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Carbon cycling and storage in world forests: biome patterns related to forest age

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Abstract

Forest age, which is affected by stand-replacing ecosystem disturbances (such as forest fires, harvesting, or insects), plays a distinguishing role in determining the distribution of carbon (C) pools and fluxes in different forested ecosystems. In this synthesis, net primary productivity (NPP), net ecosystem productivity (NEP), and five pools of C (living biomass, coarse woody debris, organic soil horizons, soil, and total ecosystem) are summarized by age class for tropical, temperate, and boreal forest biomes. Estimates of variability in NPP, NEP, and C pools are provided for each biome-age class combination and the sources of variability are discussed. Aggregated biome-level estimates of NPP and NEP were higher in intermediate-aged forests (e.g., 30–120 years), while older forests (e.g., $>$120 years) were generally less productive. The mean NEP in the youngest forests (0–10 years) was negative (source to the atmosphere) in both boreal and temperate biomes ($-$0.1 and –1.9 Mg C ha^{-1} yr^{-1}, respectively). Forest age is a highly significant source of variability in NEP at the biome scale; for example, mean temperate forest NEP was $-$1.9, 4.5, 2.4, 1.9 and 1.7 Mg C ha^{-1} yr^{-1} across five age classes (0–10, 11–30, 31–70, 71–120, 121–200 years, respectively). In general, median NPP and NEP are strongly correlated ($R^2 = 0.83$) across all biomes and age classes, with the exception of the youngest temperate forests. Using the information gained from calculating the summary statistics for NPP and NEP, we calculated heterotrophic soil respiration (R_h) for each age class in each biome. The mean R_h was high in the youngest temperate age class (9.7 Mg C ha^{-1} yr^{-1}) and declined with age, implying that forest ecosystem respiration peaks when forests are young, not old. With notable exceptions, carbon pool sizes increased with age in all biomes, including soil C. Age trends in C cycling and storage are very apparent in all three biomes and it is clear that a better understanding of how forest age and disturbance history interact will greatly improve our fundamental knowledge of the terrestrial C cycle.

Keywords: carbon cycling, climate change, fluxes, forest succession, global change, pools, synthesis

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Introduction

Globally, forests store vast pools of carbon (C) and even small shifts in the balance between photosynthesis and ecosystem respiration can result in a large change in the uptake or emission of carbon dioxide (CO_2) from forests to the atmosphere. Tropical, temperate, and boreal forests cover about 4.1 billion hectares of the earth's land surface, with forest ecosystems containing up to 80% of all aboveground terrestrial carbon (C) and $\sim$ 40% of all belowground terrestrial C (Dixon, 1994). Rates of both plant production and decomposition are related to latitudinal climatic gradients spanning the poles to the equator (Reich & Bolstad, 2001). However, the net C accumulation by an ecosystem over the decadal time frame depends more heavily on time since disturbance than on climate (Chapin *et al*., 2002). Large quantities of C stored in forest ecosystems for decades to centuries can be released to the atmosphere over short time steps following disturbance (Schulze *et al*., 2000; Page *et al*., 2002; Körner, 2003). Therefore, net C

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accumulation by forest ecosystems depends fundamentally on forest age (i.e. time since disturbance) and natural disturbance regimes, and land-use practices play a key role in regulating C cycling and storage (Houghton, 2001). The objectives of this mini-review were: (1) to synthesize C pools and fluxes by age class for the boreal, temperate, and tropical forest biomes; and (2) to empirically model biome changes in pools and fluxes over time in order to better understand the overall role of disturbance in the regulation of global forest C cycling and storage.

Rates of forest net primary productivity (NPP; gross photosynthesis minus plant respiration) and net ecosystem productivity (NEP; gross photosynthesis minus ecosystem respiration) change over the course of stand development. Younger forests are inherently more productive than older forests (Ryan *et al*., 1997) and models clearly predict that successional changes in NPP influence rates of NEP through time (Thornton *et al*., 2002). The ideal approach to understanding age-dependent trends in NEP is the simultaneous study of a carefully selected age sequence of stands, the so-called chronosequence approach. However, at the biome level, this approach is inevitably limited by the cost of establishing the many replicate chronosequences necessary to understand biome variability and by the elapsed sampling time needed to sort out disturbance-related trends in NEP from interannual variability in NEP caused by short-term climatic variability.

Disturbance also has a large impact on ecosystem C storage. Beginning with the succession of vegetation following disturbance, forest ecosystems can accrue C in four major pools: vegetation, coarse woody debris (CWD), organic soil horizons, and soil. The four pools of C in forest ecosystems are rarely discrete, individual pools are sometimes absent (e.g. organic soil horizons, CWD), and intraecosystem transfers among pools occur on a variety of time steps as forests mature. Periods of C accrual following disturbance typically range from decades to millennia and depend greatly on the growth rate (NPP) of the dominant trees and the frequency and intensity of natural or human-regulated disturbance regimes. Many trees have long average life expectancies (>100 years) and most wood and many leaves/needles/small roots are naturally resistant to decay. Thus, pools of total ecosystem C in mature forests can be impressive, routinely ranging from 100–200 $\mathrm{Mg\,C\,ha^{-1}}$, and sometimes exceeding $500\,\mathrm{Mg\,C\,ha^{-1}}$ (Janisch & Harmon, 2002). Because vast quantities of C are stored in forests over long periods of time, the global management of forest C reserves has become quite controversial as nations and multinational corporations struggle to balance their internal economic and social agendas against the realization that combustion of fossil fuels and land-use practices are altering the Earth's climate system (Schulze *et al*., 2002).

Our underlying hypothesis is that disturbance (time) trends are so fundamental in regulating NPP, NEP, and C storage that they will be apparent at the biome level in spite of the tremendous variability in C pools and fluxes at this scale. In other words, the modeled age trends apparent across an individual chronosequence (Thornton *et al*., 2002) should be apparent at the biome scale where sufficient data are available to model biome age trends. We also discuss the pitfalls of our synthesis and emphasize statistical variability in C pools and fluxes. Most biome-level reviews of forest C cycling and storage produce estimates averaged across age classes (but see Schulze *et al*., 1999) and many lack statistical estimates of variability and information on one or more storage pools, typically CWD and soil C; thus, it has been difficult to appreciate the overall effect of disturbance (age) on biome pools and fluxes of C. By synthesizing global information on forest NPP and NEP, we were able to calculate age trends in heterotrophic soil respiration (R_h) for each biome.

Methods

Database compilation

Our database includes information pertaining to carbon pools (C in the total ecosystem, living biomass, CWD, organic soil horizons, and soil) and carbon fluxes (NPP and NEP) for the boreal, temperate, and tropical biomes (Appendix A). It includes deciduous, coniferous, and evergreen species encompassing a broad range of stand ages and geographic locations. We deliberately included both managed and unmanaged forests as well as studies that incorporated varying methodologies in order to acquire the broadest possible array of data. The entire database is comprised of approximately 1200 entries, taken from 120 references, 15 of which are chronosequence studies. The primary decisive factor for including data was availability in the peer-reviewed, open literature, and sufficient documentation of the field measurements as well as the age and location of the stand under consideration. Review papers that followed these same guidelines are also included (e.g., Harmon *et al*., 1986; Gower *et al*., 1994; Clark *et al*., 2001; Gower *et al*., 2001; Law *et al*., 2002). Those papers that estimated the above parameters based primarily on models were excluded. None of the data reported come from unpublished sources. The data were summarized as reported and no assumptions or corrections were made to the original data. If more than one method was applied to estimate a given pool or flux in a particular study, we used the estimate(s) that the authors deemed more accurate. We converted all the data to standard units, $Mg\,C\,ha^{-1}$ (pools) or $Mg\,C\,ha^{-1}\,yr^{-1}$ (fluxes), and when necessary, applied a conversion factor of 0.5 to estimate the amount of carbon from a given oven-dry biomass.

The soil C database reports measurements made to different cumulative depths, including both organic and mineral soils. No attempt was made to correct soil C for the depth of measurement, although we recognize that total soil C increases with depth (Jobbagy & Jackson, 2000). However, we do report the depth(s) to which soil samples were collected in Appendix A. We chose to synthesize organic layer soil horizon data separately from the underlying soil horizons because there is a rich literature on C content in the organic soil horizons ('forest floor'), and these measurements are often independent of mineral soil horizon C measurements (i.e. the 'forest floor' C content is often reported independently without subsequent reports of the C content of the underlying soil horizons). We tabulated organic layer soil horizon pool sizes when these layers were explicitly identified in the literature and we made no attempt to reinterpret whether or not the organic soil horizons were properly identified according to standard soil survey procedures, which are explained in Soil Taxonomy (Soil Survey Staff, 1975).

The total ecosystem, living biomass, and NPP data were restricted to those studies that included actual measurement of both above- and belowground components, and only NPP data reported on a per unit area basis were utilized. Restricting data in this way should minimize the effects of changes in stand management and self-thinning on estimates of NPP. The data pertaining to NEP primarily include values obtained via micrometerological techniques (e.g., eddy covariance). Three studies in the database used biometric methods to calculate NEP, and two of these were chronosequence studies. We attempted to perform a thorough review of the literature, but understand that valuable references may have been unintentionally omitted. We also recognize that our results depend fundamentally on the number of observations and the literature included in the database.

Statistical analyses

The deciduous, coniferous, and evergreen species for each biome were pooled to attain sufficient data to examine trends over time. The data were then divided into five age classes to (1) represent key developmental periods over the course of forest succession, and (2) ensure that each age class would generally contain enough data to perform meaningful statistical analyses. As such, the age classes for the boreal forest were slightly different from those for the temperate and tropical forests to take into account the slower growing nature of the boreal trees. For example, those data in the youngest age class for boreal forests range from 0 to 30 years, while those in the temperate and tropical forest range from 0 to 10 years.

For all the carbon pools and fluxes, summary statistics by age class and for all age classes combined were computed and Duncan's multiple range test was performed using PROC ANOVA of the SAS software (SAS Institute, 1990,version 6.0) to check for significant differences in the mean values of NEP and NPP across age classes for a given biome. Empirical nonlinear functions were then fit to the median values of the carbon flux and carbon pool data by age groups (excluding those with two or fewer observations) using the iterative Gauss–Newton method with specified ranges of starting values in PROC NLIN of the SAS software (SAS Institute, version 6.0). In each case, several different models were tested and compared for fit using *F*-tests (Rice, 1995). Plots of the fitted values vs. the residuals were visually examined for heteroscedacity to aid in validating the models. The functions were deliberately not fitted to the mean values of the carbon pool and flux data because of outliers in many of the age classes. Details of the precise models implemented are presented in Table 1.

