Implications of a large global root biomass for carbon sink estimates and for soil carbon dynamics

David Robinson*

School of Biological Sciences, University of Aberdeen, Aberdeen AB24 3UU, UK

Recent evidence suggests that significantly more plant carbon (C) is stored belowground than existing estimates indicate. This study explores the implications for biome C pool sizes and global C fluxes. It predicts a root C pool of at least 268 Pg, 68% larger than previously thought. Although still a low-precision estimate (owing to the uncertainties of biome-scale measurements), a global root C pool this large implies stronger land C sinks, particularly in tropical and temperate forests, shrubland and savanna. The land sink predicted from revised C inventories is 2.7 Pg yr⁻¹. This is 0.1 Pg yr⁻¹ larger than current estimates, within the uncertainties associated with global C fluxes, but conflicting with a smaller sink (2.4 Pg yr⁻¹) estimated from C balance. Sink estimates derived from C inventories and C balance match, however, if global soil C is assumed to be declining by 0.4–0.7% yr⁻¹, rates that agree with long-term regional rates of soil C loss. Either possibility, a stronger land C sink or widespread soil C loss, argues that these features of the global C cycle should be reassessed to improve the accuracy and precision of C flux and pool estimates at both global and biome scales.

Keywords: carbon; biome; global; root; sink; soil

1. INTRODUCTION

Potential carbon (C) sources and sinks are quantified using 'top-down' or 'bottom-up' approaches (Houghton 2003). Top-down approaches include monitoring largescale spatial and temporal changes in atmospheric CO_2 to infer locations and sizes of source and sink C fluxes to produce a global C balance. Bottom-up methods involve cataloguing land-use changes (e.g. deforestation, including burning) as a potential source of C emissions, and compiling C inventories for terrestrial biomes (Saugier *et al.* 2001; Houghton 2003; Grace 2004). Inventories estimate the amount of C held in the biosphere at the time when foliage, wood, debris, roots and soils are sampled. C fluxes can be derived from data if temporal changes in the C contents of soil and vegetation are measured or assumed (Taylor & Lloyd 1992).

Uncertainty surrounds inventory data especially for roots. These have, for decades, been major weaknesses in ecosystem models (Geider *et al.* 2001). The main uncertainties are spatial and temporal heterogeneity, uneven sampling, methodological differences among studies, and errors in estimating land cover and biome areas. The most recent synthesis accounting for such uncertainties as far as this is practicable at biome and global scales suggests that the best estimate for the total C pool in terrestrial biomes is approximately 650 Pg (Saugier *et al.* 2001; table 1). Of this, 160 Pg is thought to be belowground in root and associated fungal (mostly mycorrhizal) material, but recent evidence suggests that 160 Pg is a significant underestimate.

Allometric (or metabolic) scaling theory (West *et al.* 1997; Enquist & Niklas 2002) indicates that inventorybased estimates of root C probably account for only 60%, on average, of the true values (Robinson 2004). This discrepancy is caused mainly by incomplete sampling and mass loss during sample storage and preparation. An average 40% global underestimate in the root C pool might initially seem improbable, but it has support from several sources as follows:

- (i) Meticulous root extraction from beneath single poplar (Friend *et al.* 1991) or beech (Le Goff & Ottorini 2001) trees recovered only 65% of the total root mass.
- (ii) Only 64% of wheat roots were recovered by direct sampling following ¹³C-labelling as a sensitive indicator of belowground C allocation (Subedi *et al.* 2006).
- (iii) Data compiled (Poorter & Nagel 2000) from many experiments on individual plants indicate a geometric mean root mass/shoot mass quotient (R/S) of 0.45 (95% CI 0.42–0.47, n=426), falling within the range (0.4–0.6) given by the allometric model (Robinson 2004).
- (iv) Spatially detailed sampling of coarse and fine roots of loblolly pine (Albaugh *et al.* 2006) yielded *R/S* quotients matching those predicted by the allometric model (Robinson 2004).
- (v) An analysis (Mokany *et al.* 2006) of *R/S* data that excluded values obtained by 'inadequate or unverifiable' methods concluded that at least 240 Pg C was stored in roots, agreeing with the allometric model (Robinson 2004).

