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Critical analysis of root : shoot ratios in terrestrial biomes

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Abstract

One of the most common descriptors of the relationship between root and shoot biomass is the root : shoot ratio, which has become a core method for estimating root biomass from the more easily measured shoot biomass. Previous reviews have examined root : shoot ratio data, but have only considered particular vegetation types and have not always critically reviewed the data used. Reliable root : shoot ratios are needed for a wide range of vegetation types in order to improve the accuracy of root biomass estimates, including those required for estimating the effects of land management and land use change in National Greenhouse Gas Inventories.

This study reviewed root : shoot ratios in terrestrial biomes. A key facet of our analysis was a critical methodological review, through which unreliable data were identified and omitted on the basis of specific criteria. Of the 786 root : shoot ratio observations collated, 62% were omitted because of inadequate or unverifiable root sampling methods. When only the reliable data were examined, root : shoot ratios were found to be negatively related to shoot biomass, mean annual precipitation, mean annual temperature, forest stand age, and forest stand height.

Although a single allometric equation derived in this study reliably predicted root biomass from shoot biomass for forests and woodlands, in general, the use of vegetation-specific root : shoot ratios were found to be a more accurate method for predicting root biomass. When the root : shoot ratio data collated here were applied to an analysis of the global carbon budget, there was a 50% increase in estimated global root carbon stock, and a 12% increase in estimated total carbon stock of terrestrial vegetation. The use of the vegetation-specific root : shoot ratios presented in this study is likely to substantially improve the accuracy of root biomass estimates for purposes such as carbon accounting and for studies of ecosystem dynamics.

Keywords: biomass, carbon accounting, critical review, global carbon stocks, root, shoot, vegetation

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Introduction

Aboveground and belowground biomass are important components of terrestrial ecosystem carbon stocks. Patterns of aboveground biomass distribution in terrestrial ecosystems are reasonably well understood, whereas knowledge of belowground biomass and its distribution is still quite limited (McNaughton *et al*., 1998). This disparity in knowledge is essentially because of methodological difficulties associated with observing and measuring root biomass (Vogt *et al*., 1996; Titlyanova *et al*., 1999).

Knowledge of root biomass dynamics is fundamental to improving our understanding of carbon allocation and storage in terrestrial ecosystems (Cairns *et al*., 1997). One approach to gaining a greater understanding of root biomass distribution has been to explore the relationship between root biomass and shoot biomass, most commonly through the root : shoot ratio (defined as the root biomass divided by the shoot biomass). The distinction between 'root' and 'shoot' biomass is generally made at the ground surface level, with the term 'root' referring to all biomass below the ground surface, and 'shoot' being all biomass above the ground surface. Root : shoot ratios may be applied to individual plants,

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but more often are applied to stands of vegetation at varying scales from local, to landscape, region or biome.

From a physiological perspective, root : shoot ratios have been interpreted as reflecting the differential investment of photosynthates between the aboveground and belowground organs (Titlyanova *et al*., 1999). Although root : shoot ratios may reflect the cumulative response of vegetation to biotic, abiotic, and management influences, the physiological interpretation of root : shoot ratios is not straight forward. One reason for this is that existing root and shoot biomass only represents the net effects of carbon allocation, and does not incorporate the considerable loss of carbon resulting from respiration and senescence (turnover). Another issue is that the distinction between 'root' and 'shoot' biomass is based on the arbitrary position of the ground surface, which has relatively little meaning for plant functional compartmentalization (Körner, 1994). In some ecosystems, a considerable proportion of roots occur above the ground surface (Jenik, 1971) and likewise, a portion of stem biomass sometimes occurs below the soil surface.

Within the belowground biomass component, organs perform a range of functions, including structural support, storage, transport, and absorption (Schulze, 1983; Körner, 1994). Likewise, aboveground biomass includes organs performing a variety of functions, including support, transport, storage, photosynthesis, and reproduction. Root : shoot ratios are also greatly affected by the accumulation of dead biomass in woody tissue over time, such as in the stems of forest trees (Sanford & Cuevas, 1996; Litton *et al*., 2003). These factors combine to make the functional interpretation of root : shoot ratios difficult (Klepper, 1991). A more appropriate approach would involve examining biomass compartments on the basis of their physiological function, such as the 'fine-root : foliage' biomass ratio (Shackleton *et al*., 1988; Litton *et al*., 2003).

Although root : shoot ratios may only be coarse indicators of physiological processes affecting carbon allocation, they are of high value in providing estimates of belowground plant biomass from aboveground biomass. Multiplying the aboveground biomass by the root : shoot ratio relevant to that vegetation type is the primary method used by nations to estimate belowground biomass and carbon stocks for National Greenhouse Gas Inventory purposes (Cairns *et al*., 1997; Snowdon *et al*., 2000; Australian Greenhouse Office, 2002; Eamus *et al*., 2002).

While models and allometric equations of root dynamics can be important for predicting temporal change in root biomass at specific sites, it is currently not practical to apply these models across large temporal and spatial scales. The practical interim approach currently used for broadscale carbon accounting (IPCC, 1996; IPCC, 2003) utilizes default values of root : shoot ratios to estimate root carbon stocks. Root : shoot ratios also provide useful constraints for the calibration and testing of dynamic carbon-cycling models. Reliable estimation of root biomass assumes that the root : shoot ratio applied is representative of the system under study (Snowdon *et al*., 2000).

Current analysis

Although there have been a number of valuable reviews of root–shoot biomass dynamics (Rodin & Bazilevich, 1967; Santantonio *et al*., 1977; De Angelis *et al*., 1981; Jackson *et al*., 1996; Kurz *et al*., 1996; Vogt *et al*., 1996; Cairns *et al*., 1997; Snowdon *et al*., 2000; Li *et al*., 2003), they have had some limitations. Many of the past reviews have focused on particular biomes, such as forests, and excluded other major vegetation types (e.g. shrublands, grasslands). More importantly, these reviews have not generally applied or presented a systematic approach to evaluating the limitations of the data used in their analyses. Although the reviews by Jackson *et al*. (1996) and Cairns *et al*. (1997) did omit some data because of methodological deficiencies, they provided little detail on the criteria applied, and as discussed later, appear not to have omitted all data likely to be erroneous. The lack of clear critical methodological review in previous studies will have clouded the interpretation of root : shoot ratio data, because there are many factors that can lead to erroneous estimates of root biomass at the ecosystem scale.

Some of the more obvious methodological pitfalls associated with sampling root biomass distribution include: sampling to insufficient soil depth to capture the majority of roots; not sampling the root crown of woody plants; not sampling fine root biomass; and sampling with inadequate replication to enable a reliable estimate of root biomass. Studies affected by these factors may well have underestimated root biomass and generated unreliable root : shoot ratios. Inclusion of unreliable data may obscure identification of the main biotic and abiotic factors affecting root : shoot ratios, and yield poor estimates of root biomass for the purposes of carbon accounting.

