miller, P. C. & Ng, E. (1977) *Madroño* **24**, 215–223.
- Ares, A. & Peinemann, N. (1992) *Can. J. For. Res.* **22**, 1575–1582.
- Fogel, R. (1983) *Plant Soil* **71**, 75–85.
- Gehrmann, J., Gerriets, M., Pühe, J. & Ulrich, B. (1984) *Berichte des Forschungszentrums Waldökosysteme/Waldsterben* (Univ. Bayreuth, Bayreuth, Germany).
- Hendriks, C. M. A. & Bianchi, F. J. J. A. (1995) *Neth. J. Agric. Sci.* **43**, 321–331.
- McClagherty, C. A., Aber, J. D. & Melillo, J. M. (1982) *Ecology* **63**, 1481–1490.
- Moir, W. H. & Bachelard, E. P. (1969) *Ecology* **50**, 658–662.
- Reynolds, E. R. C. (1970) *Plant Soil* **32**, 501–517.
- Safford, L. O. & Bell, S. (1972) *Can. J. For. Res.* **2**, 169–172.
- van Praag, H. J., Sougnez-Remy, S., Weissen, F. & Carletti, G. (1988) *Plant Soil* **105**, 87–104.
- Vogt, K. A., Edmonds, R. L. & Grier, C. C. (1981) *Can. J. For. Res.* **11**, 223–229.
- Vogt, K. A., Moore, E. E., Vogt, D. J., Redlin, M. R. & Edmonds, R. L. (1983) *Can. J. For. Res.* **13**, 429–437.
- Aber, J. D., Melillo, J. M., Nadelhoffer, K. J., McClagherty, C. A. & Pastor, J. (1985) *Oecologia* **66**, 317–321.
- Burke, M. K. & Raynal, D. J. (1994) *Plant Soil* **162**, 135–146.
- Fahey, T. J. & Hughes, J. W. (1994) *J. Ecol.* **82**, 533–548.
- Farrish, F. W. (1991) *Soil Sci. Soc. Am. J.* **55**, 1752–1757.
- Hendrick, R. L. & Pregitzer, K. S. (1993) *Can. J. For. Res.* **12**, 2507–2520.
- Joslin, J. D. & Henderson, G. S. (1987) *For. Sci.* **33**, 330–346.
- Nadelhoffer, K. J., Aber, J. D. & Melillo, J. M. (1985) *Ecology* **66**, 1377–1390.
- Powell, S. W. & Day, F. P., Jr. (1991) *Am. J. Bot.* **778**, 288–297.
- Symbula, M. & Day, F. P., Jr. (1988) *Am. Midl. Nat.* **120**, 405–415.
- Ulrich, B. (1986) in *Raten der Deposition, Akkumulation und des Austrags toxischer Luftverunreinigungen als Maß der Belastung und Belastbarkeit von Waldökosystemen*, ed. Ulrich, B.
- Yin, X., Perry, J. A. & Dixon, R. K. (1989) *For. Ecol. Manage.* **27**, 159–177.
- Barker, D. J., Zhang, D. M. & McKay, A. D., (1988) *N. Z. J. Exp. Agric.* **16**, 73–76.
- Dahlman, R. C. & Kucera, C. L. (1965) *Ecology* **46**, 84–89.
- Dumortier, M. (1991) in *Plant Root Growth: An Ecological Perspective*, ed. Atkinson, D. (Blackwell, Oxford), pp. 301–309.
- Hayes, D. C. & Seastedt, T. R. (1987) *Can. J. Bot.* **65**, 787–791.
- Liang, Y. M., Hazlett, D. L. & Lauenroth, W. K. (1989) *Oecologia* **80**, 148–153.
- Old, S. M. (1969) *Ecol. Monogr.* **39**, 355–384.
- Rychnovská, M. (1993) in *Ecosystems of the World: 8B Natural Grasslands*, ed. Coupland, R. T. (Elsevier, Amsterdam), pp. 125–166.