This mounting evidence for a larger-than-suspected root C pool prompts the reassessment of global and biome C inventories presented here. Alternative assumptions about the distribution of the 'extra' root C among biomes are assessed. These are based on an application of allometric

	area (10 ⁶ km ²)	plant mass $(g m^{-2})$		plant C ^a (Pg)			soil C^{c}	biome C ^d	$C sink^e$ (Pg vr ⁻¹)
biome		above	below	above	below	total ^b	- (- 8)	(- 8)	(-8)-)
				$C_{\rm A}$	$C_{\mathbf{R}}$	$C_{ m V}$	Cs	C_{B}	S
tropical forest	17.5	30 400	8400	266	74	340	214	553	0.66
temperate forest	10.4	21 000	5700	109	30	139	153	292	0.35
Boreal forest	13.7	6100	2200	42	15	57	338	395	0.47
Mediterranean shrubland	2.8	6000	6000	8	8	17	71	88	0.11
tropical savanna and grassland	27.6	4000	1700	55	23	79	247	326	0.39
temperate grassland	15.0	250	500	2	4	6	176	182	0.22
deserts	27.7	350	350	5	5	10	159	169	0.20
tundra	5.6	250	400	1	1	2	115	117	0.14
crops	13.5	530	80	4	1	4	11	15	0.02
ice	15.5								
total	149.3			492	160	652	1485	2137	2.56

Table 1. Current best estimates of (oven-dry) above- and belowground vegetation mass and C pools of vegetation and soils in terrestrial biomes, and of the land C sink, derived from C inventories (Saugier *et al.* 2001; Grace 2004; Grace *et al.* 2006).

^a Plant C is assumed to be 50% of dry mass (Saugier *et al.* 2001).

^b Total plant C (C_V) = aboveground C content (C_A) + root C content (C_R).

^c Soil C is calculated for a depth of 1 m (Saugier *et al.* 2001).

^d Biome C content (C_B) = vegetation C content (C_V) + soil C content (C_S).

^e C sink (S) = C_{Ba} , where $a = 0.0012 \text{ yr}^{-1}$ (§2 and table 1 of Grace (2004), but corrected to remove errors in that table (cf. table 4 of Grace *et al.* (2006)).

scaling theory (Robinson 2004) or on a recent reassessment of published data on root mass allocation (Mokany *et al.* 2006). The effects of revised C pool sizes on estimates of the global land sink for C (i.e. the C flux from the atmosphere into vegetation) are explored, as is the extent to which soils could be gaining or losing C and thereby influencing size of the net sink.

One of the strengths of allometric scaling theory is that it is mechanistic and predictive, based on fundamental biophysical principles that transcend data variability. It can reveal underlying trends that are often undetectable using purely empirical approaches. This is especially valuable when dealing with biome-scale data which are inevitably more variable than the differences among alternative estimates of C pool sizes. Ecosystem C models are based on those estimates (Cramer et al. 2001), so it is important that they are known as accurately as possible. Empirical analyses usually cannot distinguish between alternative estimates of C pools because relatively small differences between them are swamped by enormous data scatter. This limits the extent to which such estimates can be improved by conventional approaches. Allometric scaling theory is one of the few ways of dealing with this problem.

2. MATERIAL AND METHODS

(a) Data sources

Baseline plant mass and C data, biome classifications and land areas were as reported previously (Saugier *et al.* 2001; table 1).

Soil C pools were derived from Grace (2004) and are based on a standard depth of 1 m. That depth includes, on average, two-thirds of the planet's soil organic C (Jobbágy & Jackson 2000) and 97% of global root biomass (Jackson *et al.* 1996). The global soil C pool (C_S) calculated in table 1 on a biome basis (1485 Pg) falls within the range (1462–1548 Pg) calculated by Batjes (1996), also for a soil depth of 1 m. The total C content of each biome (C_B) was calculated as the sum of the vegetation C aboveground (C_A) and belowground (C_R) , and that in soil (C_S) .

The database of the Global Carbon Project (2006) provided annual C flux data with which inventory-based C sinks were compared.

(b) C sink calculations

Taylor & Lloyd (1992) estimated the size of the potential land C sink (S, Pg yr⁻¹) as

$$S = P\tau a, \tag{2.1}$$

where *P* is a biome's net primary productivity $(Pg yr^{-1})$; τ is the mean residence time (yr) of C in soil and vegetation; and *a* is a rate constant (yr⁻¹) to account for productivity changes caused mainly by increase in atmospheric CO₂ concentration. If atmospheric CO₂ concentration is increasing by approximately 0.4% yr⁻¹ and if *P* can increase by up to 30% in response to a doubling of CO₂ concentration (Grace 2004; Norby *et al.* 2005), the global mean rate at which *P* changes is, therefore, 0.0012 yr⁻¹; this is *a*.