We performed a comprehensive review of root biomass and root : shoot ratios for the major terrestrial biomes of the world. This included a comprehensive critical analysis of the methods used in each study, so that unreliable data could be omitted from the final analysis. The specific questions addressed by this study were: what effect does the omission of unreliable data have on the estimates of root biomass and root : shoot ratios?; how do the results of this review compare with those of earlier reviews which have not used specific criteria for the omission of unreliable data?; how do root : shoot ratios vary across the world's terrestrial biomes?; how do biotic and abiotic variables affect root biomass and root : shoot ratios?; and, can root biomass be estimated more accurately from allometric equations rather than by root : shoot ratios?

Methods

The database

We assembled 786 estimates of root and shoot biomass from 266 sources (books, journals, conference proceedings, published reports, and theses). Unpublished data were not included in this analysis because they are generally inaccessible to other researchers, cannot be fully critically analyzed, and the methods used are often difficult to verify. Many of the references obtained for this study were sourced from reference lists in published reviews of root–shoot biomass dynamics, including those of De Angelis *et al*. (1981), Jackson *et al*. (1996), Sanford & Cuevas (1996), Vogt *et al*. (1996), Cairns *et al*. (1997), and Snowdon *et al*. (2000). Other studies, including those published more recently, were identified through keyword searches on global databases such as Current Contents and CAB Abstracts.

It is highly probable that some relevant references were missed through the searching process described here, particularly for vegetation types such as grassland for which no major review of root–shoot biomass dynamics could be found. However, a strong effort was made to locate all available data sources.

Only studies presenting data on both the root biomass and shoot biomass of an area of vegetation were included in the analysis. References presenting root and shoot biomass data for individual plants only, from pot studies, or root biomass determined by modeling, were not included in the analysis.

Data collation

From the relevant references assembled, a range of biomass data and supporting information were recorded (available from the authors on request), including:

- Root and shoot biomass (dry weight of biomass per unit area). [Note: – where both live and dead root biomass values were provided, the combined live and dead root biomass value was used – for vegetation types such as grassland, where root and shoot biomass data were collected more than once over a time period, data were taken for the time of peak aboveground biomass. This approach eliminated the effects of highly varying shoot biomass caused by climatic variation and by disturbance such as grazing and fire.]
- Vegetation description (including vegetation type, dominant species, age, height, density of stems, mean diameter at breast height (DBH), basal area, any treatments imposed, disturbance history).
- Site description (including locality, country, latitude and longitude, elevation, mean annual temperature, mean annual precipitation, mean annual potential evapotranspiration (PET), soil texture).
- Shoot biomass sampling methods (including description of sampling methods, sample size, whether existing allometrics were applied).
- Root biomass sampling methods (including description of sampling methods, dimensions of soil cores or soil pits, depth of sampling, number of replicate samples, minimum root size sampled, whether root crowns were sampled).

Where studies did not provide climatic data for the site they examined (i.e. mean annual precipitation, mean annual rainfall, mean annual PET) these data were estimated using *LocClim* (FAO, 2002), which estimates basic climate variables from latitude, longitude, and altitude. The accuracy of *LocClim* in estimating mean annual temperature and mean annual precipitation was assessed by comparing climatic data predicted by *LocClim* with actual data, for those sites where actual data were presented by a study. Mean annual temperature predicted by *LocClim* was not significantly different to actual data ($P = 0.247$, $n = 94$). Mean annual precipitation predicted by *LocClim* was not significantly different to actual data for all sites where mean annual precipitation was $< 5000\ \mathrm{mm\ yr^{-1}}$ ($P = 0.74$, $n = 169$). *LocClim* was less accurate in predicting mean annual precipitation where values were $> 5000\ \mathrm{mm\ yr^{-1}}$; however, precipitation only exceeded this level for one site in the retained data. We were therefore confident in applying *LocClim* to estimate climatic data in this study.

Categorization of data by biome

The categorization of data by biome relied primarily upon the information provided in each study regarding the type of vegetation examined. The information reported varied widely, from detailed vegetation descriptions to simply providing a name of the broad vegetation type. The highly variable quality and quantity of vegetation descriptions available placed restrictions on the categorization of data by biome, and resulted in an inability to simply apply an existing biome classification system (e.g. FAO, 2001). The biome categories applied here are therefore based on existing classification systems, adapted to make use of the non-uniform information that was available. The biomes used in this study were first categorized by major growth form, then by climate zone (based on the Köppen–Trewartha system (Bailey, 1998)). Where required, data were further categorized by broad moisture regime, the dominant taxa, and the shoot biomass.

The forest biomes were further subcategorized by the amount of shoot biomass. This was done because root : shoot ratios have been shown to vary with forest stand development (e.g. Litton *et al*., 2003), and accumulated shoot biomass is more physiologically meaningful than other measures such as vegetation age, because growth rate can vary greatly. The shoot biomass categories for the forest biomes were established following assessment of a plot of root : shoot ratios as a function of shoot biomass for each forest type. For most of the forest biomes, the data clearly disaggregated into several shoot biomass categories with clearly distinct ranges in root : shoot ratios. The level of biome categorization for this study was conducted so as to maintain an adequate sample size (generally $n > 5$) within each category.

Criteria for omitting data

The reliability of root : shoot ratio data was determined by applying a number of criteria to each study (full description and justification of these criteria are available as an electronic supplement). On the basis of this methodological review and specific criteria, data were allocated to three categories: 'unverifiable'; 'inadequate', or; 'retained'. Table 1 describes the criteria for omitting data.

Data analysis

One-way ANOVA was used to evaluate the statistical significance of categorical data, followed by *a posteriori* Tukey's tests (SYSTAT, 1994). For frequency data, χ^2 analyses were applied, and where appropriate, adjusted residuals were calculated (Everitt, 1994). Simple linear and nonlinear regression was used to analyze relationships between variables. The significance of differences between constants and slopes was evaluated by analysis of variance (Zar, 1984). Where necessary, data were log or power transformed in order to correct for data displaying heteroscedasticity.

Some statistical issues can arise in analysis of data when in ratio format. Ratio data is often not normally distributed, hence violating the assumptions of many statistical tests (Sokal & Rohlf, 1981). As the analysis of root : shoot ratios was a key focus of this study, data were maintained in ratio form but were log transformed for statistical analyses to correct for skewness. All data were analyzed using SYSTAT 5.05 (1994), and GenStat (2003, 7th edn).

Results

Consequences of omitting unreliable data

Of the 786 data points assembled in this study, only 301 (38%) were deemed to be adequate and hence retained for analysis. Of the 485 data points omitted, 308 (39%) were judged to be inadequate, while 177 (23%) were unverifiable.

For the inadequate data, the main reasons for omission were inadequate replication in root sampling, and the root crown not being sampled (Fig. 1a). For the unverifiable data, the most common reason data were omitted was that the source publication was unobtainable (Fig. 1b).

