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

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

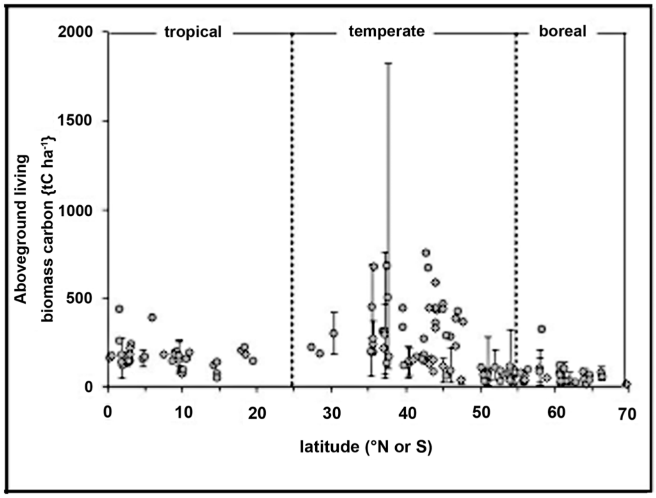

Fig. 2. Global forest site data for above-ground biomass carbon (tC·ha^{-1}) in relation to latitude (north or south). Points are values for individual or average of plots, and bars show the range in values at a site. The O'Shannassy Catchment has a mean of 501 tC·ha^{-1} and ranges from 104 to 1,819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

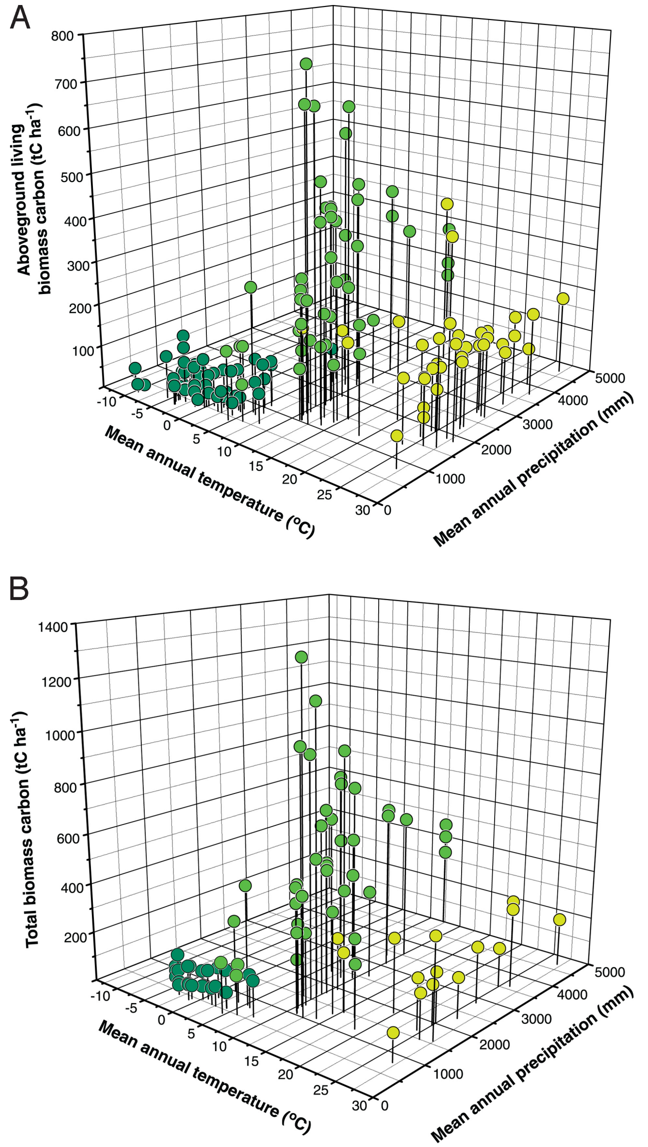

Fig. 3. Global forest site data for above-ground living biomass carbon (tC·ha^{-1}) (*A*) and total biomass carbon (tC·ha^{-1}) (*B*), in relation to mean annual temperature and mean annual precipitation for the site. Site data are shown in relation to their distribution among biomes of boreal (dark 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·ha^{-1}		Root + dead biomass carbon, tC·ha^{-1}		Total living + dead biomass carbon, tC·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 $W \cdot m^{-2}$. 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.