Taylor & Lloyd (1992) defined the mean residence time of C in a biome as

$$\tau = C_{\rm B}/P. \tag{2.2}$$

Therefore, τ and *P* can be eliminated from equation (2.1). The calculation of *S* simplifies to

$$S = C_{\rm B}a. \tag{2.3}$$

The calculation depends, therefore, on accurate estimates of $C_{\rm B}$ from C inventories and of *a* from physiological measurements; neither mean residence times of C nor primary productivity rates need to be specified.

This simple and transparent approach to estimating the land C sink can be criticized on at least two points, however. First, arguments can be made for biome-specific values of a to reflect geographical variations in the responsiveness of primary production to environmental change and seasonality

(Taylor & Lloyd 1992). Second, increases in primary production of mature deciduous trees exposed to elevated CO_2 could be much less than the assumed 30% increase for a doubling in concentration (Körner *et al.* 2005), implying global *a* values significantly smaller than 0.0012 yr⁻¹. Nevertheless, despite the limitations of this approach, a global mean *a* value of 0.0012 yr⁻¹ was used here to allow direct comparisons with existing sink estimates that were calculated using it (Saugier *et al.* 2001; Grace 2004).

(c) Assumptions for root C estimation

Effects of the size of root C pools on C inventories were explored by modifying the root C data in table 1 according to various assumptions as follows:

- (i) Root masses reported for forests are 60% of the true values, but those for other biomes are accurate. Corrected root masses of tropical, temperate and boreal forests were derived by dividing those in table 1 by 0.6 (Robinson 2004). This assumes that root masses of forests are underestimated by direct sampling mainly because the root systems of large trees are so extensive, rendering complete recovery impossible, but that this is a negligible problem elsewhere. Root C was assumed throughout to be 50% of root mass (Saugier et al. 2001).
- (ii) Root masses of all biomes are 60% of the true values. Corrected root masses were derived by dividing all those in table 1 by 0.6. This assumes that poor root sampling and post-sampling handling problems apply equally to all biomes. The nature of these sources of error makes it difficult to verify this. However, these problems are unlikely to apply to biomes (e.g. tundra) containing relatively small plants with shallow root systems (Jackson *et al.* 1996) and not to forests. Even small root systems can be impossible to estimate accurately if they are embedded in an intractable medium like peat, and fine roots are always undersampled (Jackson *et al.* 1996). There is, therefore, a strong argument for applying the allometric correction to all biomes and not just those dominated by large trees.
- (iii) Root masses of all biomes are underestimated because inappropriate R/S quotients were used in earlier analyses. Biome root masses are often calculated as the products of aboveground masses (which can usually be estimated with greater accuracy than those of roots) and R/Squotients. Mokany et al. (2006) provided improved R/S quotients for the main terrestrial biomes from numerous reported measurements. Biome-specific quotients were derived as the geometric means of those reported in table 2 of Mokany et al. (2006) with the exceptions of those for tropical savanna (mean R/S = 2.02; Grace *et al.* 2006) and crops for which R/S=0.15 was assumed, as in Saugier et al. (2001). Biome classes used by Mokany et al. (2006) were narrower than those in table 1. R/S data relevant to narrowly defined biomes were combined; for example, the four tropical woodland or plantation classes defined by Mokany et al. (2006) were combined into a single 'tropical forest' biome. This was done to allow comparison with a previous analysis based on broad biome definitions (Saugier et al. 2001). The resulting mean R/S quotients were multiplied by the aboveground vegetation masses in table 1 to obtain new root masses for each biome. The allometric correction of 0.6 (see above) was not applied. This assumes that

Proc. R. Soc. B (2007)

above- and belowground masses in the studies screened by Mokany *et al.* (2006) were accurate.

- (iv) Root masses of all biomes are underestimated because inappropriate R/S quotients were used in earlier analyses and because root masses reported for forests are 60% of the true values. This assumption combines assumptions (i) and (iii). All root masses were recalculated using biomespecific R/S quotients (Mokany et al. 2006) and aboveground masses in table 1. The allometric correction was then applied to the root masses of only the forest biomes, but not elsewhere. The logic behind this is that the R/S quotients selected to be the most representative of each biome (Mokany et al. 2006) were still likely to have been underestimated during measurement, but that the error was most serious for forests, as argued previously (Robinson 2004 and above).
- (v) Root masses of all biomes are underestimated because inappropriate R/S quotients were used in earlier analyses and because reported root masses of all biomes are 60% of the true values. This assumption combines assumptions (ii) and (iii). All root masses were recalculated using the biome-specific R/S quotients (Mokany et al. 2006) and the aboveground masses in table 1. The allometric correction was then applied to the root masses of all biomes. This assumes that errors in measuring root mass apply equally to all biomes, and not just to forests, again based on the arguments given previously (Robinson 2004 and above).