75. Schulze, E.-D., Mooney, H. A., Sala, O. E., Jobbagy, E., Buchmann, N., Bauer, G., Canadell, J., Jackson, R. B., Loreti, J., Oesterheld, M. & Ehleringer, J. R. (1996) *Oecologia* **108**, 503–511.
76. Singh, J. S. & Coleman, D. C. (1973) *Can. J. Bot.* **51**, 1867–1870.
77. Singh, J. S. & Coleman, D. C. (1974) *J. Ecol.* **62**, 359–363.
78. Jenik, J. (1971) in *Productivity of Forest Ecosystems*, ed. Duvingneaud, P. (UNESCO, Paris), pp. 323–331.
79. Kellman, M. (1990) *J. Trop. Ecol.* **6**, 355–370.
80. Lawson, G. W., Armstrong-Mensah, K. O. & Hall, J. B. (1970) *J. Ecol.* **58**, 371–398.
81. Kummerow, J., Castillanos, J., Maas, M. & Larigauderie, A. (1990) *Vegetatio* **90**, 75–80.
82. Singh, K. P. & Singh, R. P. (1981) *Oikos* **37**, 88–92.
83. Srivastava, S. K., Singh, K. P. & Upadhyay, R. S. (1986) *Can. J. For. Res.* **16**, 1360–1364.
84. Arunachalum, A., Pandey, H. N., Tripathi, R. S. & Maithani, K. (1996) *Vegetatio* **123**, 73–80.
85. Berish, C. W. (1982) *Can. J. For. Res.* **12**, 699–704.
86. Gower, S. T. (1987) *Biotropica* **19**, 171–175.
87. Huttel, C. (1975) in *Tropical Ecological Systems*, eds. Golley, F. B. & Medina, E. (Springer, Berlin), pp. 123–130.
88. Klinge, H. (1973) *Trop. Ecol.* **14**, 29–38.
89. Lugo, A. E. (1992) *Ecol. Monogr.* **62**, 1–41.
90. Mensah, K. O. A. & Jenik, J. (1968) *Preslia* **40**, 21–27.
91. Nepstad, D. C., de Carvalho, C. R., Davidson, E. A., Jipp, P. H., Lefebvre, P. A., Negreiros, G. H., da Silva, E. D., Stone, T. A., Trumbore, S. E. & Vieira, S. (1994) *Nature (London)* **372**, 666–669.
92. Silver, W. L. & Vogt, K. A. (1993) *J. Ecol.* **81**, 729–738.
93. Vance, E. D. & Nadkarni, N. M. (1992) *Plant Soil* **142**, 31–39.
94. Fiala, K. & Herrera, R. (1988) *Folia Geobot.* **23**, 225–237.
95. Lawson, G. W., Jenik, J. & Armstrong-Mensah, K. O. (1968) *J. Ecol.* **56**, 505–522.
96. Le Roux, X., Bariac, T. & Mariotti, A. (1995) *Oecologia* **104**, 147–155.
97. Pandey, C. B. & Singh, J. S. (1992) *Can. J. Bot.* **70**, 1885–1890.
98. Watts, S. E. (1993) M.S. dissertation (Texas A&M University, College Station).
99. Dennis, J. G., Tieszen, L. L. & Vetter, M. A. (1978) in *Vegetation and Production Ecology of an Alaskan Arctic Tundra*, ed. Tieszen, L. L. (Springer, Berlin), pp. 113–140.