When we examined the relationship between NEP and NPP, we removed all biometric estimates of NEP from the database in order to create NPP and NEP data sets that were independent in terms of how measurements were taken. Consequently, for this analysis, all NPP data were developed from biometric ground measurements through time, while the subset of NEP data all comes from published eddy flux measurements.

Measurement of heterotrophic soil respiration (R_h) at the ecosystem level has been problematic for many years (Hanson *et al.*, 2000). Nevertheless, because we developed independent average measurements of NPP and NEP for different age classes at the biome level, we were able to calculate average R_h for each age class in each biome as

$$Rh_{age,\,biome} = NPP_{age,\,biome} - NEP_{age,\,biome}. \qquad (1)$$

Results

Carbon fluxes

NPP. The mean boreal forest NPP across all age classes was 2.8 ($\pm$ 1.6) $Mg\,C\,ha^{-1}\,yr^{-1}$ and increased from 7.1 ($\pm$ 3.5) in temperate forests to 8.3 ($\pm$ 5.2) in tropical forests. NPP peaked at intermediate ages in boreal and

Table 1 Parameters, sum of squared errors, and *P*-values from curves fitted to the medians of components of the forest carbon budgets across five age classes

C budget component	Biome	Function*	*a*	*b*	*c*	SSE†	*P*-value
Living biomass	Boreal‡	Sigm	15134	9306	–	8.8	<0.05
	Temperate	Hyp	206.0	131.0	–	108.3	<0.05
	Tropical	Pow	11.69	0.39	–	88.0	<0.05
	Boreal‡	Pow	4.28	0.089	–	0.2	<0.05
CWD	Temperate	Mix	161.5	0.094	2.55	98.3	0.08
	Tropical	Pow	102.3	−0.628	–	40.4	<0.05
Organic soil horizons	Boreal	Logn	21.91	0.80	177.4	25.7	<0.05
	Temperate	Sigm	8856	3170	–	92.9	<0.05
	Tropical	Logn	28.45	0.21	183.9	69.2	0.13
	Boreal‡	Mix	−219.4	0.201	109.2	427.5	0.20
Soil	Temperate	Mix	178.6	0.092	52.29	446.7	0.30
	Tropical‡	Hyp	111.0	11.05	–	554.6	<0.05
	Boreal	Hyp	119.2	8.1	–	1677.9	<0.05
Total ecosystem	Temperate	Sigm	427786	212025	–	14280	<0.05
	Tropical	Pow	53.7	0.26	–	446.2	<0.05
NPP	Boreal	Logn	2.8919	0.7163	66.4462	0.2	<0.05
	Temperate	Logn	8.0826	0.9850	27.9749	1.4	<0.05
	Tropical§	–	–	–	–	–	–
NEP	Boreal	Logn	2.74376	0.1100	47.6843	0.1	0.13
	Temperate¶	Logn	6.7021	0.1617	38.4328	7.5	0.20
	Tropical§		–	–	–	–	–
NEP vs. NPP	All biomes	Linear	−0.90	0.57	–	0.70	<0.001

*Explanation of functions used: A. Lognormal, 'logn', $Y = a \times \exp\{-0.5[\ln(A/c)/b]^2\}$; B. Sigmoidal, 'sigm', $Y = (a \times A)/(A^2 + b)$; C. Mixed, 'mixed', $Y = (a/A) + (b \times A) + c$; D. Power, 'pow', $Y = a \times A^b$; E. Hyperbolic, 'hyp', $Y = (a \times A)/(b + A)$, where *a*, *b*, and *c* are estimated parameters, *A* is the age of the ecosystem, and *Y* is the predicted pool or flux.

†SSE, sum of squared errors. R^2 for all models was 0.9 or above, where R^2 for the nonlinear models is defined as (1−SSE/CSS), where SSE is the variance of the full model, and CSS (corrected sum of squares) is the variance of the mean model.

‡These models do not include data from either age class '*D*' or '*E*' because of the low number of observations.

§NPP and NEP for the tropical forest were not modeled because of lack of data for most age classes.

¶Constants were subtracted and added to the lognormal function when fitting this model to eliminate the constraints imposed on the tails of the lognormal curve. More precise methods of parameterizing the NEP distribution curve can be found in Euskirchen *et al*. (2002). CWD, coarse woody debris; NPP, net primary productivity; NEP, net ecosystem productivity.

temperate forests, but there were insufficient data to determine whether this trend also occurs in tropical forests (Fig. 1). In the boreal forest, peak NPP occurred in the 71–120 years age class, while NPP peaked in the 11–30 years age class in temperate forests. Across all age classes and biomes, NPP was variable (Fig. 1), with coefficients of variation ranging from a low of 19% (boreal forests 120–200 years old) to a high of 117% (boreal forests 0–30 years old).

NEP. The mean NEP across all age classes was 0.3 (±1.1) Mg C ha^{-1} yr^{-1} in boreal forests, 1.7 (±3.2) in temperate forests, and 3.6 (±2.9) in tropical forests. NEP also peaked at intermediate ages in boreal and temperate forests and the pattern of NEP through stand development mirrored that for NPP (Fig. 1). The youngest age class in boreal forests exhibited mean rates of NEP that were negative (source to the atmosphere; −0.1 Mg C ha^{-1} yr^{-1}). The 120–200 years age class in boreal forests also had a negative rate of NEP (−0.9 Mg C ha^{-1} yr^{-1}), primarily because of a 150-year-old spruce stand in European Russia, which acted as a strong carbon source for 3 years in a row (Milyukova *et al*., 2002). There were insufficient data from tropical forests to study the trends in NEP through time and only one age class is reported (Fig. 1). In general, rates of NEP across all age classes and biomes were much more variable than rates of NPP (Fig. 1). Coefficients of variation ranged from an overall low of 61% in temperate forests 11–30 years old to an overall high of −1087% in temperate forests 0–11 years old. Potential explanations for this variability in NEP are discussed below. Regardless of variability, two important points are clear (Fig. 1): (1) time trends in

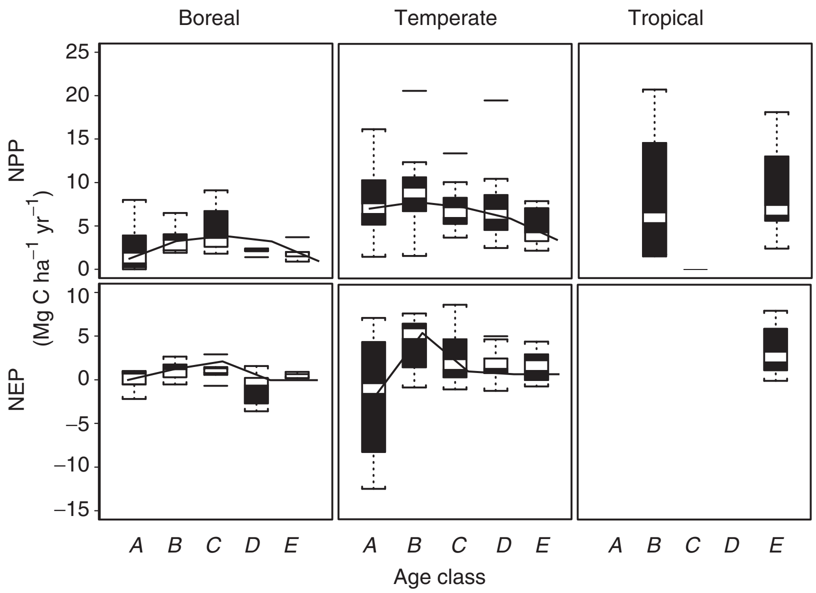

Fig. 1 Variation in net primary productivity (NPP) and net ecosystem productivity (NEP) ($Mg\,C\,ha^{-1}\,yr^{-1}$) over time across boreal, temperate, and tropical forest biomes. Lines are fitted through the medians (horizontal white lines in the interior of the boxplots) of each age class with associated functions and parameter estimates detailed in Table 1. The height of the boxes is equal to the interquartile distance with the dotted lines from the top and bottom extending to the extreme values of the data, or a distance of 1.5 × interquartile distance, whichever is less. The single horizontal lines outside the boxes are the outliers. Age classes, in years, are as follows: for the boreal biome, *A* = 0–30; *B* = 31–70, *C* = 71–120; *D* = 121–200; *E* = >200, and for the temperate and tropical biomes, *A* = 0–10; *B* = 11–30; *C* = 31–70; *D* = 71–120; *E* = 121–200.

boreal and temperate NEP follow those of NPP, with a peak at intermediate ages; and (2) boreal forests, regardless of age, hover about zero NEP. More studies are needed in tropical forests, especially young and middle-aged tropical forests, to determine whether forests in all three biomes follow the same general developmental trends through time.

Relationship between NPP and NEP. In general, median NPP and NEP were strongly correlated across all age classes and biomes, with one notable exception (Fig. 2). The highly significant linear relationship between NPP and NEP depicted in Fig. 2 depends on the omission of one outlier, the median of NPP plotted against the median of NEP for the youngest age class of the temperate forests. In this case, NPP is around $7\,Mg\,C\,ha^{-1}\,yr^{-1}$, but NEP is negative ($-1\,Mg\,C\,ha^{-1}\,yr^{-1}$) due in large part to high rates of woody debris decomposition following harvest in Florida slash pine plantations (Gholz & Fisher, 1982; Thornton *et al*., 2002). This observation agrees with the overall high variability in NEP for the youngest age class of the temperate forests (Fig. 1), which we believe is because of the wide range of management activities associated with timber harvest and site preparation, as discussed below.

Heterotrophic soil respiration (R_h). Average rates of R_h (Eqn (1)) range from 1.5 to $3.5\,Mg\,C\,ha^{-1}\,yr^{-1}$ in boreal forests (Fig. 3). In temperate forests, rates decline from $9.7\,Mg\,C\,ha^{-1}\,yr^{-1}$ in the youngest age class to $2.8\,Mg\,C\,ha^{-1}\,yr^{-1}$ in the oldest forests (Fig. 3). Tropical forests >120 years old exhibit rates of R_h that average $4.6\,Mg\,C\,ha^{-1}\,yr^{-1}$ (Fig. 3), an amount that is 164% greater than the same age class of temperate forests.

Carbon pool sizes

Living biomass. Living biomass C increased with age across boreal, temperate, and tropical forests, as would be expected (Fig. 4). High variability in temperate biomass C in the oldest age class (Fig. 4) results from the inclusion of several studies from the Pacific Northwestern Region of North America. Living forest biomass C reaches its peak globally in this region and many old-growth stands are dominated by massive trees reaching ages exceeding 400 years (Harmon *et al*., 1990). With the exception of this age class (temperate – old), it is interesting how predictable changes in living tree biomass are across the age class – biome categories (Table 1, Fig. 4). There were no studies in the database for tropical forests 71–120 years old.