(d) Accuracy and precision of C pool estimates

The numbers in table 1 are the best estimates currently available for each category of the global C budget. Although believed to be reasonably accurate (with the notable exception of the root C pools), the estimates in table 1 are inevitably imprecise. They were derived originally from data reflecting the great heterogeneity of soils, vegetation and environmental conditions within biomes, measurement errors and errors generated when scaling-up from small to large areas. Saugier et al. (2001) attached no specific uncertainties to their estimates of biome C pools; nor did uncertainties feature in later analyses based on those estimates (Prentice et al. 2001, p. 192; Royal Society 2002). A typical coefficient of variation for inventory-based estimates of biome net primary productivity is 70%, bracketed by a low CV of 41% for temperate forests and a high of 128% for deserts (Cramer et al. 2001). Equally wide CVs apply to the organic C contents (to 1 m depth) of FAO/UNESCO soil units, ranging from 43% in podzoluvisols to 136% in fluvisols (Batjes 1996). Therefore, the C pool estimates in table 1, and those derived from them, are likely to have uncertainties of the order of 70%. For clarity, these are not included explicitly in the analyses below, but the estimates of C pools derived here (and elsewhere) should be viewed accordingly. Large variations in biome C data do not negate the value of producing better (i.e. more accurate) estimates of biome C pools even if those estimates will always be less precise than is desirable.

3. RESULTS

The predicted increases in the size of the global root C pool $(C_{\rm R})$ above the currently accepted figure of 160 Pg are 80–317 Pg (table 2). The increases depend on the assumptions applied to the data in table 1.

		root C (C _R) (Pg) assumption						
biome	table 1	(i)	(ii)	(iii)	(iv)	(v)		
tropical forest	74	123	123	88	148	148		
temperate forest	30	49	49	33	55	55		
Boreal forest	15	25	25	13	22	22		
Mediterranean shrubland	8	8	14	15	15	26		
tropical savanna and grassland	23	23	39	112	112	186		
temperate grassland	4	4	6	8	8	13		
deserts	5	5	8	12	12	21		
tundra	1	1	2	3	3	6		
crops	1	1	1	1	1	1		
total	160	240	268	286	376	477		

Table 2. Root C pools of terrestrial biomes revised from those in table 1 by applying each of the five assumptions detailed in §2. The original data from table 1 are included to allow direct comparisons with the revised figures.

Table 3. Revised biome C inventories if the root C pool (C_R) of each biome is increased according to assumption (ii) and table 2, from those in table 1.

	plant C (Pg)					
	above	below	total	soil C ^a (Pg)	biome C (Pg)	C sink ^b (Pg yr ⁻¹)	C sink increase ^c (%)
biome	C_{A}	C _R	$C_{ m V}$	Cs	$C_{\rm B}$	S	
tropical forest	266	123	389	214	602	0.72	9
temperate forest	109	49	159	153	312	0.37	7
Boreal forest	42	25	67	338	405	0.49	3
Mediterranean shrubland	8	14	22	71	94	0.11	6
tropical savanna and grassland	55	39	94	247	342	0.41	5
temperate grassland	2	6	8	176	185	0.22	1
deserts	5	8	13	159	172	0.21	2
tundra	1	2	3	115	118	0.14	1
crops	4	1	4	11	15	0.02	2
total	492	268	759	1485	2244	2.69	5

^a Soil C is calculated for a depth of 1 m (Saugier et al. 2001), see table 1.

^b C sinks estimated as described in §2 and table 1.

^c Increases in the C sink are expressed as percentages of those in table 1.

The smallest increase (under assumption (i)) is the more conservative of the figures proposed by the allometric approach (Robinson 2004) and matches that suggested by Mokany et al. (2006) from a literature analysis and reassessment of the Saugier et al. (2001) data. However, that analysis was based on reported root masses (which are always underestimated; Robinson 2004). Therefore, the predicted 80 Pg larger root C pool is probably still smaller than the true global figure. The increase under assumption (ii) is the larger of the allometric scaling estimates reported by Robinson (2004) and implies that the global root C pool is 108 Pg larger than the current figure. A slightly larger pool is predicted by assumption (iii). Very large increases are implied under assumptions (iv) and (v). A global root C pool of 400-500 Pg rivals that for the aboveground component (C_A ; table 1) and would require that, globally, R/S is approximately unity. This is unlikely. The R/Squotients of most plants lie between 0.3 and 0.8 (Poorter & Nagel 2000). Allometric scaling (Robinson 2004) predicts R/S quotients between 0.4 and 0.6.