100. Hobbie, S. E. (1995) Ph.D. dissertation (University of California, Berkeley).
101. Ignatenko, I. V. & Khamizyanova, F. I. (1971) *Ekologiya* **4**, 17–24.
102. Khodachek, E. A. (1969) *J. Bot.* **54**, 1059–1073.
103. Shaver, G. R. & Billings, W. D. (1975) *Ecology* **56**, 401–409.
104. Caldwell, M. M., Manwaring, J. H. & Durham, S. (1991) *Funct. Ecol.* **5**, 765–772.
105. Jastrow, J. D. & Miller, R. M. (1993) *Ecology* **74**, 561–569.
106. Reinhardt, D. R. & Miller, R. M. (1990) *New. Phytol.* **116**, 129–136.
107. Clemensson-Lindell, A. & Asp, H. (1995) *Plant Soil* **173**, 147–155.
108. Eissenstat, D. M. (1992) *J. Plant Nutr.* **15**, 763–768.
109. Ford, E. D. & Deans, J. D. (1977) *Plant Soil* **47**, 463–485.
110. Håland, B. & Braekke, F. H. (1989) *Scand. J. For. Res.* **4**, 307–316.
111. Hendrick, R. L. & Pregitzer, K. S. (1992) *Ecology* **73**, 1094–1104.
112. Mason, G. F., Bhar, D. S. & Hilton, R. J. (1970) *Can. J. Bot.* **48**, 43–47.
113. van Rees, K. C. J. & Comerford, N. B. (1986) *Soil Sci. Soc. Am. J.* **50**, 1042–1046.
114. Ahlström, K., Persson, H. & Börjesson, I. (1988) *Plant Soil* **106**, 179–190.
115. Berg, B. (1984) *Soil Biol. Biochem.* **16**, 609–617.
116. Bloomfield, J., Vogt, K. A. & Vogt, D. J. (1993) *Plant Soil* **150**, 233–245.
117. Camiré, C., Côté, B. & Brulotte, S. (1991) *Plant Soil* **138**, 123–132.
118. Cuevas, E. & Medina, E. (1988) *Oecologia* **76**, 222–235.
119. Khiewtan, R. S. & Ramakrishnan, P. S. (1993) *For. Ecol. Manage.* **60**, 327–344.
120. McLaugherty, C. A., Aber, J. D. & Melillo, J. M. (1984) *Oikos* **42**, 378–386.
121. McKay, H. M. & Malcolm, D. C. (1988) *Can. J. For. Res.* **18**, 1416–1426.
122. Majdi, H. & Rosengren-Brinck, U. (1994) *Plant Soil* **162**, 71–80.
123. Nambiar, E. K. S. (1987) *Can. J. For. Res.* **17**, 913–918.
124. Remezov, N. P. (1959) *Soviet Soil Sci.* **1**, 59–67.
125. Ůlehlová, B. (1990) *Ekológia* **9**, 193–206.
126. Whittaker, R. H. (1975) *Communities and Ecosystems* (Macmillan, London).
127. Dittmer, H. J. (1938) *Science* **88**, 482.
128. Schlesinger, W. H. (1991) *Biogeochemistry: An Analysis of Global Change* (Academic, San Diego).
129. Stone, E. L. & Kalisz, P. J. (1991) *For. Ecol. Manage.* **46**, 59–102.
130. Canadell, J., Jackson, R. B., Ehleringer, J. R., Mooney, H. A., Sala, O. E. & Schulze, E.-D. (1996) *Oecologia* **108**, 583–595.
131. Coupland, R. T., ed. (1993) *Ecosystems of the World: 8A and B Natural Grasslands* (Elsevier, Amsterdam).
132. Shalyt, M. S. (1950) *Tr. Bot. Inst. Akad. Nauk SSSR, Ser. III Geobot.* **6**, 205.
133. Ehleringer, J. R. & Field, C. B. (1993) *Scaling Physiological Processes* (Academic, San Diego).
134. Jackson, R. B. & Caldwell, M. M. (1993) *J. Ecol.* **81**, 683–692.
135. Wilson, E. O. (1992) *The Diversity of Life* (Norton, New York).
136. Körner, C. (1994) in *Biodiversity and Ecosystem Function*, eds. Schulze, E.-D. & Mooney, H. A. (Springer, Berlin), pp. 117–140.