For the analysis of root–shoot biomass relations, forest and woodlands were examined separately from shrubland and grasslands (including savannas), as the latter possessed a much greater range in root : shoot ratios (0.34–26.03). This broad separation was undertaken primarily to enhance the clarity of the subsequent analyses.

The mean shoot biomass of retained data (116 Mg ha^{-1}) was significantly lower ($P < 0.001$) than for either inadequate (177 Mg ha^{-1}) or unverifiable (206 Mg ha^{-1}) data for forest and woodland (data not shown).

The number of retained root : shoot ratio data points per unit area for the major biomes of the world were calculated based on areas presented by Saugier *et al.* (2001). Temperate forests had by far the highest number of retained data per unit of biome area (Fig. 2). Biomes such as tropical forests, tropical savannas and woodlands, and deserts had markedly less retained data per unit of biome area than the average for all biomes (Fig. 2).

For forest and woodland, the regression of root biomass as a function of shoot biomass for the retained data had a significantly greater slope (and hence greater root : shoot ratio) compared with all data combined (retained, inadequate, and unverifiable) and compared with the omitted data (inadequate and unverifiable) ($P < 0.05$) (Fig. 3). The regression for retained data also had a greater slope than the relationship presented by Cairns *et al*. (1997) (Fig. 3). Although the linear regression for the retained data provided a reasonable fit ($R^2 = 0.78$), applying a power function to the shoot data (Eqn (1)) provided an improved model for relating root biomass (y) to shoot biomass (x) for forests and woodlands ($R^2 = 0.93$):

$$y = 0.489x^{0.890}. \qquad (1)$$

Table 1 Criteria for rejecting data examined in this study (the number of data points omitted for each category are shown in Fig. 1)

Data category	Criteria for allocation to category
Unverifiable	Publication not in English*
	The publication could not be located or obtained using standard library global document searches
	The methods presented were of insufficient clarity to allow allocation to either of the categories 'inadequate' or 'retained'
Inadequate	All or part of the root biomass was estimated by the application of existing allometric relationships (i.e. new independent root data were not collected)
	The root crowns of woody plants were not sampled for vegetation with a shoot biomass >8 Mg ha^{-1}†
	Root sampling did not include roots of diameter‡:
	• <2 mm, where the shoot biomass was <135 Mg ha^{-1}
	• <5 mm, where the shoot biomass was 135–215 Mg ha^{-1}
	• <10 mm, where the shoot biomass was >215 Mg ha^{-1}
	The maximum depth of root sampling was§:
	• <75 cm belowground level for deserts and very arid ecosystems
	• <50 cm belowground level for woodlands, savannas, and shrublands
	• <50 cm belowground level for temperate and tropical forests where the shoot biomass was >30 Mg ha^{-1}
	• <30 cm belowground level for temperate and tropical forests where the shoot biomass was <30 Mg ha^{-1}
	• <30 cm belowground level for grasslands and boreal forests
	• <20 cm belowground level for tundra
	There was no, or inadequate, replication in the sampling of root biomass by excavation, soil cores, or soil pits.¶
	The aboveground vegetation was subject to recent major disturbance (e.g. fire, heavy grazing, harvesting)

*Criterion applied with the exception of several key Russian and German publications, which were translated and assessed similarly to publications in English.

†The proportion of root biomass occurring in the root crown, was analyzed as a function of shoot biomass. We arbitrarily set a maximum of 15% of total root biomass permitted to be missed because of no sampling of the root crown, which equated to a shoot biomass of approximately 8 Mg ha^{-1}.

‡The distribution of root biomass in different root size categories was analyzed as a function of shoot biomass. We arbitrarily set a maximum of 15% total root biomass permitted to be missed because of no sampling of particular root size categories, and determined the level of shoot biomass below which this proportion of root biomass was exceeded.

§A maximum of 15% root biomass was permitted to be missed because of inadequate soil sampling depth. The data of Jackson et al. (1996) was used to determine the soil depth at which the cumulative proportion of the root biomass sampled equalled 85% of the total root biomass for each biome. For young and low biomass forests, we determined the soil depth below which the cumulative root biomass was >85% of the total root biomass using compiled data on root biomass distributions for low biomass forests. These data were also used to establish the level of shoot biomass (30 Mg ha^{-1}) distinguishing high and low biomass forests for this purpose.

¶Precise criteria for judging the adequacy of replication in root sampling could not be defined, because of the wide range in root sampling methods applied in the studies we reviewed. The omission of data because of inadequate replication was judged for each study, using the following as a guide to minimum requirements: $\geq$10 soil cores of 5 cm diameter; $\geq$3 soil pits 50 cm long by 50 cm wide; entire root systems excavated for $\geq$3 woody plants.

For the shrubland and grassland data, the relationship between root biomass and shoot biomass was highly variable and not significantly different ($P>0.05$) for the retained data, the omitted data, and all data combined (Fig. 4).

Factors influencing root–shoot biomass relationships

Further analyses of root–shoot biomass interrelations involved examining only the retained data. The range in root : shoot ratios across all vegetation types varied by two orders of magnitude, from as low as 0.1 in some forest types to as high as 26 in a cool temperate grassland (Table 2). The median values of root : shoot ratios for each vegetation type are given rather than the mean values, because of the skewed distribution of data for many of the vegetation types. Root : shoot ratios were greater in grasslands than in forests or other woody vegetation. For forests, the root : shoot ratios tend to be higher in the forests with low shoot biomass (Table 2). The median root : shoot ratio of grasslands tended to increase from tropical to temperate to cool temperate climates (Table 2).

It was difficult to examine the relationship between root : shoot ratios and various biotic and abiotic factors (e.g. shoot biomass, precipitation), because each root : shoot

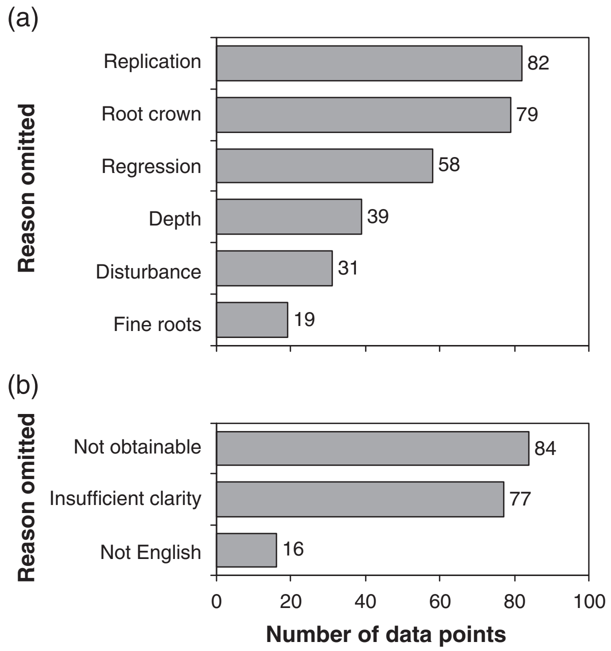

Fig. 1 The number of data points in each omission subcategory for: (a) inadequate data and (b) unverifiable data. For (a), the subcategories are: root crown (root crown not sampled); replication (inadequate replication); regression (allometric equation used to determine root biomass); depth (root sampling to inadequate depth in the soil); disturbance (aboveground biomass disturbed); and, fine roots (fine roots inadequately sampled). For (b), the subcategories are: not obtainable (reference for data was not obtainable); insufficient clarity (the methods published for the data were insufficiently clear); and, not English (reference not published in English).