These arguments lead to the rejection of root C estimates derived using assumptions (iv) and (v) as being unreasonably large, and to suspect that predicted from

assumption (i) as being too small. Assumptions (ii) and (iii) predict a probable root C pool of 268–286 Pg, approximately 15 Pg of which are probably in the mycorrhiza-forming fungi associated with the roots of most plant species (Robinson 2004). It is proposed that a figure approximately 270–280 Pg is now accepted as the best estimate of the global root C pool pending the collection of better data or more definitive analyses. The conservative implications of this larger root C pool are now explored, using the smaller figure in the most probable range, 268 Pg.

A global root C pool of 268 Pg implies a stronger terrestrial C sink. The current sink estimate based on biome C inventories is 2.56 Pg yr^{-1} (table 1). Recalculating this using a root C pool of 268 Pg gives a sink of 2.69 Pg yr⁻¹ (table 3). Although now based on more accurate root C data than its predecessor, this estimate remains a low-precision one owing to the uncertainty attached to inventory-based estimates of biome C pools (see §2*d*).

The global C sink in table 3 represents, on average, a 5% increase on the existing estimate, but this is not distributed uniformly across biomes (table 3). The sink strengths of some biomes (e.g. tundra, desert and temperate grassland) barely change from those in table 1. Those of other biomes

	$b\!=\!0.4\%~{ m yr}^{-1}$		$b = 0.7\% \text{ yr}^{-1}$		
	soil C ^a (Pg)	$C sink^b (Pg yr^{-1})$	soil C (Pg)	$\frac{C \text{ sink } (Pg \text{ yr}^{-1})}{S}$	
biome	C_{S}	S	$C_{\rm S}$		
tropical forest	197	0.70	185	0.69	
temperate forest	142	0.36	133	0.35	
Boreal forest	313	0.46	293	0.43	
Mediterranean shrubland	66	0.11	62	0.10	
tropical savanna and grassland	229	0.39	214	0.37	
temperate grassland	163	0.21	153	0.19	
deserts	147	0.19	138	0.18	
tundra	107	0.13	100	0.12	
crops	10	0.02	9	0.02	
total	1374	2.56	1286	2.45	

Table 4. Biome soil C pools and the resulting C sinks calculated assuming two yearly rates of soil C loss (b) over a 20-year period and including the root C pools in table 3.

^a Soil C pools at time zero are assumed to be those in table 3 and which represent the case b=0% yr⁻¹. Soil C is calculated for a depth of 1 m (Saugier *et al.* 2001).

^b C sinks estimated as described §2 and table 1.

(e.g. tropical and temperate forests, Mediterranean shrubland, and tropical savanna and grassland) increase by up to 9%. The relative sink strengths of different biomes remain unchanged if their areas remain constant. For example, the sink fraction contributed by tropical forests is 27% of the total, irrespective of any recalculated root masses. If the sizes of root C pools are of the scale suggested here, they are still smaller than that in the soil and are usually exceeded by that aboveground, especially in the forests that dominate the sink calculation (60% of the total).

4. DISCUSSION

(a) A stronger terrestrial C sink?

How does a land C sink of 2.69 $Pg yr^{-1}$ compare with topdown estimates that do not rely exclusively on biomass inventories? The 1990–2005 mean (\pm 95% CI) land sink derived as the residual balance of other C fluxes (Houghton 2003) was $2.45 \pm 0.66 \text{ Pg yr}^{-1}$ (Global Carbon Project 2006). Compared with the land sink, other C fluxes are relatively well constrained: fossil fuel emissions = $6.4 \pm$ 0.24 Pg yr^{-1} ; other emissions = $0.25 \pm 0.02 \text{ Pg yr}^{-1}$; land-use change = 1.5 ± 0.04 Pg yr⁻¹; oceanic uptake = 2.2 ± 0.1 Pg yr⁻¹; and atmospheric increase = $3.5\pm$ 0.66 Pg yr^{-1} (Global Carbon Project 2006). Therefore, the mean net land sink (land-use change-residual sink) was -0.9 Pg yr^{-1} , consistent with estimates obtained from atmospheric inversion models (Prentice et al. 2001, pp. 210-212). This consistency gives confidence in the global C balance even if a weakness of that approach is that it cannot distinguish between certain key fluxes such as those associated with burning (mainly in tropical forest and savanna) and those caused by ecosystem respiration.