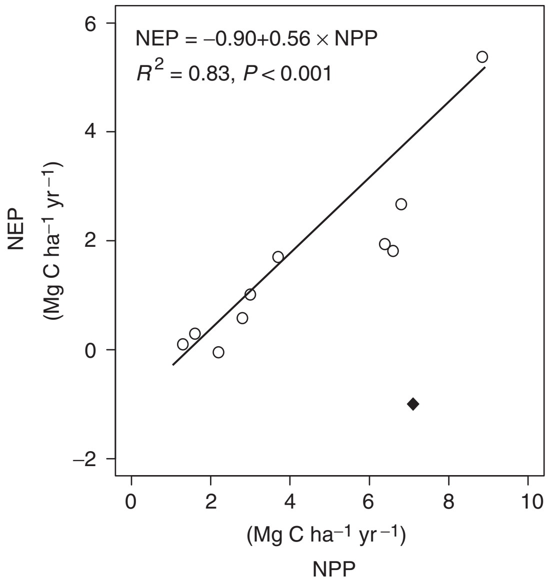

Fig. 2 Relationship between the median values of net ecosystem productivity (NEP) and net primary productivity (NPP) (Mg C ha^{-1} yr^{-1}), with the line representing the fitted linear least-squares relationship. The solid black point represents the young age class for the temperate forests, and was not included in the model. The NEP data represent only those data obtained via micrometeorological techniques (e.g., as measured by the eddy covariance method) so that the methods of collecting the NPP and NEP data are independent. Detailed parameter estimates are given in Table 1. Age classes, in years, are as follows: for the boreal biome, $A = 0$–30; $B = 31$–70, $C = 71$–120; $D = 121$–200; $E = >200$, and for the temperate and tropical biomes, $A = 0$–10; $B = 11$–30; $C = 31$–70; $D = 71$–120; $E = 121$–200.

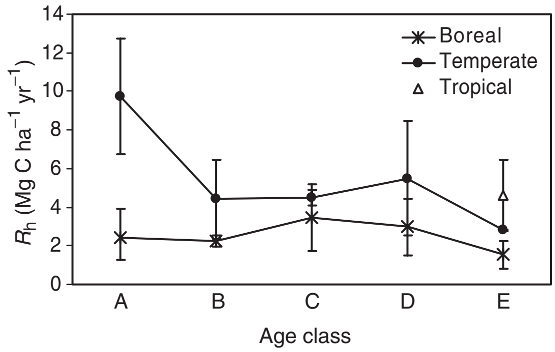

Fig. 3 R_h (Mg C ha^{-1} yr^{-1}) calculated from average net primary productivity (NPP) subtracted from average net ecosystem productivity (NEP) across all age classes. The error bars are calculated as $R_h = (\text{NPP} \pm \sigma\text{NPP}) - (\text{NEP} \pm \sigma\text{NEP})$. NEP data were unavailable for age classes A–D in the tropical biome. Age classes, in years, are as follows: for the boreal biome, $A = 0$–30; $B = 31$–70, $C = 71$–120; $D = 121$–200; $E = >200$, and for the temperate and tropical biomes, $A = 0$–10; $B = 11$–30; $C = 31$–70; $D = 71$–120; $E = >121$.

Organic soil horizons. Mean and median organic soil horizon pool sizes increased with age in boreal, temperate and tropical forests, reaching a peak in the 71 or older age classes (Fig. 4). The standard deviations within an age class (data not shown) and the box plots in Fig. 4 clearly demonstrate that organic soil horizon pool sizes are highly variable across all three biomes.

Soil. The overall mean C content of soil, excluding the surface organic soil horizons ('forest floor'), across all age classes, was 151.6 (± 175.2), 82.3 (± 39.5), and 84.2 (± 49.6) Mg C ha^{-1} for the boreal, temperate, and tropical forests, respectively. The soil C pools were highly variable, particularly within the boreal biome. Across all biomes, there was an overall trend for soil pool sizes to increase through time (Fig. 4).

CWD. The pool size of CWD across all age classes was relatively small in boreal forests (mean 7.9 ± 7.5 Mg C ha^{-1}) and accounted for an average of about 5% of the total ecosystem C. The stage of stand development appears, on the average, to have little overall influence on the pool size of CWD in boreal forests (Fig. 4). The mean pool size of CWD averaged across all temperate age classes was 42.0 (± 45.8) Mg C ha^{-1}, or about 18% of the total ecosystem C. Pools of CWD were much more variable in temperate forests, especially in the youngest and oldest age classes (Fig. 4). In the tropics, the mean CWD pool size across all age classes was 17.5 (± 15.9) Mg C ha^{-1}, or roughly 10% of the total ecosystem C. The youngest age class was the most variable pool of CWD in the tropics (Fig. 4).

Total ecosystem carbon. Total ecosystem C increased with age in the boreal forest (Fig. 4) and C peaked in the 120–200 years age class, following the same pattern described for living biomass. The mean total ecosystem C across all boreal age classes was 143 (± 93) Mg C ha^{-1}. Older boreal age classes were more variable than younger age classes (Fig. 4). Total ecosystem C also increased with age in temperate forests (Fig. 4); the mean total ecosystem C across all temperate age classes was 239 (± 101) Mg C ha^{-1}). Variability in total temperate ecosystem C was relatively low through the first four age classes, but was very high in the oldest age class (Fig. 4), once again presumably because of the inclusion of several studies from the Pacific Northwestern Region of North America, where pools of living biomass and CWD are high in old-growth forests (Janisch & Harmon, 2002). The mean tropical total ecosystem C was 174 (± 54) Mg C ha^{-1} and total ecosystem C increased

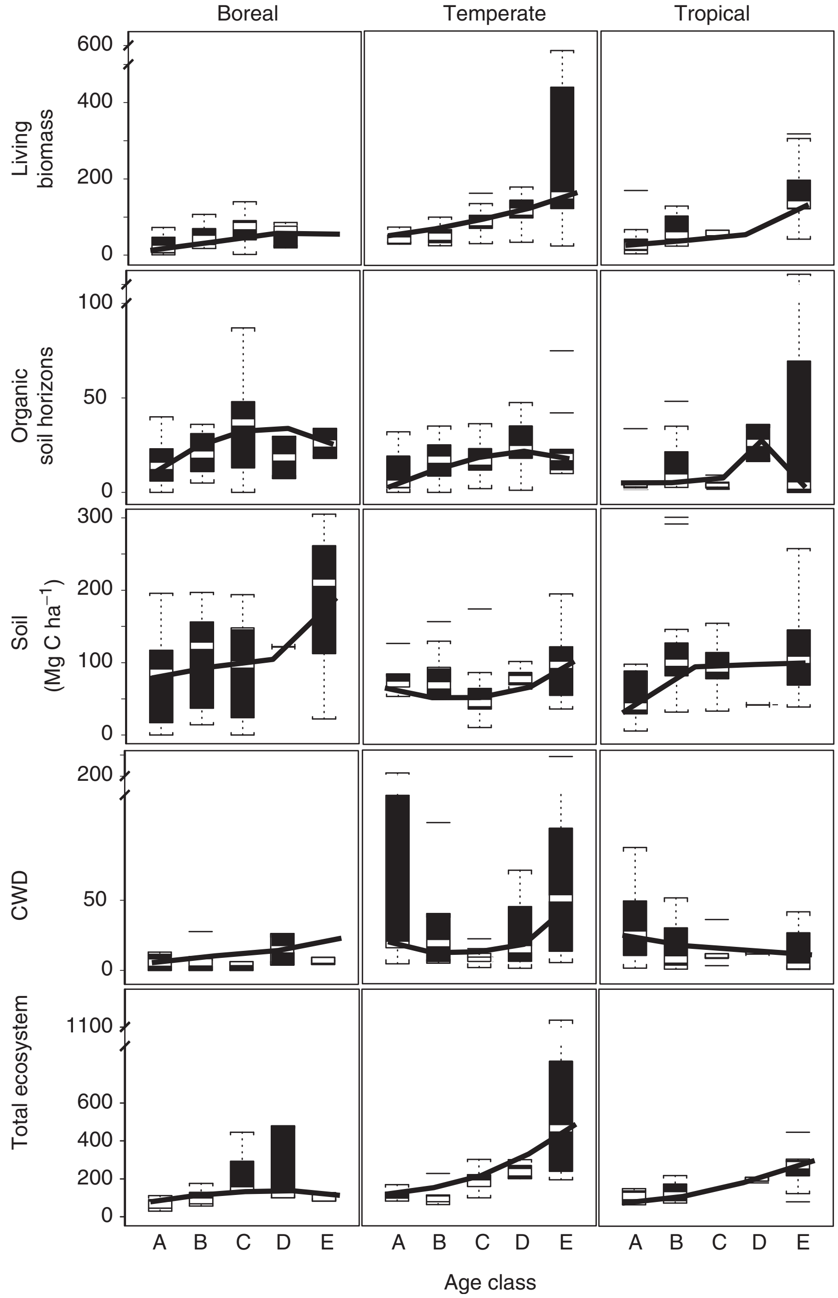

Fig. 4 Variation in the pools (Mg C ha^{-1}) of living biomass, organic soil horizons, soil, coarse woody debris (CWD), and total ecosystem carbon over time across boreal, temperate, and tropical forest biomes. Lines are fitted through the medians (horizontal lines in the interior of the boxplots) of each age class with associated functions and parameter estimates detailed in Table 1. The height of the boxes is equal to the interquartile distance with the dotted lines from the top and bottom extending to the extreme values of the data, or a distance of 1.5 × interquartile distance, whichever is less. The single horizontal lines outside the boxes are the outliers. Age classes, in years, are as follows: for the boreal biome, $A = 0–30$; $B = 31–70$, $C = 71–120$; $D = 121–200$; $E = >200$, and for the temperate and tropical biomes, $A = 0–10$; $B = 11–30$; $C = 31–70$; $D = 71–120$; $E = 121–200$.

with age class (Fig. 4). Variability in the total ecosystem C was relatively low in tropical forests compared with temperate and boreal forests, especially when comparing the older age classes among the biomes (Fig. 4).