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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Supporting Information

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SI Text

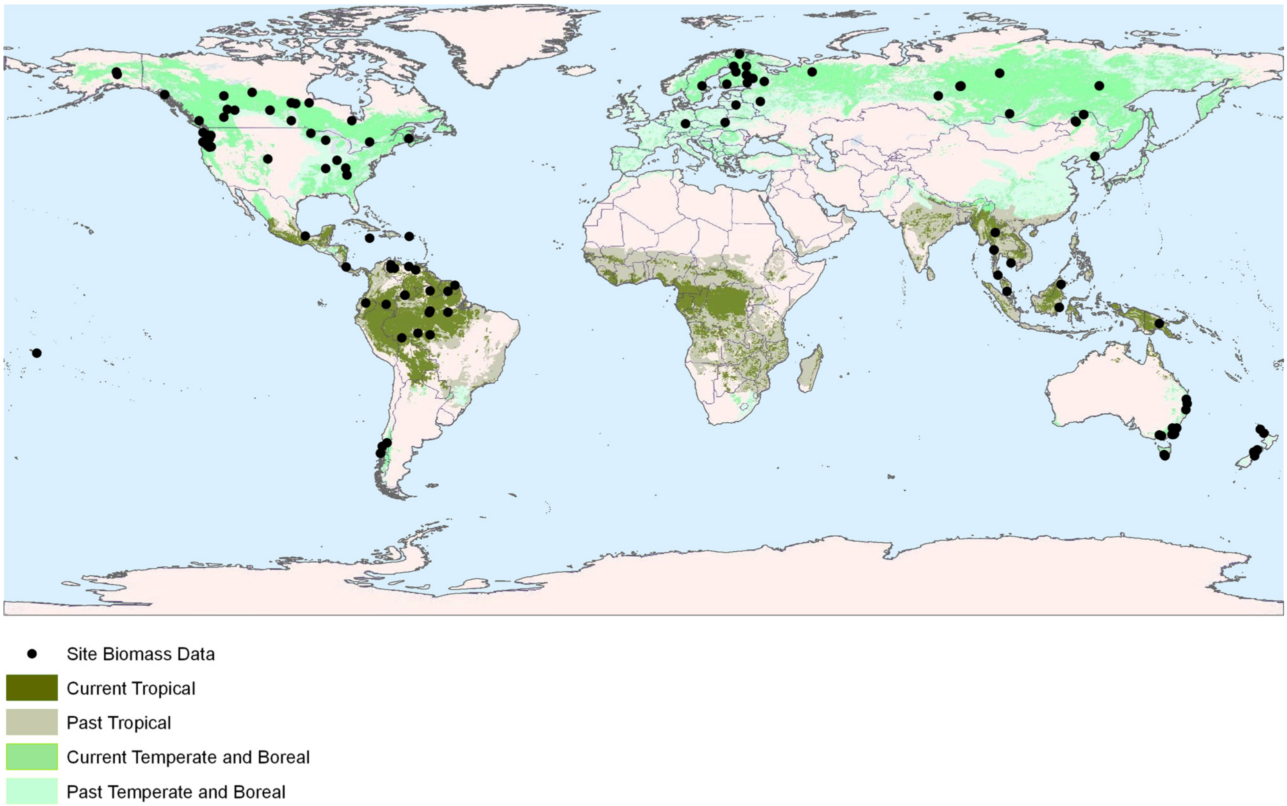

Fig. S1. Distribution of sites with data for biomass carbon from the published literature is shown in relation to global biomes of tropical, temperate, and boreal forest, with their current and original extent. The map of the global distribution of current and original forest areas was obtained from United Nations Environment Programme, World Conservation Monitoring Centre, Global Forest Cover Map.

Table S1. Global sites with biomass data used to analyze trends across forest biomass and to compare with *E. regnans* forests in Australia

