Re-evaluation of forest biomass carbon stocks and lessons from the world's most carbon-dense forests

Heather Keith[1], Brendan G. Mackey, and David B. Lindenmayer

The Fenner School of Environment and Society, Australian National University, Canberra, ACT 0200, Australia

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From analysis of published global site biomass data (n = 136) from primary forests, we discovered (*i*) the world's highest known total biomass carbon density (living plus dead) of 1,867 tonnes carbon per ha (average value from 13 sites) occurs in Australian temperate moist *Eucalyptus regnans* forests, and (*ii*) average values of the global site biomass data were higher for sampled temperate moist forests (n = 44) than for sampled tropical (n = 36) and boreal (n = 52) forests (n is number of sites per forest biome). Spatially averaged Intergovernmental Panel on Climate Change biome default values are lower than our average site values for temperate moist forests, because the temperate biome contains a diversity of forest ecosystem types that support a range of mature carbon stocks or have a long land-use history with reduced carbon stocks. We describe a framework for identifying forests important for carbon storage based on the factors that account for high biomass carbon densities, including (*i*) relatively cool temperatures and moderately high precipitation producing rates of fast growth but slow decomposition, and (*ii*) older forests that are often multiaged and multilayered and have experienced minimal human disturbance. Our results are relevant to negotiations under the United Nations Framework Convention on Climate Change regarding forest conservation, management, and restoration. Conserving forests with large stocks of biomass from deforestation and degradation avoids significant carbon emissions to the atmosphere, irrespective of the source country, and should be among allowable mitigation activities. Similarly, management that allows restoration of a forest's carbon sequestration potential also should be recognized.

Eucalyptus regnans | climate mitigation | primary forest | deforestation and degradation | temperate moist forest biome

Deforestation currently accounts for ≈18% of global carbon emissions and is the third largest source of emissions (1). Reducing emissions from deforestation and degradation (REDD) is now recognized as a critical component of climate change mitigation (2). A good understanding of the carbon dynamics of forests (3) is therefore important, particularly about how carbon stocks vary in relation to environmental conditions and human land-use activities. Average values of biomass carbon densities for the major forest biomes (4) are used as inputs to climate-carbon models, estimating regional and national carbon accounts, and informing policy debates (5). However, for many purposes it is important to know the spatial distribution of biomass carbon within biomes (6) and the effects of human land-use activities on forest condition and resulting carbon stocks (refs. 3 and 7 and www.fao.org/forestry/site/10368/en).

Primarily because of Kyoto Protocol rules (ref. 8; http://unfccc.int/resource/docs/convkp/kpeng.pdf), interest in carbon accounting has been focused on modified natural forests and plantation forests. It has been argued that primary forests, especially very old forests, are unimportant in addressing the climate change problem because (*i*) their carbon exchange is at equilibrium (9, 10), (*ii*) carbon offset investments focus on planting young trees as their rapid growth provides a higher sink capacity than old trees, and/or (*iii*) coverage and hence importance of modified forest is increasing. Recent research findings have countered the first argument for all 3 major forest biomes (namely, tropical, temperate, and boreal forests) and demonstrated that old-growth forests are likely to be functioning as carbon sinks (11–13). The long time it takes new plantings to sequester and store the amount of carbon equivalent to that stored in mature forests counters the second argument (14). The third argument about the unimportance of old forest in addressing climate change relates, in part, to the diminishing extent of primary forest caused by land-use activities (15) and associated depletion of biomass carbon stocks (16). However, significant areas of primary forest remain (17), and depleted carbon stocks in modified forests can be restored.

It is useful to distinguish between the carbon carrying capacity of a forest ecosystem and its current carbon stock. Carbon carrying capacity is the mass of carbon able to be stored in a forest ecosystem under prevailing environmental conditions and natural disturbance regimes, but excluding anthropogenic disturbance (18). It is a landscape-wide metric that provides a baseline against which current carbon stocks (that include anthropogenic disturbance) can be compared. The difference between carbon carrying capacity and current carbon stock allows an estimate of the carbon sequestration potential of an ecosystem and quantifies the amount of carbon lost as a result of past land-use activities.