If this global C balance is broadly correct, an inventorybased land sink of 2.69 Pg yr⁻¹ that included a root C pool of 268 Pg demands a mean net sink of -1.2 Pg yr⁻¹ to achieve C balance. Net sinks this strong have been detected in certain years in the 1990–2005 period (Global Carbon Project 2006), but such a large mean value sits uncomfortably with the global C balance. This suggests that sink estimates based on C inventories, and which include the larger root C pool, could be incorrect. Rather than a stronger land sink, a large root C pool of 268 Pg could indicate global losses of soil C.

(b) Significant soil Closs?

The sink calculation used here assumes that the global soil C pool is constant. This assumption is usually reasonable over short (inter-annual) periods. But on decadal time scales, significant variations in soil C can be detected. These are caused by changes in land-use, which include deforestation (Guo & Gifford 2002; Murty *et al.* 2002) and burning (leading to the loss of both oxidizable organic C and of oxidation-resistant elemental C; Bird *et al.* 1999), or in climate, especially if warmer temperatures accelerate organic matter decomposition (Davidson & Janssens 2006).

A net C loss from the global soil pool would reduce the size of the potential land sink. By how much must the size of the soil C pool change to align the inventory-based C sink (2.69 Pg yr⁻¹), and which includes the larger root C pool, with those estimated from existing inventories (2.56 Pg yr⁻¹; table 1) or from the global C balance (2.45 Pg yr⁻¹; Global Carbon Project 2006)? This question was addressed by simulating a uniform and constant C loss from the top 1 m of soil for each of the past 20 years, taking the soil C pools in table 1 as the starting points. Soil C contents (C_S) at time t+1 were computed for each biome as

$$C_{\rm S}(t+1) = C_{\rm S}(t) - [bC_{\rm S}(t)], \qquad (4.1)$$

where b is the annual rate (yr^{-1}) of soil C change. Values of b leading to sink estimates matching the inventory-based value in table 1 or that derived from the global C balance after 20 years were computed numerically. A soil C loss rate of b=0.4% yr⁻¹ (table 4) matches the inventory-based sink that includes the 268 Pg root C pool with the original sink estimate based on a root C pool of 160 Pg (table 1). Alternatively, if soil C has been declining faster, at b=0.7% yr⁻¹, the inventory-based sink matches that given by the global C balance for 1990–2005 (Global Carbon Project 2006).

These assumed rates of soil C loss are realistic. For example, since the late 1970s, the mean rate of soil C loss in England and Wales has been $0.6\% \text{ yr}^{-1}$ (range $0-2\% \text{ yr}^{-1}$; Bellamy *et al.* 2005). Mean loss rates within this range have

been measured in diverse ecosystems: North American grasslands (Jackson et al. 2002); Belgian cropland (Sleutel et al. 2003); tundra and boreal forest (Thompson et al. 2006); sub-Saharan fields (Ouattara et al. 2006); and New Zealand pastures (Schipper et al. 2007). But such loss rates are not uniform across the globe. Soil C is accumulating in some areas at significant rates, as in some undisturbed, old-growth forests in China where soil C is increasing by $2\% \text{ yr}^{-1}$ (Zhou *et al.* 2006). There is strong evidence for general latitudinal differences in soil C residence times (Bird et al. 1996), influencing how rapidly the C content of soil organic matter, and of its size-and age-fractions, can change in specific biomes. It is, therefore, probable that large areas of land could be losing or gaining soil C significantly faster than the global average. There is currently no consensus about whether the world's soils are losing C overall, but the evidence presented here suggests that a global net loss of soil C is a serious possibility.

5. CONCLUSIONS

The evidence for a larger-than-suspected root C pool of approximately 270–280 Pg is compelling, despite the scale of the discrepancy between it and current estimates based on biome C inventories. A larger root C pool of this magnitude has implications for the global C cycle. To accommodate the larger root C pool, the land C sink must be stronger (by 0.1-0.2 Pg yr⁻¹) than current C balance estimates indicate. Alternatively, and to achieve agreement between the various sink estimates based on inventories or on global C balance, global soil C pools must be declining (on average by up to 0.7% yr⁻¹). Either possibility argues for a critical reassessment of these key features of the C cycle and for better precision of C flux and C pool estimates at both biome and global scales.

I thank Ruth Hasty, Clare Trinder, Pete Smith and John Grace for their help, Hendrik Poorter and Karel Mokany for providing data and supplementary information, and three anonymous referees for their comments.