Region	Site	Species	Latitude	Longitude	Mean annual temperature, °C	Mean annual precipitation, mm	Aboveground living biomass carbon, tC·ha^{-1}	Total living + dead biomass carbon, tC·ha^{-1}	Ref.
Tropical forest									
Tropical wet									
Central America	Los Tuxtlas, Mexico	tropical, tall evergreen	18.58°N	95.08°W	27.0	4700	181	195	1
	La Selva Biological Station, Costa Rica	tropical wet rainforest	9.85°N	83.60°W	26.0	4000	87		2
South America	Tapajos NF, Brazil	tropical rainforest	3.04°N	54.95°W	25.0	2000	141	202	3,4,5
	Northern Rôndonia State	tropical moist forest	8.75° S	63.38°W	26.2	2300	143	163	6
	Rondonia	upland tropical evergreen forest	9.20°S	60.05°W	25.2	2354	195		7
	Manaus, Central Amazon	tropical evergreen forest	2.50°S	60.00°W	26.7	2200	162		8
	Manaus, Central Amazon	tropical upland moist forest	2.97°S	60.18°W	26.7	2285	180		9
	Rio Negro, Venezuela	tropical moist forest	1.93°N	67.05°W	24.9	3500	117	159	10
	Venezuela	tropical moist forest	9.00°N	64.00°W	25.5	2850	179	227	11
	San Carlos, Venezuela	evergreen sclerophyllous woodland	1.92°N	67.07°W	26.0	3600	182	320	12
	San Carlos, Venezuela	tropical evergreen lowland forest	1.92°N	67.07°W	26.0	3600	138	350	13
	Araracuara, Colombia	ombtophilous tropical rainforest	0.63°S	72.37°W	25.5	2998	175		14
	French Guiana	tropical wet rainforest	4.75°N	53.00°W	25.8	2757	155		15
Oceania	Tutuila Island, Samoa	lowland tropical rainforest	14.30°S	170.68°W	26.9	3207	122		16
Asia	Khao Chong, peninsular Thailand	tropical rainforest	7.50°N	99.80°E	27.2	2700	182		17
	Cheko, Cambodia	evergreen seasonal forest	10.93°N	103.40°E	27.8	3726	191		18
	Ulu Segama FR, Sabah, Malysia	dipterocarp hill forest	5.00°N	117.50°E	26.7	2700	165		19
	Marafunga, New Guinea	lower montane rainforest	6.00°S	145.18°E	13.0	4000	387		20
Tropical moist									
Central America	Eastern Jamaica	montane rainforest	18.00°N	77.00°W	24.4	1685	204	204	21
	Luquillo, Puerto Rico	*Prestoea montana,* tropical palm forest	18.42°N	65.92°W	19.7	1885	224	298	22
South America	Manaus, Central Amazon, Brazil	tropical rainforest	3.10°N	60.03°W	27.4	1571	237	399	23
	Tapajos, Central Amazon	tropical forest	2.85°S	54.97°W	25.0	1920	153	161	24
	Tapajos, Central Amazon	tropical upland moist forest	2.85°S	54.97°W	24.5	1909	141		9
	Rio Branco, western Amazon	open forest	10.12°S	68.00°W	25.0	1940	95		9
	Venezuela	tropical transition moist to dry forest	9.50°N	70.00°W	26.0	1500	148	178	11
Asia	Sebulu, East Kalimantan, Indonesia	tropical lowland evergreen dipterocarp rainforest	1.50°S	116.97°E	27.0	1862	254		25
	Sebulu, East Kalimantan, Indonesia	tropical lowland evergreen dipterocarp rainforest	1.50°S	116.97°E	27.0	1862	436		26
	Pasoh FR, Negeri Sembilan, Malaysia	lowland tropical rainforest	2.97°N	102.30°E	28.0	1842	215		27,28
	Thong Pha Phum NF, Thailand	tropical rainforest	14.67°N	98.68°E	25.0	1650	138		29
	Thong Pha Phum NF, Thailand	dry evergreen forest	14.67°N	98.68°E	25.0	1650	70		29
	Thong Pha Phum NF, Thailand	mixed deciduaous forest	14.67°N	98.68°E	25.0	1650	48		29
	Ping Kong, northwestern Thailand	monsoon forest	19.50°N	99.00°E	24.0	1364	146		17
Tropical dry									
South America	Venezuela	tropical dry forest	10.00°N	66.00°W	27.0	800	70	111	11
Tropical montane									
South America	Venezuela	tropical lower montane moist forest	9.50°N	71.00°W	15.0	1487	173	235	11
	Venezuela	tropical montane wet forest	10.50°N	71.00°W	10.5	1968	157	211	11
	Eastern Andean Mts., Ecuador	*Polylepis incana,* high altitude	0.22°S	78.05°W	7.2	1500	163		30
Temperate forest									
Warm temperate moist									
North America	Alaskan coast	*Tsuga heterophylla, Chamaecyparis nootkatensis, T. mertensiana*	58.37°N	134.72°W	10.0	3550	325	582	31
	Oregon Cascades	*Pseudotsuga menziesii*	44.00°N	122.50°W	10.1	1789	331	526	32
	Oregon coast	*Tsuga heterophylla-Picea sitchensis*	45.00°N	123.93°W	10.1	3115	436	626	32