This study re-evaluates the biomass carbon densities of the world's major forest biomes based on a global synthesis of site data of biomass measurements in forest plots from publicly available peer-reviewed articles and other reputable publications. Site data were selected that (*i*) provided appropriate measurements of biomass and (*ii*) sampled largely mature and older forests to provide an estimate of carbon carrying capacity. The most reliable nondestructive source of biomass carbon data are from field measurements of tree and dead biomass structure at sites that sample a given forest type and condition. These structural measurements are converted to biomass carbon densities by using allometric equations. Standard national forestry inventories contain site data but they are not always publicly available and their suitability for estimating carbon stocks at national and biome-levels has been questioned (5, 6).

We identify those forests with the highest biomass carbon densities and consider the underlying environmental conditions and ecosystem functions that result in high carbon accumulation. These results (*i*) provide a predictive framework for identifying forests with high biomass carbon stocks, (*ii*) help clarify interpretation of average forest biome values such as those published by the Intergovernmental Panel on Climate Change (IPCC), and (*iii*) inform policies about the role of forests in climate change mitigation.

Australian *Eucalyptus regnans* Forests Have the World's Highest Biomass Carbon Density

Evergreen temperate forest dominated by *E. regnans* (F. Muell.) (Mountain Ash) in the moist temperate region of the Central

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[1]To whom correspondence should be addressed. E-mail: heather.keith@anu.edu.au.

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Fig. 1. *E. regnans* forest with midstory of *Acacia* and understory of tree ferns. The person in the bottom left corner provides a scale.

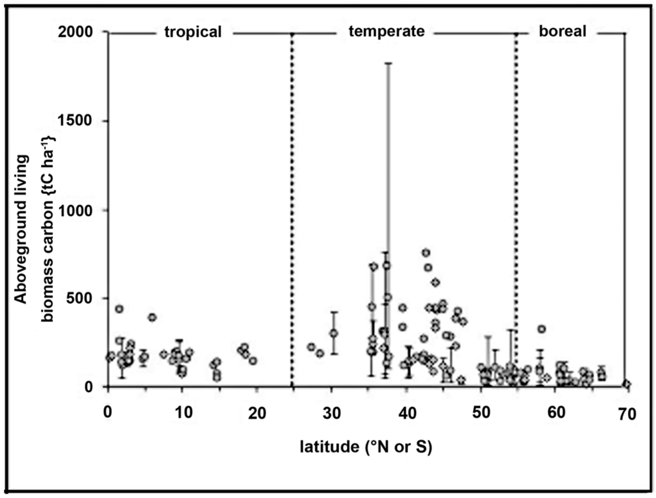

Fig. 2. Global forest site data for above-ground biomass carbon (tC·ha^{-1}) in relation to latitude (north or south). Points are values for individual or average of plots, and bars show the range in values at a site. The O'Shannassy Catchment has a mean of 501 tC·ha^{-1} and ranges from 104 to 1,819 tC·ha^{-1}. The highest biomass carbon occurs in the temperate latitudes.

Highlands of Victoria, southeastern Australia has the highest known biomass carbon density in the world. We found that *E. regnans* forest in the O'Shannassy Catchment of the Central Highlands (53 sites within a 13,000-ha catchment) contains an average of 1,053 tonnes carbon (tC)·ha^{-1} in living above-ground biomass and 1,867 tC·ha^{-1} in living plus dead total biomass in stands with cohorts of trees >100 years old sampled at 13 sites. We examined this catchment in detail because it had been subject to minimal human disturbance, either by Indigenous people or from post-European settlement land use. We compared the biomass carbon density of the *E. regnans* forest with other forest sites globally by using the collated site data (Table S1). No other records of forests have values as high as those we found for *E. regnans*.

Our field measurements and calculations revealed that maximum biomass carbon density for a *E. regnans*-dominated site was 1,819 tC·ha^{-1} in living above-ground biomass and 2,844 tC·ha^{-1} in total biomass from stands with a well-defined structure of overstory and midstory trees (see Fig. 1) consisting of multiple age cohorts with the oldest ≈250+ years (19). There was substantial spatial variability in total biomass carbon density across the sites in the catchment within an ecologically mature forest type, ranging from 262 to 2,844 tC·ha^{-1}. Unexpectedly, we found the highest values were from areas experiencing past partial stand-replacing natural disturbances.