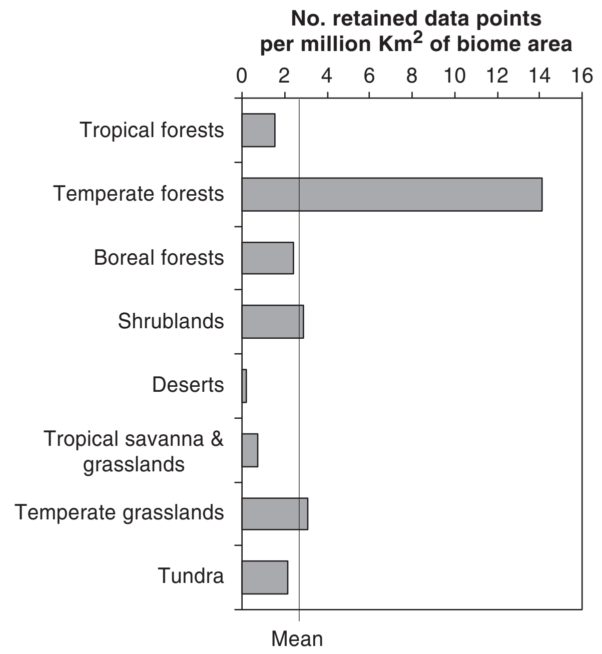

Fig. 2 The relative amount of retained root : shoot ratio data points for the major biomes of the world.

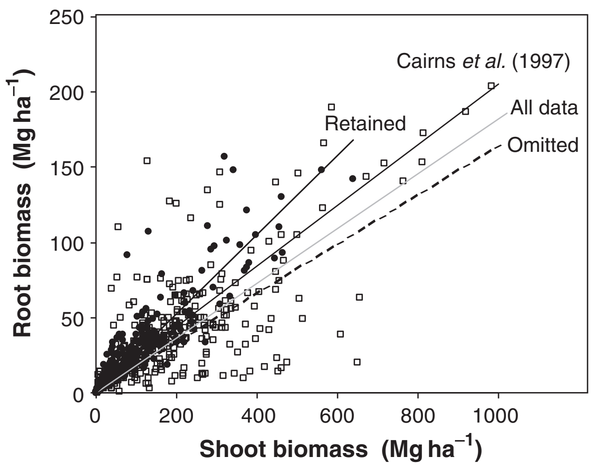

Fig. 3 Root biomass as a function of shoot biomass for data from forests and woodlands. Data shown are for retained data (•) and omitted data (inadequate and unverifiable data combined) (□). Regressions are shown for retained data ($y = 0.26x$; $R^2 = 0.78$), omitted data ($y = 0.16x$; $R^2 = 0.38$), all data (retained and omitted data combined) ($y = 0.18x$; $R^2 = 0.44$), and the relationship presented by Cairns *et al*. (1997) (Fig. 3 from that study). The slope for retained data is significantly greater ($P < 0.05$) than that for both all data and omitted data. The relationship for all data is not significantly different to that for omitted data ($P = 0.64$).

ratio data point often did not have data available for one or more of the independent factors. As a consequence, many root : shoot data points were omitted from a multiple regression analysis. Independent factors associated with root : shoot ratios were therefore examined separately.

For both forest and woodland (Fig. 5a), and shrubland and grassland (Fig. 5e), root : shoot ratios decreased significantly ($P < 0.001$) as shoot biomass increased. Similarly, root : shoot ratios decreased significantly ($P < 0.001$) as annual precipitation increased for both forest and woodland (Fig. 5b), and for shrubland and grassland (Fig. 5f). Although root : shoot ratios decreased significantly ($P < 0.001$) with increasing mean annual temperature for shrubland and grassland (Fig. 5g), there was no trend with temperature for root : shoot ratios in forest and woodland (Fig. 5c).

There was a general trend for root : shoot ratios to increase as soil texture changes from clay to sand for forest and woodland (Fig. 5d), with root : shoot ratios from sand and sandy loam soils significantly greater ($P < 0.001$) than those from clay or loam soils. Root : shoot ratios were significantly greater ($P < 0.001$) for clay loam soil texture than for other soil textures for forest

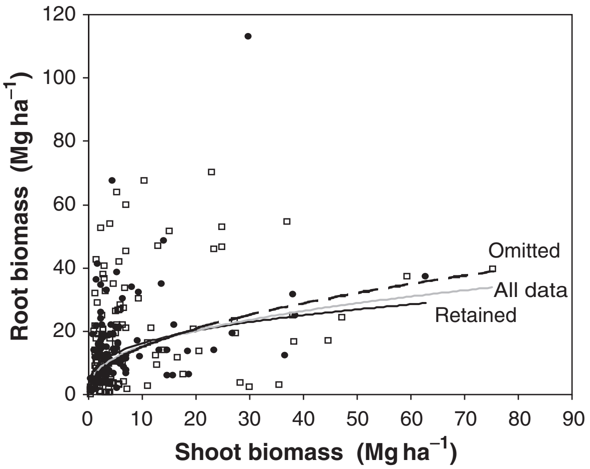

Fig. 4 Root biomass as a function of shoot biomass for data from shrublands and grasslands. Data shown are for retained data (●) ($y = 7.83x^{0.32}$; $R^2 = 0.15$), and omitted data (inadequate and unverifiable data combined) (□) ($y = 5.01x^{0.47}$; $R^2 = 0.17$). The regression is also shown for all data (retained and omitted data combined) ($y = 6.22x^{0.39}$; $R^2 = 0.14$). None of the regressions shown are significantly different from each other ($P > 0.05$); however, all slopes are significant ($P < 0.05$).

and woodland, however this result may be influenced by the low number of data points for clay loam soils. There was no significant ($P = 0.31$) influence of soil texture on root : shoot ratios for shrubland and grassland (Fig. 5h).