Discussion

Critical appraisal of the data and its limitations

There are numerous problems associated with binning data collected by a multitude of investigators using varying methodologies. One clear example is the data on soil organic horizons and soil. The soil organic horizons ('forest floor') are technically a part of the soil profile, and the 'O layer' is typically subdivided into the fibric (Oi), hemic (Oe), and/or sapric (Oa) layers in the USA (Soil Survey Staff, 1975). However, the 'forest floor' has been variously defined and the distinction between the forest floor and soil is artificial. Some of the variability in C pools in the organic soil horizons and soil that we report is undoubtedly related to how these layers are defined and reported in the literature. The distinction in the literature between the forest floor and soil is particularly problematic for imperfectly and poorly drained soils. Furthermore, the soil C database we compiled reports measurements made to different cumulative depths, including both organic and mineral soils. Obviously, some of the variability in the soil organic horizon and soil C stocks we report is simply because of the way in which we summarized the data and the different methods of sampling and reporting soil C in the literature.

The three biomes also contain different proportions of managed and unmanaged forests. In general, the temperate forests are more intensively managed than the tropical and boreal biomes at this time in history. Controlling species composition, genetic improvement of growing stock, fertilization, weed control, and irrigation are all examples of cultural practices applied ever more frequently in forest plantation culture. Intensively cultured plantation forests with high rates of NPP can accumulate C stocks in living biomass in just a few years, which are typical of mature naturally regenerated forests in the region (Madeira *et al*., 2002).

Forests in different regions within a biome are also influenced by inherently different rates of NPP related to many site factors such as climate, soil, and drainage. The life-history attributes of different native and exotic species can also play an important role in regulating C storage in living biomass (Jackson *et al*., 2000). Binning data across different sites by species combinations add to the inherent variability within the database and should mask age-related patterns in C cycling and storage.

Can we meaningfully interpret the influence of disturbance (age) on biome-scale C cycling and storage using such a wide array of information? Our synthesis and interpretation certainly have limitations; nonetheless, the patterns related to forest age discussed below transcend all the variability inherent in our database. The fact that age-related patterns in C cycling and storage are very apparent, in spite of the caveats we discuss above, suggest that we need to pay more attention to the role of disturbance in regulating C cycling and storage. For example, many of the current sites in the networks measuring NEP tend to be located in undisturbed, mature, 'representative' forests, but, as we discuss below, these sites, on the average, have low rates of NEP compared with younger stands. Obviously, as new data from existing studies become available we will be able to refine our understanding of how disturbance regulates C cycling and storage in forests located along edaphic and climatic gradients.

NPP

Our results demonstrate that the pattern of decline in forest productivity with age, apparent at the stand level (Ryan *et al*., 1997), can be seen in average rates of boreal and temperate NPP aggregated to the biome level (Fig. 1). Because we only used studies reporting both above- and belowground NPP data expressed on a per unit land area basis, these results should be robust in the face of different stand densities and management histories. There is some debate about how much more productive young forests are compared with older forests, centering on management history, stand density, and assumptions made in models of forest growth (Carey *et al*., 2001; Knohl *et al*., in press). Our analysis of NPP makes no assumptions whatsoever and the data cut across all types of temperate and boreal forests, including forests that are even-aged and those that are of mixed ages and species composition from virtually every habitat ever reported in the literature. Nonetheless, the pattern of decline in NPP with age is clear (Fig. 1), although the reasons for this are not fully apparent (Ryan *et al*., 1997).

NEP

Variability in NEP within boreal, temperate, and tropical forests is high (Fig. 1). Some of this variability is driven by the same set of factors that drive changes in photosynthesis (Gu *et al*., 2003) and plant respiration (Clark *et al*., 2003). However, much of the variability in NEP is related to changes in the factors that drive R_h (Goulden *et al*., 1998; Valentini *et al*., 2000). Heterotrophic soil respiration (R_h) is regulated by the enzymatic and metabolic activity of the soil foodweb. The factors limiting R_h are not the same as those that limit photosynthesis. The chemical composition of plant detritus is important in regulating the rate of soil organic matter decomposition (Cadish & Giller, 1997), as are soil temperature, soil moisture (including drainage class), and soil oxygen content.

Different soil environmental conditions, for example, the depth of thaw in permanently frozen boreal soils, can also change from year to year, making labile soil C available for decomposition in 1 year and not the next

(Goulden *et al*., 1998). Thus, NPP and NEP are not always coupled in time. However, in general, median NEP was strongly correlated to median NPP across all age classes and biomes (Fig. 2). This makes sense, because soil microbial metabolism is normally tightly linked to the availability of labile substrates coming primarily from leaf and fine root litter and root exudates (Zak & Pregitzer, 1998; Högberg *et al*., 2001). Ecosystem NEP can only be decoupled from NPP if the conditions regulating the availability of labile substrates or the environmental conditions limiting microbial enzymatic and metabolic activity somehow change. Our results suggest that, on the average, this occurs most routinely just following disturbance, when biome R_h is high and median and mean NEP are negative (source to the atmosphere; Fig. 3).

During the intermediate stages of stand development when NPP and NEP are highest (Fig. 1), variability in NEP is lower. Although it is not possible to separate these sources of variation explicitly given the information we currently have available, we can infer that the 390% cv for the young age class is due primarily to the time since disturbance, when decomposition rates are high at first and depend on the intensity and type of disturbance (Chapin *et al*., 2002; Thornton *et al*., 2002). As forests reorganize their internal biogeochemical cycles and mature (intermediate age classes), NPP and NEP are high (Fig. 1) and appear to be primarily responding to interannual climatic variation, favoring either increased photosynthesis or decreased respiration (Myneni *et al*., 1997; Schimel *et al*., 2000). On the whole, the greatest amount of variability in NEP over the course of succession appears to be attributable to time since disturbance rather than interannual variations in climate or long-term environmental trends (Chapin *et al*., 2002), underscoring the importance of land-use history and forest management practices in the regulation of global pools and fluxes of forest C.

Heterotrophic soil respiration (R_h)

Disturbance-induced increases in R_h early in succession appear to be very important in temperate forests, with mean rates of R_h at 9.7 Mg C ha^{-1} yr^{-1} in the 0–10-year age class (Fig. 3). Obviously, any forest management practice that reduces the pulse of R_h associated with disturbance will accelerate the development of positive NEP. We expect that tropical forests will exhibit a pattern of R_h through time similar to the pattern exhibited by temperate forests in Fig. 3, with a peak early in succession and a decline through time, but the data are insufficient to test this hypothesis at this time. Because NPP (Fig. 1) and R_h (Fig. 3) decline as forests age, total ecosystem respiration must also decline during the later stages of forest succession. If soil respiration is dominated by plant respiration and microbial respiration of labile C substrates (Zak & Pregitzer, 1998; Högberg *et al*., 2001), there is no reason to expect the oldest forests to exhibit the highest rates of ecosystem respiration as Odum (1969) originally hypothesized.

Carbon pool sizes

Living biomass. Living biomass C increased through time, peaking in the 71–120-year age class in boreal forests, but increasing steadily with age in temperate and tropical forests (Fig. 4). The older age classes contained two to 10 times as much living biomass C as the youngest age class. Boreal biomass C peaks at an earlier age compared with the temperate or tropical biomes, presumably because catastrophic wildfire is the predominant form of disturbance across the boreal landscape (Kasischke & Stocks, 2000), and because many poorly drained forests lose tree cover as moss biomass increases and soil temperature declines during the advanced stages of forest succession (Van Cleve & Viereck, 1981).

Organic soil horizons. In many forest soils, surface layers accumulate, which are rich in organic matter composed primarily of plant litter in various stages of decay. These 'forest floor' layers are believed to be highly active in forest C cycling, especially in response to disturbance (Covington, 1981; Yanai *et al*., 2003). At the biome level, it is clear that average forest floor C contents either remain relatively constant or increase with age, and median forest floor C reached a peak in all three biomes after about 70 years of stand development (Fig. 4). Yanai *et al*. (2003) review the reasons why the common assumption of increased forest floor decay following disturbance may not be valid in many instances.

Soil carbon. Carbon is stored in soil when it is unavailable for use by microorganisms. The formation of mineral soil C with a relatively long residence time (stable or passive soil C) is thought to be primarily controlled by three mechanisms: (1) chemical stabilization, (2) physical protection, and (3) biochemical stabilization (Six *et al*., 2002). All three of the soil C stabilization mechanisms co-vary across the landscape with changes in soil parent material and vegetation type. This is one reason why soil C pools are so variable within a given biome (Fig. 4). Other factors controlling variability in soil C are soil drainage, soil temperature, and variability in C inputs through time. Poorly drained and cold soils accrue significant C contents because lack of oxygen and low temperatures inhibit rates of decomposition. These two phenomena are much more frequent in boreal forests where pools of soil C are both high and highly variable because of the greater frequency of cold and saturated soils (Fig. 4; Gower *et al*., 1997; Harden *et al*., 1997; Chapin *et al*., 2002). Labile soil C also cycles back to the atmosphere on longer time steps in boreal forests compared with temperate and tropical forests (Trumbore, 2000), which means that a greater proportion of the total C pool in wet and cold boreal soils has not been stabilized by one of the three mechanisms discussed above. This soil C could be susceptible to further decomposition if the conditions that currently limit microbial respiration change. Interestingly, median soil C at the biome level increased with time (cumulative inputs) in all three biomes (Fig. 4), a finding contrary to the notion that soil C contents often vary little through time (Johnson & Curtis, 2001).

CWD. The factors regulating the decomposition of CWD are essentially the same as those that regulate R_h in the soil: detrital substrate quality, temperature, moisture, and oxygen content (Wang *et al*., 2002). Decomposition of CWD can directly influence how rapidly forests become sinks for C following disturbance (Thornton *et al*., 2002). Although temperature and moisture can change following disturbance and this can accelerate rates of decomposition (Amiro, 2001), changes in the environment probably play a minor role in regulating CWD pool size compared with disturbance history. We believe that the amount of residual CWD following disturbance and its size and incorporation into the mineral soil play a key role in defining the wide range of variability in pool sizes in the youngest age class of forests (Fig. 4). Consequently, this variability in the youngest temperate age class is probably because of differences in forest management activities.

In old forests, the main factor regulating a change in CWD pool size is the continued recruitment of new CWD into this pool, not changes in the environmental factors that drive decomposition during succession or following disturbance. When old forests are harvested, it is primarily the storage term (pool size) of CWD that is altered in subsequent years, not the rate of decomposition. In other words, the pool declines primarily because recruitment of new CWD has halted, not because rates of decomposition are greatly altered. This is true for the forest floor as well (Yanai *et al*., 2003). Eventually, recruitment of significant amounts of new CWD begins as stands age and pools of CWD recover. This process explains the bowl-shaped trend of CWD seen in the temperate forest data (Fig. 4). High levels of CWD following disturbance in the youngest age class and in old-growth forests are also a trend observed in other studies (Spies *et al*., 1988; Sturtevant *et al*., 1997; Janisch & Harmon, 2002). In boreal forests, CWD dynamics appear to be driven mostly by stand-replacing wildfires that reoccur on relatively short time steps (Kasischke & Stocks, 2000); thus, pool sizes never account for as great a proportion of total ecosystem C as in temperate forests.