In February 2009, extensive areas of the O'Shannassy Catchment and elsewhere in the Central Highlands of Victoria were burned in a major conflagration. We will be undertaking a major survey of the network of permanent field sites in the catchment (20) to assess changes in postfire carbon stocks. It will be important that these sites are not subject to postfire salvage logging over the coming years to prevent the extensive removal of dead biomass carbon (21).

Some Temperate Moist Forest Types Can Have Higher Biomass Carbon Density Than Both Boreal and Tropical Forests

Average values of the collated global site biomass data from largely mature or primary forests were much higher for the sampled temperate moist forests ($n = 44$) than they were for the sampled tropical ($n = 36$) and boreal ($n = 52$) forests, where n is the number of sites in each forest biome (Table S1) (Fig. 2). The locations of the global site biomass data are shown in Fig. S1. They do not represent all forest types or environmental conditions within a given biome (reflecting the difficulty of finding published field data) and therefore are insufficient to calculate biome spatial averages. We related site values of above-ground living biomass carbon (tC·ha^{-1}) and total biomass carbon (tC·ha^{-1}) to temperature and precipitation (Fig. 3).

Fig. 3 shows that temperate moist forests occurring where temperatures were cool and precipitation was moderately high had the highest biomass carbon stocks. Temperate forests that had particularly high biomass carbon density included those dominated by *Tsuga heterophylla*, *Picea sitchensis*, *Pseudotsuga menziesii*, and *Abies amabilis* in the Pacific Northwest of North America [range in living above-ground biomass of 224−587 tC·ha^{-1} and total biomass of 568–794 tC·ha^{-1} (22–25)]. A synthesis of site data for the Pacific Northwest gave an average for evergreen needle leaf forest of 334 tC·ha^{-1} (26), and this is used as the continental biome value by the IPCC (4). An upper limit of biomass accumulation of 500–700 tC·ha^{-1} in the Pacific Northwest of the United States has been derived from an analysis of global forest data of carbon stocks and net ecosystem productivity in relation to stand age (11, 27). In New Zealand, the highest biomass carbon density reported is for *Agathis australis* [range in living above-ground biomass of 364–672 and total biomass of 400–982 tC·ha^{-1} (28)]; and a synthesis based on forest inventory data gave a mean of 180 tC·ha^{-1} with a range in means for forest classes of 105–215 tC·ha^{-1} (29). In Chile, the highest biomass carbon densities reported are for *Nothofagus*, *Fitzroya*, *Philgerodendron*, and *Laureliopsis* [range in living above-ground biomass 142–439 and total biomass of 326–571 tC ha^{-1} (30–33)].

IPCC Tier-1 Biome Default Values

IPCC biome default values are shown in Table 1 alongside the published global site biomass data (Table S1). The site data were averaged for each biome but they are not equivalent to a spatial average for each biome. The comparison helps identify biomes where site averages differ significantly from default values. The biome-averaged values of the global site biomass carbon data were 2.5–3 times higher than the IPCC biome default values for warm and cool temperate moist forests (Table 1). The IPCC default