For the forest and woodland data, root : shoot ratios were correlated with a range of factors associated with stand development. They decreased significantly ($P < 0.01$) with the related factors of age (Fig. 6a), height (Fig. 6b), and mean DBH (Fig. 6d). Root : shoot ratios also increased significantly ($P = 0.01$) with tree density (Fig. 6e), but there was no significant ($P = 0.18$) relationship with tree basal area (Fig. 6c). There was no significant difference ($P > 0.05$) in root : shoot ratios between conifer and angiosperm-dominated forest ($P = 0.97$) (Fig. 6f), or between natural forest and plantation forest ($P = 0.31$) (Fig. 7).

Application of root : shoot ratios for estimation of root biomass

When the median root : shoot ratios were compared with the default values recommended by the IPCC (1996) for carbon accounting purposes, there were often large differences (Table 2). In addition, there are no IPCC default root : shoot ratio values for some vegetation types (e.g. tundra, cool temperate arid shrubland/desert).

Discussion

Consequences of omitting unreliable data

Of the 786 root : shoot ratio data points collated in this review, only 301 (38%) were considered reliable and included in the final analysis. From the large amount of data deemed to be methodologically inadequate (39%) or unverifiable (23%), it is apparent that much of our current knowledge of root–shoot biomass relations has been clouded by unreliable data.

Although the inadequate and unverifiable data were omitted from the final analysis, there is value to be gained in examining the properties of the omitted data, and in comparing them with the retained data. For data omitted because of inadequate methods, the most common reason for omission was that there was inadequate replication in the root sampling methodology (Fig. 1a). Root biomass is often heterogeneously distributed throughout the soil, so adequate replication in root sampling is essential. Much data were also omitted because the study did not sample the root crown. This is a major issue for root biomass studies in woody systems such as forests, where we observed the root crown to comprise on average 41% of total root biomass (range = 11–63%; SE = 3.1%; $n = 21$). Root sampling in woody vegetation (including shrublands and savannas) must include root crowns.

We were able to minimize the number of data points omitted as a consequence of publication in non-English languages (Fig. 1b) by translating some key Russian and German publications. This reduced the bias from omitting studies examining boreal forests, many of which are published in Russian. Unfortunately, resource limitations prevented translation of all non-English publications.

In examining root–shoot relations, forest and woodland vegetation types were separated from those of shrubland and grassland. This improved the clarity of the analysis of root–shoot data. The retained root : shoot ratios for forests and woodlands (ranging from 0.1 to 1.2) were much lower than those for shrublands and grasslands (ranging from 0.1 to 26.0) (Table 2). Ideally, root–shoot biomass relations would be examined separately for each vegetation type; however, the limited amount of data for most vegetation types, and the global nature of the data, necessitated a broad approach.

For forests and woodlands, retained data had significantly lower mean shoot biomass than inadequate or unverifiable data. This suggests that root biomass sampling methods have been more thorough (and easier to apply) for forests and woodlands of lower shoot biomass. Indeed, forests of large shoot biomass

Table 2 Retained root : shoot ratios (median, standard error (SE), the low and high extremes, and the number of data points (*n*)) for major biomes

Vegetation category	Shoot biomass ($Mg\,ha^{-1}$)	Median	SE	Low	High	*n*	IPCC (1996)
Tropical/subtropical moist forest/plantation	<125	**0.205**	0.036	0.092	0.253	4	0.06–0.33
	>125	**0.235**	0.011	0.220	0.327	10	0.06–0.33
Tropical/subtropical dry forest/plantation	<20	**0.563**	0.086	0.281	0.684	4	0.23–0.85
	>20	**0.275**	0.003	0.271	0.278	2	0.23–0.85
Temperate conifer forest/plantation	<50	**0.403**	0.037	0.206	1.058	33	0.20
	50–150	**0.292**	0.017	0.236	0.502	20	0.20
	>150	**0.201**	0.030	0.122	0.492	11	0.20
Temperate Oak forest	>70	**0.295**	0.066	0.200	1.155	14	0.25
Temperate eucalypt forest/plantation	<50	**0.437**	0.048	0.286	0.810	10	0.25
	50–150	**0.275**	0.060	0.151	0.811	11	0.25
	>150	**0.200**	0.032	0.105	0.332	6	0.25
Other temperate broadleaf forest/plantation	<75	**0.456**	0.062	0.119	0.927	14	0.25
	75–150	**0.226**	0.020	0.133	0.366	12	0.25
	>150	**0.241**	0.025	0.172	0.435	10	0.25
Boreal forest	<75	**0.392**	0.059	0.226	0.963	14	0.23
	>75	**0.239**	0.015	0.152	0.369	19	0.23
Tropical/subtropical moist woodland		**0.420**	0.032	0.292	0.548	7	–
Tropical/subtropical/temperate dry woodland		**0.322**	0.085	0.259	0.710	6	–
Shrubland		**1.837**	0.589	0.335	4.250	8	–
Savanna		**0.642**	0.111	0.397	1.076	5	–
Tropical/subtropical grassland		**1.887**	0.304	0.380	4.917	15	–
Temperate grassland		**4.224**	0.518	1.586	9.871	16	–
Cool temperate grassland		**4.504**	1.337	0.827	26.027	30	–
Tundra		**4.804**	1.188	0.875	15.198	12	–
Tropical/subtropical/temperate arid shrubland/desert		**1.063**	—	1.063	1.063	1	–
Cool temperate arid shrubland/desert		**4.091**	1.324	2.200	6.765	3	–
Tidal marsh		**1.098**	0.106	0.737	1.230	4	–

The forest vegetation types are subcategorized on the basis of the shoot biomass. Root : shoot ratios published by the IPCC (1996) are also shown.

(>150 $Mg\,ha^{-1}$) have fewer retained data points than forests with lower shoot biomass, for all forest types except tropical/subtropical moist forest/plantation (Table 2). It obviously becomes more difficult to sample root biomass components such as the root crown as the size of a tree increases. The lack of reliable data for high biomass forests limits our understanding of root–shoot relationships in these systems.

When the global area of each major biome is taken into account, temperate forests have by far the greatest number of retained root : shoot ratio data points per unit biome area (Fig. 2). In contrast, there is substantially less reliable data for tropical forests. Although large areas of the earth are covered by deserts ($27.7 \times 10^6\,km^2$) and tropical savannas and grasslands ($27.6 \times 10^6\,km^2$) (Saugier *et al*., 2001), root biomass studies in these biomes have been few (Fig. 2). For desert vegetation, the amount of total biomass present per unit area is low; however, the great areal extent of these systems and their variability in structure justifies greater research attention.

When we compare the relationship between root and shoot biomass for the data allocation categories, we see that for forests and woodlands, the fitted regression for the retained data has a significantly greater slope (45%) (and hence 45% greater mean root : shoot ratio) than for all data combined (Fig. 3). Data from studies with inadequate methods have generally underestimated the root biomass, and hence provide lower root : shoot ratios. The retained data also has a lower degree of variation about the fitted regression ($R^2 = 0.78$) than for all data combined ($R^2 = 0.44$), further indicating the benefits of omitting unreliable data (Fig. 3). When compared with the relationship observed by Cairns *et al*., (1997), the retained data from this study has a greater slope (and hence a greater mean root : shoot ratio).