Total ecosystem C. Total ecosystem C pool sizes were synthesized from sites where all four pools were directly measured and reported following the criteria outlined in the methods. In the literature, it is very common for one or more of the four pools to go unmeasured at any given study site. Data depicted for each of the four pools and the ecosystem totals are somewhat independent because the data come from a

Table 2 Two estimates of total ecosystem carbon ($Mg\,C\,ha^{-1}$) for boreal, temperate, and tropical forest biomes

	Boreal		Temperate		Tropical	
Age class	Literature	Additive	Literature	Additive	Literature	Additive
A	67 ± 28	161	121 ± 27	186	111 ± 30	125
B	98 ± 45	245	106 ± 49	169	131 ± 63	210
C	214 ± 155	171	189 ± 58	158	–	178
D	233 ± 214	210	240 ± 36	248	–	80
E	102 ± 23	–	537 ± 335	487	253 ± 107	328

'Literature' refers to averages (and one standard deviation) of independent published field studies of total ecosystem carbon where all four pools were actually measured at each field site and 'additive' is the summation of mean values for the living biomass, organic soil horizons, soil, and coarse woody debris pools derived from the data compiled in this study. The number of observations by age class and biome are listed in Table 1. There was insufficient data for age class *E* of the boreal forests to calculate an 'additive' value. Age classes, in years, for the boreal biome are: *A* = 0–30; *B* = 31–70, *C* = 71–120; *D* = 121–200; *E* = >200, and for the temperate and tropical biomes: *A* = 0–10; *B* = 11–30; *C* = 31–70; *D* = 71–120; *E* = 121–200.

variety of different studies, sites, and locations. One way to check the validity of total ecosystem C is to add the mean values for each of the four pools and compare these numbers with the totals actually measured. In general, totals developed by adding together the mean pool sizes compare quite well with the totals actually measured (Table 2). Exceptions include totals in the first two age classes of boreal forests and the first age class for the temperate forests (Table 2). For the boreal forests, this is caused by the fact that total ecosystem C was measured on a greater proportion of well-drained sites, while the mean soil C included a greater percentage of poorly drained sites, sites that accrue much higher levels of soil C than well-drained boreal forests (Gower *et al*., 1997). For young temperate forests (0–10-year age class), the measured and additive totals do not compare well because of the large pools of CWD in some temperate forests following harvest, which inflates the CWD mean in this age class ($74 \pm 88\,\mathrm{Mg\,C\,ha^{-1}}$). These three discrepancies also point out why we feel it is more appropriate to model biome changes in time based on median rather than mean pool size (Table 1, Fig. 4). However, in general, the measured and additive totals compare rather well (Table 2), with the exceptions noted.

Conclusions

Biome estimates of NPP and NEP peaked at intermediate ages and declined in the older age classes. NEP studies in mature forests are not necessarily good surrogates for young forests that are rapidly increasing their biomass and accruing C in CWD and soil pools.

Heterotrophic soil respiration (R_h) depends fundamentally upon disturbance intensity, with the greatest amount of R_h occurring directly following disturbance in the youngest age class. Both temperate and boreal forests in the youngest age class had negative mean rates of NEP (source to the atmosphere) because rates of R_h were high. Understanding the processes controlling R_h following disturbance is critical to understanding time trends in NEP.

Total ecosystem respiration is highest when forests are relatively young and ecosystem respiration declines during the later stages of succession.

Disturbance history and the age class distribution of forests within a biome are very important in controlling rates of C cycling and storage. Additional mechanistic studies of NEP along chronosequences and historical reconstructions of land-use change are critical to improving our fundamental understanding of the terrestrial C cycle.

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Appendix A

Pools and fluxes of selected components of the forest carbon cycle for boreal, temperate, and tropical forests (arranged alphabetically by reference within each grouping). Pools are in units of $Mg\,C\,ha^{-1}$, and fluxes are in $Mg\,C\,ha^{-1}\,yr^{-1}$. An asterisk (*) after the reference indicates that the data are from a chronosequence study. When different ecosystem types are reported within one reference, they are separated by commas. Mixed ecosystem types (e.g., several different types of dominant tree species in one ecosystem) are indicated by a dash between the various cover types. Positive NEP values indicate a C sink (see Table A1).

Table A1

Age (range)	Location(s)	Ecosystem type(s)	Latitude(s)	Biomass (range)	Reference
Living biomass					
Boreal coniferous					
160	Finland	*Picea abies*	63°N	109.0	Finér *et al*. (2003)
28–100	Finland, Russia (Kola Penn, Mordovskaya and Siberia)	*Pinus sylvestris*	54–68°N	1.85–140.0	Gower *et al*. (1994)
20–250	Canada (Saskatchewan and Manitoba), China, Finland, Russia (Siberia), Sweden, USA (Alaska)	*Larix gmelinii*, *Picea abies*, *Picea glauca*, *Picea mariana*, *Pinus banksiana*, *Pinus sylvestris*	50–65°N	0.8–118.7	Gower *et al*. (2001)
260	Russia (Siberia)	*Larix gmelinii*	64°N	19.5	Kajimoto *et al*. (1999)
200	Russia (Siberia)	*Pinus sylvestris*	60°N	76.0	Lloyd *et al*. (2002)
Boreal deciduous					
30–90	Canada (Saskatchewan and Manitoba), Finland, USA (Alaska)	*Alnus incana*, *Betula papyrifera*, *Betula pubescens*, *Populus tremuloides*	54–65°N	17.6–106.9	Gower *et al*. (2001)
5–20	USA (Alaska)	*Alnus incana*	64°N	8.0–37.0	Van Cleve *et al*. (1971)*
Temperate coniferous					
24	USA (Florida)	*Pinus elliottii*	29°N	82.7	Clark *et al*. (1999)
50	USA (New Mexico)	*Pseudotsuga menziesii*	35°N	169.0	Gower *et al*. (1992)
8–110	Canada (British Columbia), Japan (Orita and Osaku), Scotland (Morayshire), USA (Florida, North Carolina, Wisconsin and Wyoming)	*Pinus contorta*, *Pinus densiflora*, *Pinus elliottii*, *Pinus nigra*, *Pinus resinosa*, *Pinus taeda*	30–57°N	9.5–92.3	Gower *et al*. (1994)
90–350	USA (Arizona)	*Pinus edulis*, *Juniperus monosperma*	35°N	11.9–27.0	Grier *et al*. (1992)
10–114	USA (Rhode Island)	*Pinus strobus*		8.0–183	Hooker & Compton (2003)
9–316	USA (Oregon)	*Pinus ponderosa*	44°N	6.0–205.4	Law *et al*. (2003)*
13	USA (Wyoming)	*Pinus contorta*		0.33–5.6	Litton *et al*. (2003)
16–142	Germany (Bavaria)	*Picea abies*	50°N	35.5–180.4	Mund *et al*. (2002)*
150–700	USA (Oregon)	*Abies balsamea*, *Picea sitchensis*, *Pseudotsuga menziesii*, *Thuja heterophylla*, *Tsuga heterophylla*	44–47°N	120.2–628.1	Smithwick *et al*. (2002)
Temperate deciduous					
60–90	USA (Indiana, Massachusetts, Michigan, Tennessee, and Wisconsin)	*Acer*, *Populus*, *Quercus–Acer*	35–45°N	78.6–128.6	Curtis *et al*. (2002)
1–15	India (Himalaya)	*Dalbergia sissoo*, *Populus deltoides*	28–29°N	6.1–60.4	Lodhiyal & Lodhiyal (1997, 2003)*
Old growth	Canada (Ontario)	*Acer saccharum*	47°N	104.0–122.0	Morrison (1990)
8–66	USA (Wisconsin)	*Populus tremuloides*		16.5–74	Ruark & Bockheim (1988)*

Tropical evergreen broadleaf					
12	Puerto Rico	Secondary forest	18°N	23.1	Cuevas *et al*. (1991)
Undisturbed	Latin America	Equatorial forest, dry forest, moist forest, rain forest, seasonal forest, wet forest, woodland		42.0–200.0	Houghton *et al*. (1991)
8–50	Puerto Rico	*Swietenia macrophylla*, *Tabebuia heterophylla*	18°N	21.5–128.2	Lugo (1992)
Undisturbed	Amazonia, Brazil	Rain forest	2°S	281.0	Malhi *et al*. (1999)
Undisturbed	USA (Hawaii)	*Metrosideros polymorpha*		63.0–126.0	Schuur *et al*. (2001)
1 – undisturbed	New Guinea, Peru	Secondary wet forest, seasonal forest		3.5–317.0	Street (1982)
Undisturbed	Costa Rica	Lowland forest		196.0–305.0	Van Dam *et al*. (1997)
Tropical coniferous					
12	Puerto Rico	*Pinus caribaea*	18°N	48.0	Cuevas *et al*. (1991)
4–18	Nigeria (Ibadan), Puerto Rico	*Pinus caribaea*	7–18°N	20.8–168.5	Gower *et al*. (1994)

Age (range)	Location(s)	Ecosystem type(s)	Latitude(s)	CWD (range)	Reference
CWD					
Boreal coniferous					
160	Finland	*Picea abies*	63°N	11.8	Finér *et al*. (2003)
25–155	Canada (Manitoba and Saskatchewan)	*Picea mariana*, *Pinus banksiana*	53–56°N	0–6.2	Gower *et al*. (1997)
2–155	Canada (Manitoba)	*Picea mariana*	56°N	0.0–13.0	Harden *et al*. (1997)
28–383	Siberia, Russia	*Pinus sylvestris*	60°N	4.3–26.2	Schulze *et al*. (1999)
Boreal deciduous					
53–67	Canada (Manitoba and Saskatchewan)	*Populus tremuloides*	53–56°N	6.4–9.7	Gower *et al*. (1997)
5–15	Alaska	*Alnus incana*	65°N	5.2–8.2	Van Cleve *et al*. (1971)
Temperate coniferous					
Old growth	USA (Michigan)	*Tsuga canadensis*		20.1	Goodburn & Lorimer (1998)
50	USA (New Mexico)	*Pseudotsuga menziesii*	35°N	8.2	Gower *et al*. (1992)
3–1000		*Abies amabilis*, *Abies balsamea*, *Picea–Abies*, *Picea–Tsuga*, *Pinus contorta*, *Pinus–mixed*, *Pseudotsuga–Tsuga*, *Tsuga heterophylla*, *Tsuga–Picea*		1.5–245	Harmon *et al*. (1986)
9–316	USA (Oregon)	*Pinus ponderosa*	44°N	5.1–38.0	Law *et al*. (2003)*
Temperate deciduous					
55	United States (New Hampshire)	*Acer saccharum–Fagus*		15.0	Borman & Likens (1979)
2–200	Chile (Chiloé Island)	*Nothofagus–Drimys–Podocarpus*	41°S	9.0–206.5	Carmona *et al*. (2002)*
80	USA (Indiana)	*Acer–Populus*	39°N	0.92	Curtis *et al*. (2002)
70 – old growth	USA (Wisconsin, Michigan)	Northern hardwood		5.8–13.2	Goodburn & Lorimer (1998)
10–330		*Acer–Betula*, *Acer–Fagus*, *Acer–Fraxinus*, *Fagus–Betula*, *Liriodendron*, *Prunus*		6.5–24.6	Harmon *et al*. (1986)

(*continued*)

Table A1 (Contd.)