REFERENCES

- Albaugh, T. J., Allen, H. L. & Kress, L. W. 2006 Root and stem partitioning of *Pinus taeda*. *Trees* 20, 176–185. (doi:10. 1007/s00468-005-0024-4)
- Batjes, N. H. 1996 Total carbon and nitrogen in the soils of the world. *Eur. J. Soil Sci.* 47, 151–163. (doi:10.1111/j.1365-2389.1996.tb01386.x)
- Bellamy, P. H., Loveland, P. J., Bradley, R. I., Lark, R. M. & Kirk, G. J. D. 2005 Carbon losses from all soils across England and Wales 1978–2003. *Nature* 437, 245–248. (doi:10.1038/nature04038)
- Bird, M. I., Chivas, A. R. & Head, J. 1996 A latitudinal gradient in carbon turnover times in forest soils. *Nature* 381, 143–146. (doi:10.1038/381143a0)
- Bird, M. I., Moyo, C., Veenendaal, E. M., Lloyd, J. & Frost, P. 1999 Stability of elemental carbon in a savanna soil. *Global Biogeochem. Cycles* 13, 923–932. (doi:10.1029/1999GB 900067)
- Cramer, W., Olson, R. J., Prince, S. D., Scurlock, J. M. O. & Members of the Global Primary Production Data Initiative (GPPDI). 2001 Determining present patterns of global productivity. In *Terrestrial global productivity* (eds J. Roy, B. Saugier & H. A. Mooney), pp. 429–448. San Diego, CA: Academic Press.

- Davidson, E. A. & Janssens, I. A. 2006 Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature* 440, 165–173. (doi:10.1038/nature04514)
- Enquist, B. J. & Niklas, K. J. 2002 Global allocation rules for patterns of biomass partitioning in seed plants. *Science* 295, 1517–1520. (doi:10.1126/science.1066360)
- Friend, A. L., Scarascia-Mugnozza, G., Isebrands, J. G. & Heilman, P. E. 1991 Quantification of two-year-old hybrid poplar root systems: morphology, biomass and ¹⁴C distribution. *Tree Physiol.* 8, 108–119.
- Geider, R. *et al.* 2001 Primary productivity of planet earth: biological determinants and physical constraints in terrestrial and aquatic habitats. *Global Change Biol.* 7, 849–882. (doi:10.1046/j.1365-2486.2001.00448.x)
- Global Carbon Project 2006 State of the carbon cycle: an annual update of the global carbon budget. See http://lgmacweb.env.uea.ac.uk/lequere/co2/carbon_budget.htm.
- Grace, J. 2004 Understanding and managing the global carbon cycle. *J. Ecol.* **92**, 189–202. (doi:10.1111/j.0022-0477. 2004.00874.x)
- Grace, J., San José, J., Meir, P., Miranda, H. S. & Montes, R. A. 2006 Productivity and carbon fluxes of tropical savannas. *J. Biogeogr.* 33, 387–400. (doi:10.1111/j.1365-2699.2005.01448.x)
- Guo, L. B. & Gifford, R. M. 2002 Soil carbon stocks and land use change: a meta analysis. *Global Change Biol.* 8, 345–360. (doi:10.1046/j.1354-1013.2002.00486.x)
- Houghton, R. A. 2003 Why are estimates of the terrestrial carbon balance so different? *Global Change Biol.* **9**, 500–509. (doi:10.1046/j.1365-2486.2003.00620.x)
- Jackson, R. B., Canadell, J., Ehleringer, J. R., Mooney, H. A., Sala, O. E. & Schulze, E. D. 1996 A global analysis of root distributions for terrestrial biomes. *Oecologia* **108**, 389–411. (doi:10.1007/BF00333714)
- Jackson, R. B., Banner, J. L., Jobbágy, E. G., Pockman, W. T. & Wall, D. H. 2002 Ecosystem carbon loss with woody plant invasion of grasslands. *Nature* 418, 623–626. (doi:10. 1038/nature00910)
- Jobbágy, E. G. & Jackson, R. B. 2000 The vertical distribution of soil organic carbon and its relation to climate and vegetation. *Ecol. Appl.* **10**, 423–436. (doi:10.1890/1051-0761(2000)010[0423:TVDOSO]2.0.CO;2)
- Körner, C., Asshoff, R., Bignucolo, O., Hättenschwiler, S., Keel, S. G., Peláez-Riedl, S., Pepin, S., Siegwolf, R. T. W. & Zotz, G. 2005 Carbon flux and growth in mature deciduous forest trees exposed to elevated CO₂. *Science* **309**, 1360–1362. (doi:10.1126/science.1113977)
- Le Goff, N. & Ottorini, J.-M. 2001 Root biomass and biomass increment in a beech (*Fagus sylvatica* L) stand in North-East France. *Ann. For. Sci.* 57, 1–13. (doi:10.1051/ forest:2001104)
- Mokany, K., Raison, R. J. & Prokushkin, A. S. 2006 Critical analysis of root: shoot ratios in terrestrial biomes. *Global Change Biol.* 12, 84–96. (doi:10.1111/j.1365-2486.2005. 001043.x)
- Murty, D., Kirschbaum, M. U. F., McMurtrie, R. E. & McGilvray, H. 2002 Does conversion of forest to agricultural land change soil carbon and nitrogen? A review of the literature. *Global Change Biol.* 8, 105–123. (doi:10. 1046/j.1354-1013.2001.00459.x)
- Norby, R. J. *et al.* 2005 Forest response to elevated CO₂ is conserved across a broad range of productivity. *Proc. Natl Acad. Sci. USA* **102**, 18 052–18 056. (doi:10.1073/pnas. 0509478102)
- Ouattara, B., Ouattara, K., Serpantié, G., Mando, A., Sédogo, M. P. & Bationo, A. 2006 Intensity cultivation induced effects on soil organic carbon dynamic in the western cotton area of Burkina Faso. *Nutr. Cycling Agroecosyst.* 76, 331–339. (doi:10.1007/s10705-006-9023-0)