For shrubland and grassland, the relationship between root and shoot biomass was highly variable, with no significant difference observed between the retained data and all data combined (Fig. 4). While studies that had inadequately sampled the root biomass (and thus had low root : shoot ratios) were omitted, so were those

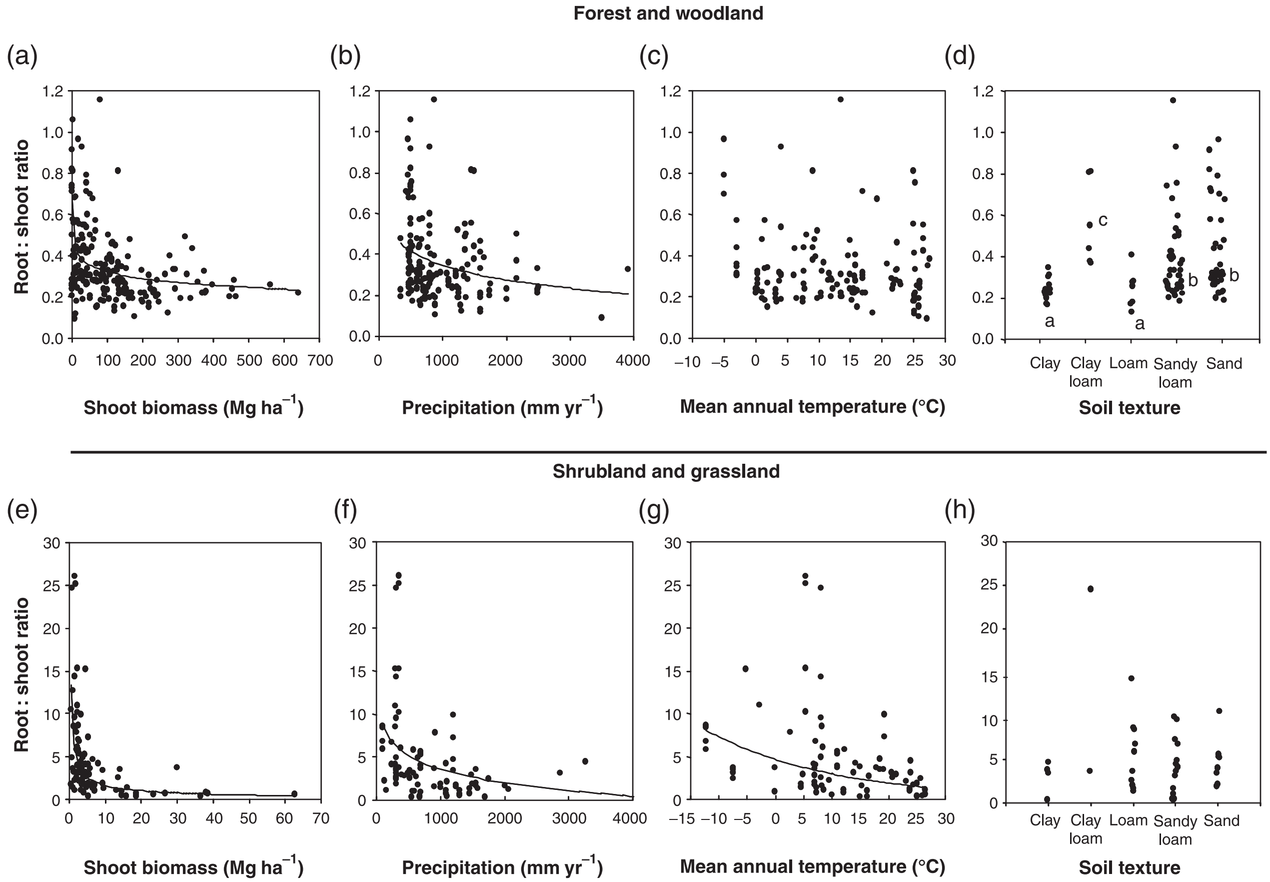

Fig. 5 Retained root : shoot ratios as a function of shoot biomass, annual precipitation, mean annual temperature, and soil texture for: Forest and Woodland (a–d), and Shrubland and Grassland (e–h). Regression slopes are significant for: (a) ($P<0.001$; $R^2=0.17$), (b) ($P<0.001$; $R^2=0.08$), (e) ($P<0.001$; $R^2=0.44$), (f) ($P<0.001$; $R^2=0.16$), and (g) ($P<0.001$; $R^2=0.17$). For (d), root : shoot ratios for soil texture groups are significantly different ($P<0.05$) when indicated by different letters (i.e. a, b). Mean root : shoot ratios for (d) are: 0.24 (clay); 0.56 (clay loam); 0.24 (loam); 0.40 (sandy loam); and 0.43 (sand).

that had been subject to recent aboveground disturbance (which results in high root : shoot ratios). The high variability in the relationship between root and shoot biomass in shrublands and grasslands (Fig. 4) indicates that use of vegetation-specific root : shoot ratios will provide a more accurate estimate of root biomass for these vegetation types.

Factors influencing root–shoot biomass relationships

We examined the relationship between the retained root : shoot ratios and a range of biotic and abiotic factors. Many factors have the potential to influence root : shoot ratios, including inherent species characteristics, site moisture and nutrient availability, regeneration strategies, and competition for light. The published studies collated here varied widely in respect to the detail they provided on site-specific biotic and abiotic data, with the resulting set of incomplete site data restricting analysis by multivariate statistics. Nonetheless, some significant results were obtained following the examination of root : shoot ratios as a function of a range of individual site factors.

Median root : shoot ratios varied widely between vegetation types, from 0.20 for temperate eucalypt forest/plantation ($>150\,\mathrm{Mg\,ha^{-1}}$) to 4.80 for tundra (Table 2). Some broad trends are evident with respect to how root : shoot ratios vary with vegetation type. For grasslands, there was an increase in median root : shoot ratio from tropical, to temperate, and then to cool temperate climates (Table 2), which may be related to the observed decrease in root : shoot ratios with increasing temperature for shrubland and grassland (Fig. 5g).