Age (range)	Location(s)	Ecosystem type(s)	Latitude(s)	Biomass (range)	Reference
		pensylvanica, *Quercus–mixed*, *Quercus–Prunus*			
1–100	USA (Indiana)	*Quercus–Acer*, *Quercus–Prunus*		19.9–69.0	Idol *et al.* (2001)*
8–63	USA (Wisconsin)	*Populus tremuloides*		4.3–7.8	Ruark & Bockheim (1988)*
Tropical evergreen broadleaf					
5–80	Congo (Yangambi), Ghana, Venezuela (San Carlos)	Dry forest, moist forest		1.25–36.0	Brown & Lugo (1990)
Undisturbed	Costa Rica (La Selva)	Wet forest	10°N	26.4	Clark *et al.* (2002)
10 to >150	New Zealand	*Nothofagus solandri*	45°S	11.3–87.4	Davis *et al.* (2002)*
Recently disturbed–undisturbed	Mexico	Dry tropical	20°N	10.3–49.8	Harmon *et al.* (1995)
Undisturbed	Brazil (Amazonia)	Rain forest	2°S	41.4	Malhi *et al.* (1999)
17 – undisturbed	Costa Rica (La Selva)	Secondary vegetation, wet forest	10°N	6.3–17.3	Raich (1983)
Undisturbed	USA (Hawaii)	*Metrosideros polymorpha*		0.3–2.3	Schuur *et al.* (2001)

Age (range)	Location (s)	Ecosystem type(s)	Latitude(s)	Organic soil horizons (range)	Reference
Organic soil horizon stocks with drainage classes when specified for boreal forests[†]					
Boral coniferous					
160	Finland	*Picea abies*	63°N	21.2	Finér *et al.* (2003)
2–16	Canada (New Brunswick)	*Picea mariana* WD, *Picea banksiana* WD	45°N	6.0–40.0	Krause (1998)*
13 to >90	Canada (Manitoba)	*Picea mariana* ID, *Picea mariana* MWD, *Picea mariana* peat ID, *Pinus banksiana* WD	56°N	0.0–48.0	Rapalee *et al.* (1998)
260	Finland (Oulu)	*Picea excelsa* PD	66°N	33.8	Reichle (1981)
30–117	Canada (Manitoba)	*Picea mariana* MWD, *Picea mariana* PD, *Pinus banksiana* WD	56°N	2.0–95.0	Trumbore & Harden (1997)
95–134	USA (Alaska)	*Picea glauca*, *Picea mariana*		22.0–78.0	Van Cleve *et al.* (1983)
0–235	Russia (Siberia)	*Pinus sylvestris*	60°N	3.7–29.6	Wirth *et al.* (2002)*
Boral deciduous					
55–77	USA (Alaska)	*Betula papyrifera*, *Populus balsamifera*, *Populus tremuloides*		78.0–195.0	Van Cleve *et al.* (1983)
Temperate coniferous					
40	USA (Minnesota)	*Picea glauca*, *Pinus banksiana*, *Pinus resinosa*	47°N	15.0–16.5	Alban *et al.* (1978)
60	USA (Washington)	*Pseudotsuga menziesii*		7.5	Harmon *et al.* (1990)
Old growth	USA (Michigan)	*Tsuga canadensis*	46°N	61.2	Hix & Barnes (1984)
10–114	USA (Rhode Island)	*Pinus strobus*		0.0–33.0	Hooker & Compton (2003)*
2–34	USA (Florida)	*Pinus elliottii*	30°N	1.5–20.0	Gholz & Fisher (1982)*

50	USA (New Mexico)	*Pseudotsuga menziesii*	35°N	21.1	Gower *et al*. (1992)
20–450	USA (Washington)	*Pseudotsuga menziesii*	45°N	12.0–16.1	Klopatek (2002)*
55	USA (Louisiana and North Carolina)	*Pinus palustris–Pinus echinata*	30–34°N	7.0–18.0	Laiho *et al*. (2003)
9–316	USA (Oregon)	*Pinus ponderosa*	44°N	7.4–20.7	Law *et al*. (2003)*
Old growth	USA (Michigan)	*Tsuga canadensis*	46°N	75.0	Liechty *et al*. (1997)
39–41	USA (Minnesota)	*Picea glauca*, *Pinus banksiana*, *Pinus resinosa*	47°N	12.5–15.5	Perala & Alban (1982)
38	USA (Michigan)	*Pinus resinosa*	42°N	10.5	Pregitzer & Palik (1997)
39	Japan (Koiwai)	*Larix leptolepis*	39°N	7.0	Reichle (1981)
23–26	New Zealand	*Pinus radiata*	38–41°S	8.0–35.0	Scott *et al*. (1999)
150–700	USA (Oregon)	*Abies balsamea*, *Picea sitchensis*, *Pseudotsuga menziesii*, *Thuja heterophylla*, *Tsuga heterophylla*,	44–47°N	9.9–19.1	Smithwick *et al*. (2002)*
23–180	USA (Washington)	*Abies amabilis*		23.9–74.8	Vogt *et al*. (1983)
50–53	Canada (Ontario)	*Pinus banksiana*	46°N	1.6–20.0	Weber *et al*. (1985)
20	Canada (British Columbia)	*Pseudotsuga menziesii*		16.0	Webber (1977)
Temperate deciduous					
40	USA (Minnesota)	*Populus*	47°N	13.5	Alban *et al*. (1978)
3–200	USA (New Hampshire)	Northern hardwoods	43–44°N	15.0–42.0	Covington (1981)*
60	USA (Massachusetts)	*Quercus rubra–Acer rubrum*	42°N	20.2	Gaudinski *et al*. (2000)
46	USA (Michigan)	*Acer–Betula*	46°N	42.3	Hix & Barnes (1984)
65	USA (New Hampshire)	*Acer–Betula–Fagus*		30.0	Huntington *et al*. (1988)
Old growth	USA (Michigan)	*Acer saccharum–Betula alleghaniensis*	46°N	22.0	Liechty *et al*. (1997)
1–15	India (Himalaya)	*Dalbergia sissoo*, *Populus deltoides*	28–29°N	1.5–4.2	Lodhiyal & Lodhiyal (1997)
Old growth	Canada (Ontario)	*Acer saccharum*	47°N	14.0–16.1	Morrison (1990)
40–49	USA (Minnesota)	*Populus tremuloides*	47°N	10.0–14.0	Perala & Alban (1982)
85–100	Denmark, Poland	*Fagus sylvatica*, *Quercus robur*	50–56°N	1.1–3.3	Reichle (1981)
8–63	USA (Wisconsin)	*Populus tremuloides*		3.6– 8.6	Ruark & Bockheim (1988)*
60	USA (Massachusetts)	*Quercus rubra–Acer rubrum*	42°N	17.0	Trumbore (2000)
1–119	USA (New Hampshire)	Northern hardwoods	43–44°N	15.0–47.5	Yanai *et al*. (2000)*
Tropical evergreen broadleaf					
10 to >150	New Zealand	*Nothofagus solandri*	45°S	16.4–35.9	Davis *et al*. (2002)*
8–52	Puerto Rico	*Swietenia macrophylla*, *Swietenia mahagoni*, *Tabebuia heterophylla*	18°N	2.4–6.6	Lugo (1992)
6	Portugal	*Eucalyptus globules*	39°N	2.8–4.8	Madeira *et al*. (2002)
Undisturbed	Brazil (Amazonia)	Rain forest	2°S	162	Malhi *et al*. (1999)
51	Australia	*Eucalyptus oliqua*	37°S	9.1	Reichle (1981)
Undisturbed	USA (Hawaii)	*Metrosideros polymorpha*		0.0–71.7	Schuur *et al*. (2001)
20 – undisturbed	Brazil (Amazonia)	*Carapa guianensis*, *Euxylophora paraensis*, *Leguminosae combin*, rain forest	2°S	3.6–4.9	Smith *et al*. (2002)
Undisturbed	Brazil (Amazonia)	Rain forest	2°S	3.25	Trumbore (2000)

(*continued*)

Table A1 (Contd.)