- Poorter, H. & Nagel, O. 2000 The role of biomass allocation in the growth response of plants to different levels of light, CO₂, nutrients and water: a quantitative review. *Aust. J. Plant Physiol.* 27, 595–607.
- Prentice, I. C. *et al.* 2001 The carbon cycle and atmospheric carbon dioxide. In *Climate change 2001: the scientific basis*, (eds J. T. Houghton, Y. Ding, D. J. Griggs, M. Noguer, P. J. Van der Linden, X. Dai, K. Maskell & C. A. Johnson). Third assessment report of the Intergovernmental Panel on Climate Change, pp. 183–238. Cambridge, UK: Cambridge University Press.
- Robinson, D. 2004 Scaling the depths: belowground allocation in plants, forests and biomes. *Funct. Ecol.* **18**, 290–295. (doi:10.1111/j.0269-8463.2004.00849.x)
- Royal Society 2001 *The role of land carbon sinks in mitigating global climate change*. London, UK: The Royal Society. See www.royalsoc.ac.uk/displaypagedoc.asp?id=11505.
- Saugier, B., Roy, J. & Mooney, H. A. 2001 Estimations of global terrestrial productivity: converging toward a single number. In *Terrestrial global productivity* (eds J. Roy, B. Saugier & H. A. Mooney), pp. 543–557. San Diego, CA: Academic Press.
- Schipper, L. A., Baisden, W. A., Parfitt, R. L., Ross, C., Claydon, J. J. & Arnold, G. 2007 Large losses of soil C and

N from soil profiles under pasture in New Zealand during the past 20 years. *Global Change Biol.* **13**, 1138–1144. (doi:10.1111/j.1365-2486.2007.01366.x)

- Sleutel, S., De Neve, S. & Hofman, G. 2003 Estimates of carbon stock changes in Belgian cropland. *Soil Use Manage*. 19, 166–171. (doi:10.1079/SUM2003187)
- Subedi, K. D., Ma, B. L. & Liang, B. C. 2006 New method to estimate root biomass in soil through root-derived carbon. *Soil Biol. Biochem.* 38, 2212–2218. (doi:10.1016/j.soilbio. 2006.01.027)
- Taylor, J. A. & Lloyd, J. 1992 Sources and sinks of atmospheric CO₂. Aust. J. Bot. 40, 407–418. (doi:10.1071/BT9920407)
- Thompson, C. C., McGuire, A. D., Clein, J. S., Chapin III, F. S. & Beringer, J. 2006 Net carbon exchange across the arctic tundra-boreal forest transition in Alaska 1981–2000. *Mitig. Adapt. Strat. Global Change* 11, 805–827. (doi:10. 1007/s11027-005-9016-3)
- West, G. B., Brown, J. H. & Enquist, B. J. 1997 A general model for the origin of allometric scaling laws in biology. *Science* 278, 122–126. (doi:10.1126/science.276.5309.122)
- Zhou, G., Liu, S., Li, Z., Zhang, D., Tang, X., Zhou, C., Yan, J. & Mo, J. 2006 Old-growth forests can accumulate carbon in soils. *Science* **314**, 1417. (doi:10.1126/science.1130168)