Shrublands had a high (1.84) median root : shoot ratio (Table 2), which is likely to be related to a wide range of factors, including their common occurrence in drier environments and their ability to resprout from root stocks following disturbance. Most of the data collated

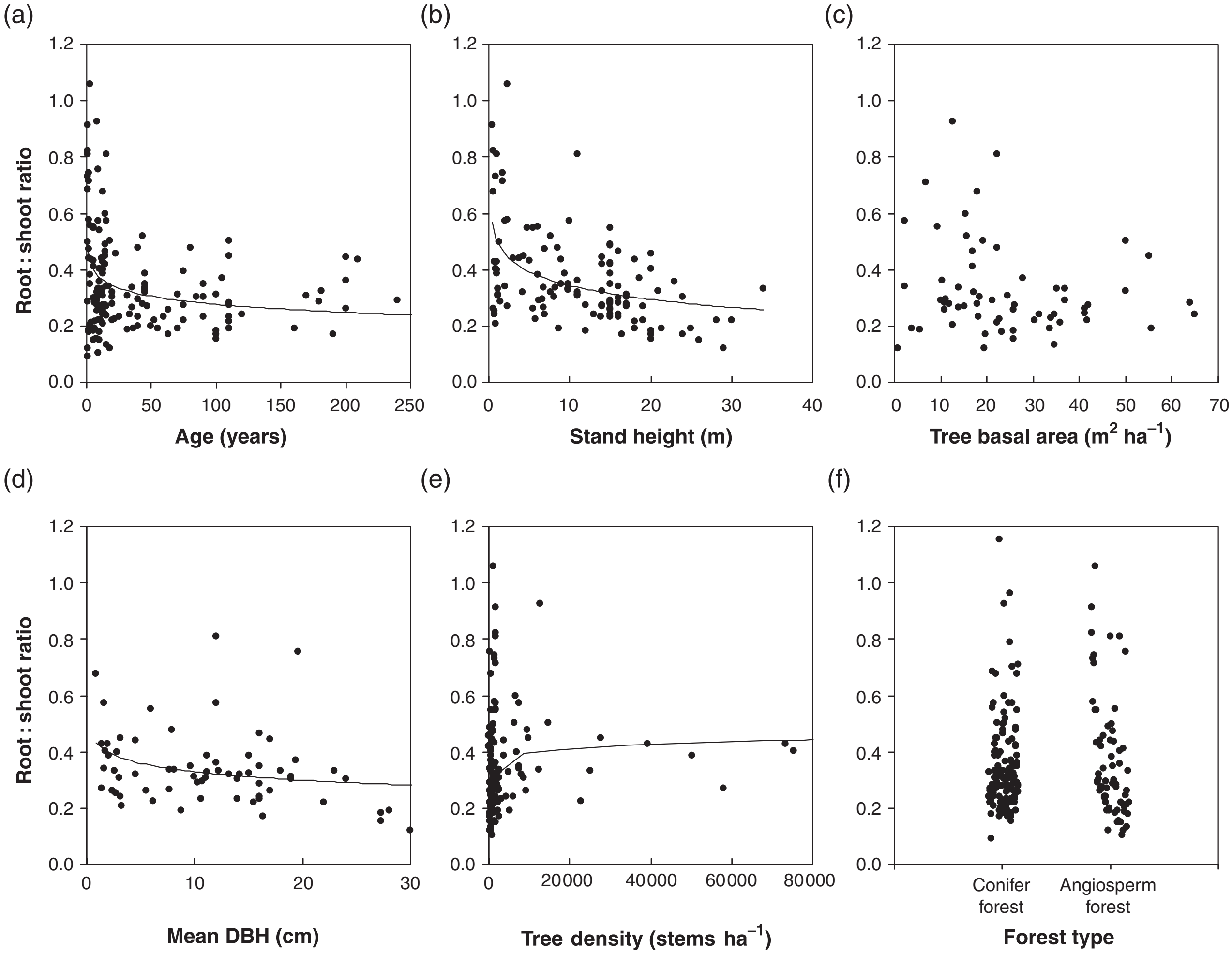

Fig. 6 Retained root : shoot ratios as a function of: (a) stand age, (b) stand height, (c) tree basal area, (d) mean diameter at breast height (DBH), (e) tree density, and (f) forest type, for forest and woodland. Regression slopes are significant for (a) ($P = 0.003$; $R^2 = 0.05$), (b) ($P < 0.001$; $R^2 = 0.21$), (d) ($P < 0.001$; $R^2 = 0.17$), and (e) ($P = 0.01$; $R^2 = 0.04$). For (f) mean root : shoot ratio for conifer forest (0.34) is not significantly different to that for angiosperm forest (0.37) ($P = 0.972$).

for shrublands were from areas that had received disturbance in the past (although generally longer than a decade before sampling).

The median root : shoot ratios presented in Table 2 are expected to be less reliable for vegetation types where the number of data points available was low. In particular, tropical dry forests, savannas, and deserts had very few root : shoot ratio data available, indicating that these systems warrant greater research attention.

For both forest and woodland and shrubland and grassland, root : shoot ratios decreased significantly as shoot biomass increased (Figs 5a and e). This widely observed phenomenon (e.g. Ovington, 1957; Ruark & Bockheim, 1987; Litton *et al*., 2003) is most obviously because of the accumulation of standing aboveground biomass, such as in the stems of forest trees.

For both forest and woodland and shrubland and grassland, root : shoot ratios decreased significantly as mean annual precipitation increased (Fig. 5b and f). This trend supports existing hypotheses and experimental evidence that root : shoot ratios become lower as moisture availability increases (e.g. Gower *et al*., 1992; Brand, 1999; Schenk & Jackson, 2002). Neither forest and woodland or shrubland and grassland showed a significant trend in root : shoot ratios as a function of PET or 'precipitation – PET' (data not shown). However, the analysis of root : shoot ratios as a function of PET and the 'precipitation – PET' index was limited by the availability of data for PET.

Although there was no significant trend observed in the relationship between root : shoot ratios and mean annual temperature for forest and woodland (Fig. 5c), there was a significant decrease in root : shoot ratios as

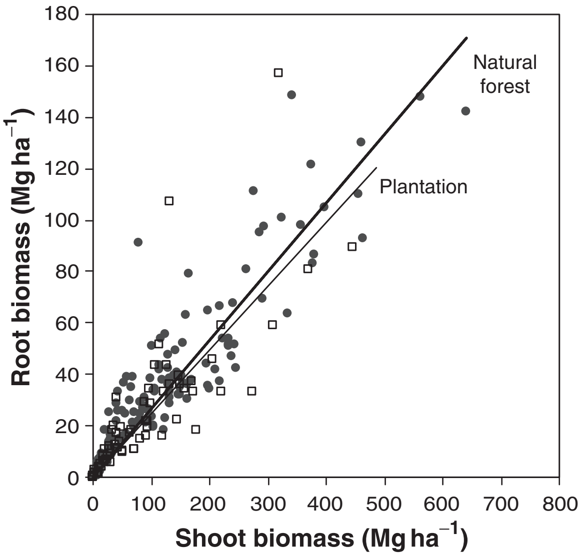

Fig. 7 Root biomass as a function of shoot biomass for retained data of natural forest (●) and plantation forest (□). There is no significant difference ($P = 0.31$) between the relationship for natural forest ($y = 0.27x$; $R^2 = 0.81$) and plantation forest ($y = 0.25x$; $R^2 = 0.64$).

mean annual temperature increased for shrubland and grassland (Fig. 5g). This trend may be related to an increase in the availability (and rate of absorption) of nutrients and water to the root system as soil temperature increases (for a given level of nutrients/water), reducing the need for extra investment in root biomass (Garkoti & Singh, 1995). The trend shown in Fig. 5g is also evident in the increase in median root : shoot ratio from tropical (1.89) to temperate (4.22) to cool temperate grasslands (4.50) (Table 2).