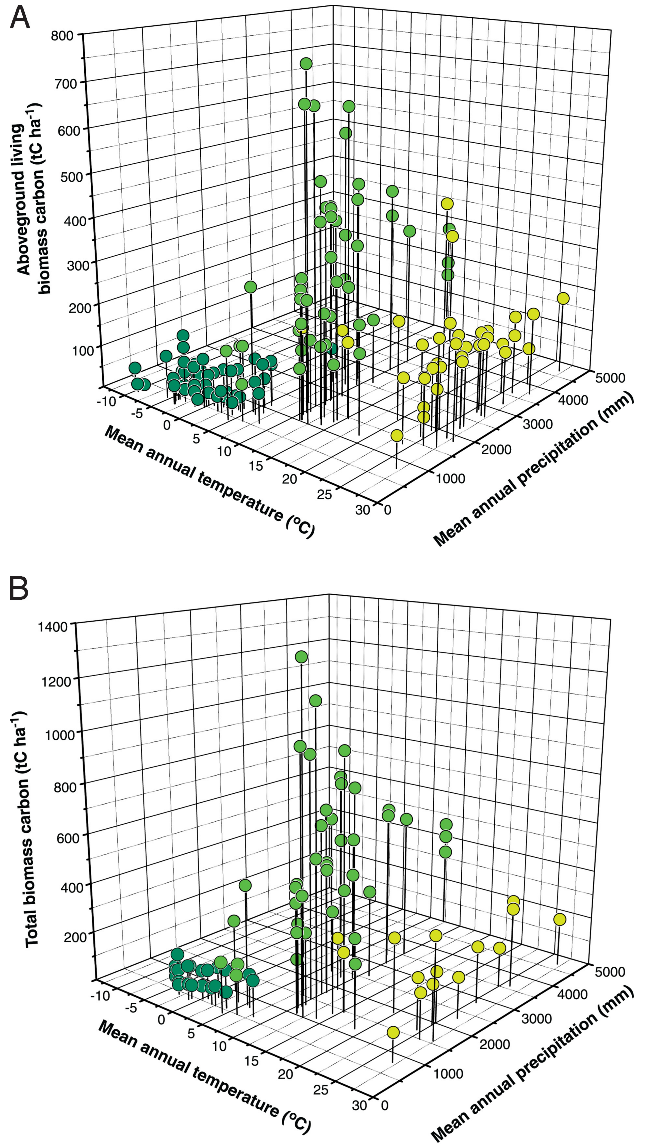

Fig. 3. Global forest site data for above-ground living biomass carbon (tC·ha^{-1}) (*A*) and total biomass carbon (tC·ha^{-1}) (*B*), in relation to mean annual temperature and mean annual precipitation for the site. Site data are shown in relation to their distribution among biomes of boreal (dark green), temperate (midgreen), and tropical (light green) forests. The highest biomass carbon density occurs in cool, moderately wet climates in temperate moist forest biomes. Some sites had values for above-ground living biomass carbon but not dead biomass, so there was no value for total biomass carbon.

values were <1 SD from the averaged site values. Average site data were comparable with IPCC default values for tropical and boreal biomes. However, the IPCC biome default value for tropical moist forest was marginally <1 SD from the averaged site values. Also, the site data for the boreal biome reflected higher above-ground living biomass carbon values but lower below-ground plus dead biomass carbon values compared with the IPCC default values (Table 1).

The differences between the collated global site biomass data and IPCC biome default values for temperate moist forests reflect the diversity of forest ecosystem types considered under the temperate biome category. Biome default values likely under-represent Southern Hemisphere evergreen temperate moist forest types and do not distinguish forest condition caused by land-use history (5). The differences between site biomass data and IPCC default values for boreal forests could reflect the effect of land-use history and fire on carbon stocks at the site level.

Toward a Predictive Framework for High Biomass Carbon Forests

We developed a framework for identifying forests with high biomass carbon stocks based on an understanding of underlying mechanisms and using the *E. regnans* forests as an example. The factors in the framework include (*i*) environmental conditions, (*ii*) life history and morphological characteristics of tree species, and (*iii*) the impacts of natural disturbance such as fire and land-use history. It is the interactions and feedbacks among these factors that influence vegetation community dynamics and ultimately lead to very high carbon densities.

Derivation of Carbon Stocks. Stock of carbon represents the net exchange of carbon fluxes in an ecosystem (net ecosystem exchange). In living biomass, the carbon stock is determined by the balance between the fluxes of carbon gain by photosynthetic assimilation by the foliage [gross ecosystem production (GEP)] and carbon loss by autotrophic respiration, which results in net primary productivity (NPP). In the total ecosystem (living plus dead biomass plus soil), the carbon stock is determined by the balance between the fluxes of carbon gain by NPP and carbon loss by decomposition of dead biomass and heterotrophic respiration. Ecosystem carbon stocks vary because environmental conditions influence the carbon fluxes of photosynthesis, decomposition, and autotrophic and heterotrophic respiration differently (34).