Age (range)	Location (s)	Ecosystem type(s)	Latitude(s)	Organic soil horizons (range)	Reference
Tropical coniferous					
4–20	Puerto Rico	*Pinus caribaea*	18°N	3.0–9.4	Lugo (1992)
13–44	South Africa and Swaziland	*Pinus patula*	26°S	48.2	Morris (1995)
23–26	New Zealand	*Pinus radiata*	38°S	6.5–35.0	Scott *et al.* (1999)
33	Brazil (Amazonia)	*Pinus caribaea*	2°S	5.4	Smith *et al.* (2002)

Age (range)	Location(s)	Ecosystem type(s)	Latitude(s)	Mineral soil (range)	Depth(s)	Reference
Mineral and deep organic soils by drainage classes when specified for boreal forests[†]; depth to which soil sample was taken in centimeters						
Boreal coniferous						
5–250	Siberia, Russia	*Pinus sylvestris* WD	56–67°N	16.9–24.3	30	Bird *et al.* (2002)
160	Finland	*Picea abies*	63°N	31.6	60	Finér *et al.* (2003)
25–155	Canada (Manitoba and Saskatchewan)	*Picea mariana* ID, *Pinus banksiana* WD	53–56°N	14.2–418	70	Gower *et al.* (1997)
13 to >90	Canada (Manitoba)	*Picea mariana* ID, *Picea mariana* peat ID, *Picea mariana* MWD, *Pinus banksiana* WD	56°N	0.0–703.0	70	Rapalee *et al.* (1998)
28–383	Russia (Siberia)	*Pinus sylvestris*	60°N	108.0–305	50	Schulze *et al.* (1999)
120	Canada (Manitoba)	*Picea mariana*	56°N	152.0	40	Trumbore (2000)
30–117	Canada (Manitoba)	*Picea mariana* MWD, *Picea mariana* PD , *Pinus banksiana* WD	56°N	13.0–190.0	70	Trumbore & Harden (1997)
95–135	USA (Alaska)	*Picea mariana*		55.0–70.0	20	Van Cleve *et al.* (1983)
Boreal deciduous						
53–67	Canada (Manitoba and Saskatchewan)	*Populus tremuloides* MWD	53–56°N	36.0–97.2	70	Gower *et al.* (1997)
55–77	USA (Alaska)	*Betula papyrifera*, *Populus balsamifera*, *Populus tremuloides*		40.0–140.0	20	Van Cleve *et al.* (1983)
Temperate coniferous						
40	USA (Minnesota)	*Picea glauca*, *Pinus banksiana*, *Pinus resinosa*	47°N	33.5–39.0	36	Alban *et al.* (1978)
2–34	USA (Florida)	*Pinus elliottii*	30°N	60.0–85.0	100	Gholz & Fisher (1982)*
50	USA (New Mexico)	*Pseudotsuga menziesii*	35°N	11.4	30	Gower *et al.* (1992
60	Washington, USA	*Pseudotsuga menziesii*		60.0		Harmon *et al.* (1990)
Old growth	USA (Michigan)	*Tsuga canadensis*	46°N	63.5	30	Hix & Barnes (1984)
10–114	USA (Rhode Island)	*Pinus strobus*		58.0–102.0	70	Hooker & Compton (2003)*

20–450	USA (Washington)	*Pseudotsuga menziesii*	45°N	97.4–174.5	20	Klopatek (2002)*
55	USA (Louisiana & North Carolina)	*Pinus palustris–Pinus echinata*	30–34°N	20.0–50.0	10	Laiho *et al.* (2003)
9–316	USA (Oregon)	*Pinus ponderosa*	44°N	40.6–127.0	100	Law *et al.* (2003)*
Old growth	USA (Michigan)	*Tsuga canadensis*	46°N	90	30	Liechty *et al.* (1997)
39–41	USA (Minnesota)	*Picea glauca, Pinus banksiana, Pinus resinosa*	47°N	33.5–45.6	100	Perala & Alban (1982)
38	USA (Michigan)	*Pinus resinosa*	42°N	113.0	50	Pregitzer & Palik (1997)
23–26	New Zealand	*Pinus radiata*	38–41°S	55	50	Scott *et al.* (1999)
150–700	USA (Oregon)	*Abies balsamea, Picea sitchensis, Pseudotsuga menziesii, Thuja heterophylla, Tsuga heterophylla*	44–47°N	36.7–365.5	100	Smithwick *et al.* (2002)
20	Canada (British Columbia)	*Pseudotsuga menziesii*		71.0	56	Webber (1977)
Temperate deciduous						
40	USA (Minnesota)	*Populus*	47°N	25.0	36	Alban *et al.* (1978)
0–80	USA (Minnesota)	*Populus tremuloides*		62.5–68.1	50	Alban & Perala (1992)
55	USA (New Hampshire)	*Acer saccharum–Fagus*		87.0		Borman & Likens (1979)
60	USA (Massachusetts)	*Quercus rubra–Acer rubrum*	42°N	67.0	80	Gaudinski *et al.* (2000)
46	USA (Michigan)	*Acer–Betula*	46°N	56.1	30	Hix & Barnes (1984)
15 – old growth	USA (Pennsylvania)	*Acer–Betula–Fagus*		45.0–86.0	30	Hoover *et al.* (2002)
65	USA (New Hampshire)	*Acer–Betula–Fagus*		130.0	>20	Huntington *et al.* (1988)
Old growth	USA (Michigan)	*Acer saccharum–Betula alleghaniensis*	46°N	70.0	30	Liechty *et al.* (1997)
Old growth	Canada (Ontario)	*Acer saccharum*	47°N	185.0–202.2	100	Morrison (1990)
40–49	USA (Minnesota)	*Populus tremuloides*	47°N	33.0 –36.5	61	Perala & Alban (1982)
8–63	USA (Wisconsin)	*Populus tremuloides*		33.0–65.0	60	Ruark & Bockheim (1988)*
60	USA (Massachusetts)	*Quercus rubra–Acer rubrum*	42°N	45.0	40	Trumbore (2000)
Tropical evergreen broadleaf						
12 – undisturbed	USA (Hawaii)	*Eucalyptus saligna, Guava–Koa acacia*	19°N	114.0–130.0	55	Bashkin & Binkley (1998)
10 – undisturbed	Puerto Rico	Dry forest, moist forest, wet forest		6.0–164.0	25 or 50	Brown & Lugo (1990)
Undisturbed	Brazil (Amazonia)	Upland wet forest		120.0	100	Cerri *et al.* (1991)
Undisturbed	Costa Rica (La Selva)	Wet forest		185.0–224.0	100	Clark *et al.* (2002)
12	Puerto Rico	Secondary forest	18°N	42.0	30	Cuevas *et al.* (1991)
10 to >150	New Zealand	*Nothofagus solandri*	45°S	29.8–42.0	10	Davis *et al.* (2002)*
24 – undisturbed	Brazil (Amazonia)	Closed secondary forest, degraded pasture, moist forest	2°S	100.0–300.0	100 or 800	De Camargo *et al.* (1999)
Undisturbed	Latin America	Equatorial forest, dry forest, moist forest, rain forest,		39.0–145.0	100	Houghton *et al.* (1991)

(*continued*)

Table A1 (Contd.)

Age (range)	Location(s)	Ecosystem type(s)	Latitude(s)	Mineral soil (range)	Depth(s)	Reference
		seasonal forest, wet forest, woodland				
17	USA (Hawaii)	*Albizia*, *Albizia–Eucalyptus saligna*, *Eucalyptus saligna*	19°N	125.0–146.0	50	Kaye *et al.* (2000)
8–52	Puerto Rico	*Swietenia macrophylla*, *Swietenia mahagoni*, *Tabebuia heterophylla*	18°N	39.0–93.0	100	Lugo (1992)
17	Costa Rica (La Selva)	Secondary vegetation	10°N	86.0	50	Raich (1983)
7–16	Puerto Rico, USA (Hawaii)	*Albizia–Eucalyptus saligna*, *Casuarina–Leucaena–Eucalyptus robusta*	18–20°N	40.0–140.0	40	Resh *et al.* (2002)
Undisturbed	Ecuador	Moist lower montane forest	0°N	61.4	15	Rhoades *et al.* (2000)
25 – undisturbed	Brazil (Amazonia)	*Carapa guianensis*, *Euxylophora paraensis*, *Leguminosae*, moist forest	2°S	78.0–114.0	20	Smith *et al.* (2002)
4 – undisturbed	New Guinea, USA (Hawaii)	Secondary wet forest, *Ohia*-treefern-wet forest		88.5 –399.0	30 or 100	Street (1982)
100	USA (Hawaii)	*Metrosideros polymorpha*		114.0–154.0	20	Townsend *et al.* (1995)
Undisturbed	Brazil (Amazonia)	Moist forest	2°S	102.0–155.0	100 or 800	Trumbore *et al.* (1995)
Undisturbed	Brazil (Amazonia)	Moist forest	2°S	51	40	Trumbore (2000)
Undisturbed	Costa Rica	Moist lowland forest		55.0–110.0	40	Van Dam *et al.* (1997)
Undisturbed	Brazil	Wet forest	22°S	126.0	70	Vitorello *et al.* (1989)
Tropical coniferous						
12	Puerto Rico	*Pinus caribaea*	18°N	41	30	Cuevas *et al.* (1991)
4–18	Puerto Rico	*Pinus caribaea*	18°N	44.0– 89.0	100	Lugo (1992)
44	South Africa	*Pinus patula*		108.5		Morris (1995)
38	Brazil (Amazonia)	*Pinus caribaea*	2°S	71	20	Smith *et al.* (2002)

Age (range)	Location(s)	Ecosystem type(s)	Latitude(s)	Total Ecosystem (range)	Reference
Ecosystem total					
Boreal coniferous					
160	Finland	*Picea abies*	63°N	175.5	Finér *et al.* (2003)
25–155	Canada (Manitoba and Saskatchewan)	*Picea mariana*, *Pinus banksiana*	53–56°N	50.5–479.4	Gower *et al.* (1997)
95	USA (Alaska)	*Picea mariana*		139.0	Van Cleve *et al.* (1983)
2–383	Russia (Siberia)	*Pinus sylvestris*	60°N	30.0–138.0	Wirth *et. al.* (2002)*
Boreal deciduous					
53–67	Canada (Manitoba and Saskatchewan)	*Populus tremuloides*	53–56°N	158.4–176.4	Gower *et al.* (1997)

Temperate coniferous					
50	USA (New Mexico)	*Pseudotsuga menziesii*	35°N	209.0	Gower *et al.* (1992)
60	USA (Washington)	*Pseudotsuga menziesii*		227.0	Harmon *et al.* (1990
10–114	USA (Rhode Island)	*Pinus strobus*		80.0–290.0	Hooker & Compton (2003)*
9–316	USA (Oregon)	*Pinus ponderosa*	44°N	79.0–304.0	Law *et al.* (2003)*
150–700	USA (Oregon)	*Abies balsamea*, *Picea sitchensis*, *Pseudotsuga menziesii*, *Thuja heterophylla*, *Tsuga heterophylla*	44–47°N	195.0–1127.0	Smithwick *et al.* (2002)
7–180	USA (Florida and Washington)	*Abies amabilis*, *Pinus elliottii*, *Pseudotsuga menziesii*		112.0–629.0	Vogt (1991)
Temperate deciduous					
0–80	USA (Minnesota)	*Populus tremuloides*		122.0–236.0	Alban & Perala (1992)
55	USA (New Hampshire)	*Acer saccharum/Fagus sp.*		210.0	Borman & Likens (1979)
60–80	USA (Indiana, Massachusetts, Wisconsin)	*Acer–Populus*, *Quercus*, *Quercus–Acer*	42°N	217.0–301.0	Curtis *et al.* (2002)
Old growth	Canada (Ontario)	*Acer saccharum*	47°N	348.0–353.0	Morrison (1990)
8–63	USA (Wisconsin)	*Populus tremuloides*		64.3–135.0	Ruark & Bockheim (1988)*
48	USA (Tennessee)	*Liriodendron tulipifera*		282.0	Vogt (1991)
Tropical evergreen broadleaf					
12	Puerto Rico	Secondary forest	18°N	73.5	Cuevas *et al.* (1991)
10 to >150	New Zealand	*Nothofagus solandri*	45°S	125.0–210.0	Davis *et al.* (2002)*
Undisturbed	Latin America	Equatorial forest, dry forest, moist forest, rain forest, seasonal forest, wet forest, woodland		81.0– 298.0	Houghton *et al.* (1991)
6	Portugal	*Eucalyptus globules*	39°N	82.0–112.0	Madeira *et al.* (2002)
Undisturbed	Brazil (Amazonia)	Rain forest	2°S	447.0	Malhi *et al.* (1999)
5 – unidsturbed	Worldwide	Agroforest, rain forest, secondary forest		65.0–305.0	Woomer *et al.* (2000)
Tropical coniferous					
12	Puerto Rico	*Pinus caribaea*	18°N	99.6	Cuevas *et al.* (1991)