There was a general trend for root : shoot ratios to increase as soil texture becomes more coarse (from clay to sand) for forest and woodland (Fig. 5d), with root : shoot ratios from sand and sandy loam soils significantly ($P < 0.001$) greater than those from clay and loam soils. Root : shoot ratios from sandier soils may be larger because of water and nutrients being less freely available than in finer soil textures. It is also much easier to sample root biomass (and more of the root biomass) in a sandy soil, and this may have resulted in higher root : shoot ratios.

For forest and woodland, root : shoot ratios were related to several factors associated with stand development. They decreased significantly with increases in shoot biomass (Fig. 5a), stand age (Fig. 6a), stand height (Fig. 6b), and mean DBH (Fig. 6d), and increased with tree density (Fig. 6e). These trends are most obviously associated with the accumulation of aboveground biomass as a stand develops. However, no significant trend was observed for root : shoot ratios as a function of tree basal area (Fig. 6c).

Similarly to Cairns *et al*. (1997), we observed no significant difference between the root : shoot ratios for conifer-dominated forests compared with angiosperm-dominated forests (Fig. 6f). Likewise, there was no significant difference between natural forests and plantation forests for the relationship between root and shoot biomass (Fig. 7). Natural forests had a slightly greater mean root : shoot ratio, which fits with the finding of Cuevas *et al*. (1991) who observed greater relative allocation to root biomass in a regenerating natural forest compared with an adjacent plantation of the same age (although it would be more appropriate to compare forests of the same shoot biomass, not age). Plantations are likely to be established in areas with fertile and moist soils, which may often be enhanced by site preparation activities. These enhanced soil conditions would be expected to enhance shoot biomass at the expense of root biomass. In our analysis however, it is likely that any differences in the root–shoot biomass dynamics of natural forests compared with plantations are clouded by a variety of covarying biotic/abiotic factors such as tree species, stand age, or tree density.

The analyses presented here generally support previous conclusions about the primary determinants of root : shoot ratios. Despite the significant relationships observed, the trends displayed in many of the analyses are weak. A large portion of the variation observed may be attributed to the limited availability of data for many vegetation types, and the subsequent need to coarsely group data from a wide range of biomes. A wide range of factors influence root : shoot ratios, and these factors interact in complex ways.

Application of root : shoot ratios for estimation of root biomass

Although vegetation-specific root : shoot ratios are the most widely accepted method for estimating root biomass for purposes such as carbon accounting, some researchers have advocated the use of allometric equations to predict root biomass from either shoot biomass or DBH (Kurz *et al*., 1996; Vogt *et al*., 1996; Cairns *et al*., 1997; Vogt *et al*., 1998; Snowdon *et al*., 2000). It is therefore relevant to examine how the new vegetation-specific root : shoot ratios presented in this study (Table 2) compare with those vegetation-specific root : shoot ratios currently in use. It is also of interest to examine whether broadly derived allometric relationships provide a simpler and more accurate means for estimating root biomass than vegetation-specific root : shoot ratios.

The retained median root : shoot ratios presented in this study were observed to differ markedly from the default root : shoot ratios provided by the IPCC (1996) for certain vegetation types, although there was no consistent trend in the nature of these differences (Table 2). Many of the default root : shoot ratios provided by the IPCC (1996) are approximations only and are better replaced by more accurate vegetation-specific values. The root : shoot ratios presented by the IPCC (1996) do not distinguish between forests of different successional stage, whereas we observed that much greater accuracy can be achieved by subcategorizing data for forest and woodland vegetation on the basis of shoot biomass. It is, therefore, evident that applying root : shoot ratios that are independent of the shoot biomass of a forest has the potential to cause significant errors in estimating root biomass.

In contrast to providing a set of root : shoot ratios, Cairns *et al*. (1997) presented an allometric equation through which the root biomass of a forest can be predicted from the shoot biomass. The application of a single allometric equation to estimate root biomass for all forests and woodlands is certainly an attractive alternative to the use of individual root : shoot ratios for different forest types. Following this approach, we developed an equation relating root biomass to shoot biomass for forests and woodlands (Eqn (1)), which possessed a remarkably good fit to the data collated ($R^2 = 0.93$).

In order to determine whether Eqn (1) would provide a better means for estimating root biomass than the application of the new vegetation-specific root : shoot ratios summarized in Table 2, we used the retained root and shoot biomass data collated in this study for forests and woodlands to compare the predictive accuracy of the two methods. We found that the median root : shoot ratios (Table 2) predicted root biomass more accurately than Eqn (1) for 13 of the 18 forest and woodland vegetation categories. Thus while Eqn (1) provides a good general description of the relationship between root and shoot biomass for forests and woodlands, individual root : shoot ratios for each specific forest and woodland type provide a more accurate means for estimating root biomass. This conclusion gives greater emphasis to the need to improve our understanding of root–shoot biomass dynamics for vegetation types which have to date received limited research attention.

Global implications

To test the possible implications of the new estimates of root : shoot ratios (Table 2) for the global carbon budget, we repeated the analysis of Saugier *et al*. (2001), but applied root : shoot ratios adapted from this study (Table 2). Our results yield an estimated global root stock of 241 PgC, a similar value to that proposed by Robinson (2004), but about 50% higher than the 160 PgC estimated by Saugier *et al*. (2001). This dramatic increase in estimated global root carbon stock corresponds to a 12% increase in estimated total carbon stock of the worlds vegetation (from 652 to 733 Pg).

More than half (46 Pg) of this estimated increase in carbon stock was for the ‘tropical grasslands and savannas’ biome. The arctic tundra, temperate grassland and desert biomes had relatively large increases in estimated root biomass (of 123%, 79%, and 79%, respectively). These latter systems all have characteristically low biomass C density, but cover large areas of the earth, so the increased estimates of root biomass contribute significantly to the global total. Previous lack of synthesis of root : shoot data for nonforest ecosystems has resulted in poor estimates of root biomass for these systems in global carbon budget analyses.

This reanalysis of the global carbon budget should be viewed with some caution, as there are some issues in adapting the root : shoot ratios from the finer biome classification in this study to the broad biomes applied by Saugier *et al*. (2001). Despite this, it is evident that root biomass has generally been underestimated in the past, in both experimental studies and broader carbon budget analyses. The sensitivity of estimates of global carbon stock to altered root : shoot ratios emphasizes the need to improve our understanding of root biomass and its dynamics.

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