Environmental Conditions. The key climatic variables of precipitation, temperature, and radiation are broadly correlated with vegetation structure and function (35, 36), although such empirical correlations do not necessarily reveal underlying biochemical processes or the dependence of these processes on environmental factors (37). Climatic influences on photosynthesis include effects of (*i*) irradiance and temperature on carboxylation rates, (*ii*) temperature and soil water status on stomatal conductance and thus diffusion of CO_2 from the atmosphere into the intercellular air spaces, and (*iii*) temperature-dependent nitrogen uptake (37). The climatic conditions and relatively fertile soils of the Central Highlands of Victoria favor rapid growth of *E. regnans* (>1 m·yr^{-1} for the first 70 years), and these trees eventually become the world's tallest flowering plant (up to 130 m) (38).

Both dark respiration and maintenance respiration are temperature dependent (37). Soil respiration is correlated with temperature and water availability, although substrate also has an important influence (34). Rates of coarse woody biomass decomposition have been found to decrease with lower temperatures in temperate forests (39) and are also related to wood density, chemistry, and size (40–42).

Climatic conditions that favor higher rates of GEP relative to rates of respiration and decomposition should, other factors being equal, lead to larger biomass carbon stocks. Table 2 gives the average and range in climatic conditions (annual precipitation and temperature) for the global site data from Table S1 and compares estimates of GEP (34) and decomposition rates (*k*) (42). Estimates of the climate conditions and derived variables are also shown for *E. regnans* forests in the Central Highlands of Victoria. Temperate forests are characterized by higher rates of GEP than boreal forests but lower decomposition rates than tropical forests. There is considerable variation evident in rates of carbon fluxes within each forest biome, along with overlap between biomes.

Life History and Morphological Characteristics of Tree Species. *E. regnans* can live for ≈450 years, with stem diameters up to 6 m (38, 43). In our analysis, the stands of *E. regnans* with high values of biomass carbon density were at least 100 years old. *E. regnans* wood density is high (450–550 g·cm^{-3}) (44), so that biomass is greater for a given volume. Limited crown development in *E. regnans* (through crown shyness or reduced crown area caused by abrasion of growing tips by neighboring crowns) and the isolateral leaf form of this

Table 1. Average published site data (from Table S1) for biomass carbon (tC·ha⁻¹) of each forest biome (mean, standard deviation, and number of sites) and default biomass carbon values (IPCC; refs. 4 and 66)

		Above-ground living biomass carbon, $tC \cdot ha^{-1}$		Root + dead biomass carbon, $tC \cdot ha^{-1}$		Total living + dead biomass carbon, $tC \cdot ha^{-1}$	
Domain	Climate region	Average site data	Biome default value*	Average site data	Biome default value†	Average site data	Biome defaul value
Tropical	Tropical wet	171 (61) *n* = 18	146	76 (72) *n* = 7	67	231 (75) *n* = 7	213
	Tropical moist	179 (96) *n* = 14	112	55 (66) *n* = 5	30	248 (100) *n* = 5	142
	Tropical dry	70 *n* = 1	73	41 *n* = 1	32	111 *n* = 1	105
	Tropical montane	127 (8) *n* = 3	71	52 (6) *n* = 3	60	167 (17) *n* = 3	112
Subtropical	Warm temperate moist	294 (149) *n* = 26	108	165 (75) n = 20	63	498 (200) *n* = 20	171
	Warm temperate dry		75		65		140
	Warm temperate montane		69		63		132
Temperate	Cool temperate moist	377 (182) *n* = 18	155	265 (162) *n* = 18	78	642 (294) *n* = 18	233
	Cool temperate dry	176 (102) *n* = 3	59	102 (77) *n* = 3	62	278 (173) *n* = 3	121
	Cool temperate montane	147 *n* = 1	61		63	153 *n* = 1	124
Boreal	Boreal moist	64 (28) *n* = 28	24	37 (16) *n* =14	75	97 (34) *n* =14	99
	Boreal dry	59 (36) *n* = 24	8	25 (12) *n* = 9	52	84 (39) *n* = 9	60
	Boreal montane		21		55		76

The site data represent an average and variance of point values whereas the default values represent a spatial average. The site data have been taken from mature and older forests with minimal human land use impact whereas the default values do not distinguish between natural undisturbed forest and regenerating forest nor forest age (unless <20 years). Domain and climate region classification are according to Table 4.5 and defined in Table 3A.5.2 (4).