Age (range)	Location(s)	Ecosystem type(s)	Latitude(s)	NPP (range)	Reference
NPP					
Boreal coniferous					
160	Finland	*Picea abies*	63°N	2.0	Finér *et al.* (2003)
28–100	Finland, Russia (Mordovskaya and Siberia)	*Pinus sylvestris*	54–60°N	1.7–3.0	Gower *et al.* (1994)
20–250	Canada (Saskatchewan and Manitoba), China, Finland, Russia (Siberia), Sweden, USA (Alaska)	*Larix gmelinii*, *Picea abies*, *Picea glauca*, *Picea mariana*, *Pinus banksiana*, *Pinus sylvestris*	50–65°N	2.2–9.1	Gower *et al.* (2001)
260	Russia (Siberia)	*Larix gmelinii*	64°N	0.9	Kajimoto *et al.* (1999)
200	Russia (Siberia)	*Pinus sylvestris*	60°N	2.1	Lloyd *et al.* (2002)

(*continued*)

Table A1 (Contd.)

Age (range)	Location(s)	Ecosystem type(s)	Latitude(s)	NPP (range)	Reference
2–383	Russia (Siberia)	*Pinus sylvestris*	60°N	<0.01–5.4	Wirth *et al.* (2002)*
Boreal deciduous					
30–90	Canada (Saskatchewan and Manitoba), Finland, USA (Alaska)	*Alnus incana*, *Betula papyrifera*, *Betula pubescens*, *Populus tremuloides*	54–65°N	2.1–8.0	Gower *et al.* (2001)
Temperate coniferous					
8–74	Canada (British Columbia), Japan (Orita and Osaku), Scotland (Morayshire), USA (Florida, North Carolina, and Wisconsin)	*Pinus contorta*, *Pinus densiflora*, *Pinus elliottii*, *Pinus nigra*, *Pinus resinosa*, *Pinus taeda*	30–57°N	4.2–12.4	Gower *et al.* (1994)
9–316	USA (Oregon)	*Pinus ponderosa*	44°N	1.5–6.6	Law *et al.* (2003)*
16–142	Germany (Bavaria)	*Picea abies*	50°N	6.1–13.4	Mund *et al.* (2002)*
290	Japan (Shigayama)	*Tsuga diversifolia–Abies mariesii*	36°N	3.3	Reichle (1981)
7–180		*Abies amabilis*, *Pinus elliottii*, *Pinus resinosa*, *Pinus strobus*, *Pinus taeda*, *Pseudotsuga menziesii*		4.3–20.6	Reich & Bolstad (2001)
Temperate deciduous					
60–90	USA (Indiana, Massachusetts, Michigan, Tennessee and Wisconsin)	*Acer*, *Populus*, *Quercus–Acer*	35–45°N	5.1–10.5	Curtis *et al.* (2002)
1–15	India (Himalaya)	*Dalbergia sissoo*, *Populus deltoides*	28–29°N	5.7–16.2	Lodhiyal & Lodhiyal (2003)*
35–78		*Acer saccharum*, *Acer–Nyssa*, *Betula*, *Liriodendron tulipifera*, *Quercus rubra*		6.3–19.5	Reich & Bolstad (2001)
50–55	USA (New Hampshire)	Northern hardwoods		3.8–6.6	Whittaker *et al.* (1974)
Tropical evergreen broadleaf					
15	USA (Hawaii)	*Albizia*, *Eucalyptus saligna*	19°N	19.4–20.7	Binkley & Ryan (1998)
Undisturbed	Worldwide			7.1–13.0	Clark *et al.* (2001)
12	Puerto Rico	Secondary forest	18°N	9.7	Cuevas *et al.* (1991)
Undisturbed	Global study			18.1	Grace *et al.* (2001)
Undisturbed	Brazil (Amazonia)	Rain forest	2°S	15.6	Malhi *et al.* (1999)
20 – undisturbed	India (Kodayar)	*Acacia mangium*, *Albizia odoratissima*, *Hevea brailiensis*, mixed forest, *Tectona grandis*	8°N	1.5–2.4	Sundarapandian *et al.* (1999)
Undisturbed	Costa Rica	Moist lowland forest		8.5–14.0	Van Dam *et al.* (1997)
Tropical coniferous					
12	Puerto Rico	*Pinus caribaea*	18°N	9.6	Cuevas *et al.* (1991)

Tropical deciduous					
Undisturbed	Mexico	Mixed forest	19°N	5.6–6.8	Martinez–Yrizar *et al.* (1996)
Undisturbed	India (Kodayar)	Mixed forest	8°N	2.6	Sundarapandian *et al.* (1999)

Age (range)	Location(s)	Ecosystem type(s)	Latitude(s)	NEE (range)	Reference
NEP					
Boreal coniferous					
120–122	Canada (Manitoba)	*Picea mariana*		–0.7 to 0.1	Goulden *et al.* (1998)
31–100	Finland, Sweden		60–64°N	–0.5 to 2.6	Law *et al.* (2002)
200	Russia (Siberia)	*Pinus sylvestris*	60°N	1.6	Lloyd *et al.* (2002)
150–152	European Russia	*Picea abies*	56°N	–3.6 to –2.4	Milyukova *et al.* (2002)
2–383	Russia (Siberia)	*Pinus sylvestris*	60°N	–2.2 to 1.3	Wirth *et al.* (2002)*
Boreal deciduous					
70–74	Canada (Saskatchewan)	*Populus tremuloides*	53°N	0.8–2.90	Black *et al.* (1996)
7	Iceland	*Populus*	63°N	1.0	Valentini *et al.* (2000)
Temperate coniferous					
8–9	New Zealand (Christchurch)	*Pinus radiata*	42°S	5.2–7.2	Arneth *et al.* (1998)
24–25	USA (Florida)	*Pinus elliottii*	29°N	6.1–7.4	Clark *et al.* (1999)
200	USA (Massachusetts)	*Tsuga canadensis*	42°N	3.0	Hadley & Schedlbauer (2002)
14–450	France, Germany, Netherlands, Scotland, USA (North Carolina, Maine, Washington)	*Picea rubens–Tsuga canadensis*, *Pinus pinaster*, *Pinus sylvestris*, *Pseudotsuga menziesii–Tsuga heterophylla*	36–56°N	–0.2 to 7.7	Law *et al.* (2002)
9–316	USA (Oregon)	*Pinus ponderosa*	44°N	–2.4 to 3.6	Law *et al.* (2003)*
97–98	Colorado, USA	*Abies lasiocarpa–Picea engelmannii*	40°N	0.6–0.8	Monson *et al.* (2002)
1–25	USA (Florida)	*Pinus elliottii*	29°N	–12.5 to 6.8	Thornton *et al.* (2002)*
Temperate deciduous					
60–90	USA (Indiana, Massachusetts, Michigan, Tennessee, and Wisconsin)	*Acer*, *Populus*, *Quercus–Acer*	35–45°N	1.7–5.8	Curtis *et al.* (2002)
80–81	USA (Indiana)	*Acer–Liriodendron*	39°N	2.3–2.9	Ehman *et al.* (2002)1
30–97	Denmark, France, USA (Tennessee, Massachusetts, and Wisconsin)	Broadleaf forests, *Fagus sylvatica*, *Quercus–Acer*	35–55°N	–0.6 to 8.7	Law *et al.* (2002)
90–93	Canada (Ontario)	*Acer–Populus*	44°N	0.8–2.7	Lee *et al.* (1999), Baldocchi *et al.* (2001)
91–92	USA (Michigan)	*Populus*	45°N	0.8–1.6	Schmid *et al.* (2000)
100	Italy	Fagus	41°N	4.7	Valentini *et al.* (1996)
50–55	USA (Massachusetts)	Northern hardwoods		2.9–4.4	Whittaker *et al.* (1974)
40–45	Japan	*Betula–Quercus*	36°N	0.7–2.1	Yamamoto *et al.* (1999), Saigusa *et al.* (2002)
Temperate mixed					
60–90	Belgium, USA (Wisconsin)	Evergreen–deciduous forests, *Pseudotsuga menziesii–Fagus sylvatica*	45–51°N	0.3–5.1	Law *et al.* (2002)

(*continued*)

Table A1 (Contd.)

Age (range)	Location(s)	Ecosystem type(s)	Latitude(s)	NEE (range)	Reference
Temperate evergreen broadleaf					
50–51	Italy		41°N	5.2–6.5	Law *et al*. (2002)
90	Italy	*Fagus sylvatica*	41°N	4.7	Valentini *et al*. (1996)
Tropical evergreen broadleaf					
Undisturbed	Brazil (Amazonia)	Lowland waterlogged rain forest, plateau rain forest	2°S	1–8	Araujo *et al*. (2002)
Undisturbed	Brazil (Amazonia)	Lowland rain forest	2°S	5.6	Carswell *et al*. (2002)
Undisturbed	Brazil (Amazonia)	Moist forest	2°S	2.2	Fan *et al*. (1990)
Undisturbed	Brazil (Amazonia)	Moist forest	10°S	1.0	Grace *et al*. (1995)
Undisturbed	Costa Rica (La Selva)	Wet forest	10°N	0.1–7.9	Loescher (2003)
Undisturbed	Brazil (Amazonia)	Moist forest	2°S	5.9	Malhi *et al*. (1998)

†Drainage classes are listed following the ecosystem type, and are abbreviated as follows: D, dry site; MD, mesic to dry site; M, mesic site; WD, well drained; MWD, moderately well drained; ID, imperfectly drained; PD, poorly drained; NPP, net primary productivity; NEP, net ecosystem productivity; CWD, coarse woody debris.