*Default values are from the IPCC (4). Above-ground biomass from Table 4.7 (4) averaged across continents for each ecological zone. Carbon fraction in above-ground biomass [Table 4.3 (4)].

†Default values are from the IPCC (4, 66). Litter carbon stocks [Table 3.2.1 (66)]. Ratio of below- to above-ground biomass [Table 4.4 (4)]. Dead wood stocks [Table 3.2.2 (66)].

species enable high levels of light to penetrate the forest floor, allowing luxuriant understory layers to grow (45). Eucalypt foliage is evergreen and minimum winter temperatures in the Central Highlands are moderate, so *E. regnans* trees can grow all year. Similarly, evergreen temperate forests of the Pacific Northwest of North America with high biomass have been found to photosynthesize throughout the year (46).

Natural Disturbance Such as Fire. Fire affects vegetation structure and biomass carbon stocks at multiple spatial scales, such as the landscape, stand, and individual tree levels. Fire can kill but not combust all of the material in trees, leading to much of the biomass carbon changing from the living biomass pool to the standing dead and fallen dead biomass pools. The amount of carbon lost from the forest floor and the soil profile may vary depending on ecosystem type, fire regimes, and postdisturbance weather conditions (47). The dead biomass then decays as the stand grows (48). Slow decomposition rates can therefore result in large total carbon stocks of dead biomass and regrowing living biomass. A study of temperate forests along a subalpine elevation gradient in the United States estimated coarse woody debris turnover time to be 580 ± 180 years (39). Large amounts of coarse woody debris biomass are also typical of old-growth forests of the Pacific Northwest of North America (40).

Unlike the majority of eucalypt species, *E. regnans* does not regenerate by epicormic growth or sprouting from lignotubers after a wildfire. Rather, a tree is killed if its canopy is completely scorched by fire. It then sheds seeds that germinate in the postfire ash-bed conditions (49). In the Central Highlands of Victoria, wetter sites on lower slopes and shaded aspects support longer fire intervals and less intense fires, leading to a greater probability of multiaged stands (50). Whether environmentally controlled or the result of stochastic processes, past partial stand-replacing wildfires produce younger cohorts of fast-growing *E. regnans* trees, mixed with an older cohort of living and dead trees, together with rejuvenating the understory of *Acacia* spp. and other tree species (Fig. 1).

Table 2. Comparison of mean and range climatic conditions for boreal, temperate, and tropical forest biomes based on the global site data (Table S1 and Fig. 3)

Condition	Mean annual temperature, ° C	Total annual precipitation, mm	GEP, $g\ CO_2\ m^{-2}\ y^{-1}$	k, $year^{-1}$
Boreal: mean	−0.6	581	822	0.01
Minimum	−10.0	213	382	0.01
Maximum	8.0	2,250	1,228	0.03
Temperate: mean	9.9	1,850	1,318	0.04
Minimum	1.5	404	923	0.02
Maximum	18.9	5,000	1,740	0.08
Tropical: mean	23.6	2,472	1,961	0.12
Minimum	7.2	800	1,190	0.03
Maximum	27.4	4,700	2,140	0.17
E. regnans: mean	11.1	1,280	1,374	0.04
Minimum	7.0	661	1,181	0.03
Maximum	14.4	1,886	1,529	0.06

Shown is the climatic profile for *E. regnans* calculated by Lindenmayer *et al.* (65). GEP is estimated from a regression correlation derived from flux tower data as a function of mean annual temperature by Law *et al.* (34). *k* is the decomposition rate constant of coarse woody debris calculated from an empirical relationship derived by Chambers *et al.* (42) using forest biome characteristic temperatures.

Land-Use Activity. The final reason for high biomass carbon densities in *E. regnans* forests is a prolonged absence of direct human land-use activity. The O'Shannassy Catchment has been closed to public access for >100 years to provide water for the city of Melbourne. It had an almost complete absence of Indigenous land use before European settlement. Natural disturbances have included wildfire, windstorms, and insect attacks. Logging has been excluded, including postwildfire salvage logging that removes large amounts of biomass in living and dead trees (thus preventing the development of multiple age cohorts) (21, 51, 52).

Some types of temperate moist forests that have had limited influence by human activities can be multiaged and do not necessarily consist exclusively of old trees, but often have a complex multiaged structure of multiple layers produced by regeneration from natural disturbances and individual tree gaps in the canopy (53). Net primary production in some types of multiaged old forests has been found to be 50–100% higher than that modeled for an even-aged stand (54). Both net primary production and net ecosystem production in many old forest stands have been found to be positive; they were lower than the carbon fluxes in young and mature stands, but not significantly different from them (55). Northern Hemisphere forests up to 800 years old have been found to still function as a carbon sink (11). Carbon stocks can continue to accumulate in multiaged and mixed species stands because stem respiration rates decrease with increasing tree size, and continual turnover of leaves, roots, and woody material contribute to stable components of soil organic matter (56). There is a growing body of evidence that forest ecosystems do not necessarily reach an equilibrium between assimilation and respiration, but can continue to accumulate carbon in living biomass, coarse woody debris, and soils, and therefore may act as net carbon sinks for long periods (12, 57–59). Hence, process-based models of forest growth and carbon cycling based on an assumption that stands are even-aged and carbon exchange reaches an equilibrium may underestimate productivity and carbon accumulation in some forest types.

Large carbon stocks can develop in a particular forest as a result of a combination and interaction of environmental conditions, life history attributes, morphological characteristics of tree species, disturbance regimes, and land-use history. Very large stocks of carbon occur in the multiaged and multilayered *E. regnans* forests of the Central Highlands of Victoria. The same suite of factors listed above operate, to varying degrees, across other evergreen temperate forests, particularly in the northwestern United States, southern South America, New Zealand, and elsewhere in southeastern Australia. Collectively, they provide the basis of a generalized framework for predicting high biomass carbon density forests. However, construction of a quantitative predictive model inclusive of all factors is complicated by a lack of process understanding (37), knowledge of species life history characteristics and dynamics, and many interactions and feedback effects (60).

Climate Change Policy Implications

Our results about the magnitude of carbon stocks in forests, particularly in old forests that have had minimal human disturbance, are relevant to negotiations under the United Nations Framework Convention on Climate Change (UNFCCC) concerning reducing emissions from deforestation and forest degradation. In particular, our findings can help inform discussions regarding the roles of conservation, sustainable management of forests and enhancement of forest carbon stocks (ref. 61; http://unfccc.int/resource/docs/2007/cop13/eng/06a01.pdf#page=8). Conserving forests with large stocks of biomass from deforestation and degradation avoids significant carbon emissions to the atmosphere, irrespective of the source country, and should be among allowable mitigation activities negotiated through the UNFCCC for the post-2012 commitment period. Similarly, where practical, management that allows restoration of a forest's carbon sequestration potential should be a recognized mitigation activity.

Our insights into forest types and forest conditions that result in high biomass carbon density can be used to help identify priority areas for conservation and restoration. The global synthesis of site data (Fig. 3 and Table 2) indicated that the high carbon densities of evergreen temperate forests in the northwestern United States, southern South America, New Zealand, and southeastern Australia should be recognized in forest biome classifications.

Concluding Comments

Our findings highlight the value of field-based site measurements in characterizing forest carbon stocks. They help reveal the variability within forest biomes and identify causal factors leading to high carbon densities. Further analyses of existing site data from forests around the world, along with new field surveys, are warranted to improve understanding of the spatial distribution of biomass carbon inclusive of land-use and fire history.

Methods

Biomass of *E. regnans* Forest. The 13,000-ha O'Shannassy Catchment (37.62° S, 145.79° E) has a mean annual rainfall of 1,670 mm, mean annual temperature of 9.4 °C, and annual radiation of 178 W·m^{-2}. Average elevation of the catchment is 830 m, and the area has a generally southerly aspect. Soils are deep red earths overlying igneous felsic intrusive parent material. These are fertile soils with high soil water-holding capacity and nutrient availability compared with most forest soils in Australia. The vegetation is classified as tall eucalypt forest with small pockets of rainforest. The forest is multilayered with an overstory of *E. regnans*, a midstory tree layer of *Acacia dealbata*, *A. frigiscens*, *Nothofagus cunninghamii*, and *Pomaderis aspera*, and a tall shrub layer that includes the tree ferns *Cyathea australis* and *Dicksonia antarctica*.

Inventory sites were established by using a stratified random design to sample the range in dominant age cohorts across the catchment. Stands were aged by a combination of methods, including historical records of disturbance events, tree diameter–age relationships, and cross-checking with dendrochronology. Ages of understory plants ranged from to 100 to 370 years, as determined by radiocarbon dating (62). Different components of the ecosystem survive and regenerate from various previous disturbance events. All living and dead plants >2 m in height and >5 cm in diameter were measured at 318 10-m × 10-m plots nested within 53 sites (each measuring 3 ha) within the catchment. Tree size ranged from 486-cm diameter at breast height (DBH) to 84 m in height (Fig. 1).

Living and dead biomass carbon for each site were calculated by using an allometric equation applied to the inventory data for the individual trees in the plots. The equation related biomass to stem volume and wood density. A reduction factor was included in the equation to account for the reduction in stem volume caused by asymmetric buttresses, based on measurements of stem cross-sections and the area deficit between the actual wood and the perimeter derived from a diameter measurement (43). A second reduction factor was included in the equation to account for decay and hollows in stems of *E. regnans* calculated as a proportion related to tree size. Trees >50 cm DBH begin to show signs of internal decomposition, and by 120 cm DBH actual tree mass is ≈50% of that predicted from stem volume (52). Accounting for decay is an important aspect of estimating biomass from allometric equations derived from stem volume that requires further research, but that is overcome by using direct biomass measurements for the derivation of the allometric equations. Selection of trees for measurement that cover the full range of conditions is also important. Unlike many allometric equations developed for forest inventory purposes, the equation used here was calculated from data representing ecologically mature *E. regnans* trees. Carbon in dead biomass was calculated by using this allometric equation for standing stems with a reduction for decay. Coarse woody debris on the forest floor was measured along 100-m transects (63). The structure of stands with high biomass was described by a bimodal frequency distribution of tree sizes that represented different age cohorts. The maximum amount of biomass carbon occurred in tree sizes 40–100 and 200–240 cm DBH. A lack of comparable high-quality soil data meant we could not provide estimates of below-ground carbon stocks nor consider associated soil carbon dynamics.

Our analyses of biomass carbon stocks used a combination of techniques including field inventory data, biomass measurements, and understanding of carbon cycling processes, as has been recommended by the IPCC (64). The relationship between reflectance from spectral bands, leaf area index, and biomass accumulation is not linear. This is exemplified by the relatively low leaf area of *E. regnans* for the high biomass accumulation in the stemwood of these tall trees. Hence, it is important that all of these types of information are used to estimate biomass carbon stocks and that models are well calibrated with site data, rather than relying solely on remote sensing.

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Global Site Biomass Data. Data on forest biomass were obtained from the literature where biomass was calculated from individual plot data at sites that represent largely mature or primary forest with minimal human disturbance (Table S1). The data were categorized into forest biomes (defined by the IPCC; Table 4.5 in ref. 4). We used field plot data that were available in the published literature as they constitute the most reliable primary data sources. We did not use modeled estimates of biomass carbon or regional estimates derived from forest inventory data and expansion factors to derive wood volume and biomass. A carbon concentration of 0.5 $gC \cdot g^{-1}$ was used where only biomass data were provided. Where site information was not given, latitude and longitude were obtained from Google Earth (http://earth.google.com) by using the described site location, and mean annual temperature and precipitation were obtained from a global dataset (www.cru.uea.ac.uk/cru/data/tmc.htm). Little or no information was provided by most of the publications concerning how internal decay in trees was accounted for in the biomass estimates. Hence, our estimates of biomass of *E. regnans* that were reduced to account for decay are considered conservative compared with the global site data.

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