Region	Site	Species	Latitude	Longitude	Mean annual temperature, °C	Mean annual precipitation, mm	Aboveground living biomass carbon, tC·ha^{-1}	Total living + dead biomass carbon, tC·ha^{-1}	Ref.
	Oregon	*Abies amabilis; Pseudotsuga menziesii*	44.00°N	122.67°W	10.1	1789	440	514	32
	Washington	*Abies amabilis; Pseudotsuga menziesii*	47.00°N	122.67°W	10.1	1789	422	496	32
	Washington	*Pseudotsuga menziesii*	46.00°N	122.00°W	12.5	1000	278	473	33
	Great Smoky Mt.	deciduous mesic	35.67°N	83.38°W	10.3	1744	199		34
	Southern Appalachians	Cove forests	35.68°N	83.42°W	12.7	1306	236		35
	Indiana	*Quercus shumardii, Liquidamber styraciflua*	39.83°N	86.18°W	11.0	1028	117		36
	Kentucky	*Fagus grandifolia, Quercus alba*	37.72°N	83.80°W	12.7	1230	165		37
	Illinois	*Carya ovata, Quercus velutina*	37.52°N	89.32°W	14.4	1270	131		38
South America	Chile	*Nothofagus dombeyi, Drimys winteri, N. nitida, Aextoxicon punctatum*	40.50°S	73.50°W	10.6	1600	142		39
Australasia	Auckland & Northland, NZ	*Agathis australis*	35.72°S	173.63°E	13.9	1640	672	982	40
	Auckland & Northland, NZ	*Agathis australis*	36.90°S	174.57°E	14.4	1341	312	400	40
	Maimai, South Island NZ	*Nothofagus truncata, Podocarpus ferrugineus*	42.16°S	171.75°E	10.9	2600	153	352	41
	Nelson, South Island NZ	*Nothofagus truncata*	41.52°S	172.75°E	10.5	1307	166	289	42
	NSW south coast, Aust.	*E. fastigata, E. sieberi, Corymbia maculata*	35.47°S	150.11°E	13.8	1097	447	615	43
	Gippsland, Aust	*E. fastigata, E. obliqua, E. cypellocarpa*	37.28°S	149.15°E	10.4	1165	310	489	P. Gibbons
	NSW south coast, Aust.	*E. fastigata, E. sieberi, Corymbia maculata*	35.60°S	149.88°E	10.8	1090	270	487	B. Mackey
	northern NSW, Aust.	*Caldluvia paniculosa, Geissois benthami*	28.50°S	153.00°E	18.9	1192	182	252	44
	NSW south coast, Aust.	*E. sieberi, E. agglomerata, E. obliqua*	37.00°S	149.50°E	11.2	1051	218	319	45
	montane, south east Aust.	*E. delegatensis*	35.37°S	148.83°E	10.3	1185	199	333	H. Keith
	southern NSW & Vict., Aust.	*E. bridgesiana, E. cypellocarpa, E. muellerana*	37.26°S	148.71°E	11.2	1041	294	433	A. Claridge
	southern Qld., Aust.	*Argyrodendron*	27.33°S	152.75°E	17.0	1448	224	310	46
	central Victoria, Aust.	*E. regnans*	37.43°S	145.18°E	10.4	1244	678	1000	47
	northern NSW, Aust.	*E. pilularis*	30.33°S	152.64°E	15.2	1467	298	477	48
Cool temperate moist									
North America	Oregon coast	*Tsuga heterophylla-Picea sitchensis*	45.00°N	123.90°W	8.6	2575	465	762	49
	Washington coast	*Tsuga heterophylla-Picea sitchensis*	47.70°N	123.90°W	8.5	3356	364	624	49
	Oregon Cascades	*Pseudotsuga menziesii* dominated	44.20°N	122.20°W	8.4	2002	432	707	49
	Washington Cascades	*Abies amabilis; Tsuga heterophylla*	46.80°N	121.70°W	6.4	2375	380	636	49
	Oregon Cascades	*Pseudotsuga menziesii*	44.00°N	122.50°W	8.5	2300	356	568	50
	Oregon Cascades	*Pseudotsuga menziesii*	44.00°N	122.50°W	8.5	2300	587	794	51
	Washington Cascades	*Abies amabilis*	46.80°N	121.70°W	5.4	2700	224	781	52
	Colorado, Rocky Mt. NP	*Picea engelmannii, Abies lasiocarpa*	40.28°N	105.63°W	1.5	1000	124	289	53
South America	Cordillera de Piuchue, Chile	*Nothofagus dombeyi, Drimys winteri, Laureliopsis philippiana*	42.50°S	74.00°W	7.2	5000	179	395	54,55,56
	Cordillera de Piuchue, Chile	*Fitzroya cupressoides*	42.50°S	74.00°W	7.2	5000	268	450	54,55,56
	Cordillera de Piuchue, Chile	*Philgerodendron uviferum, Tepualia stipularis*	42.50°S	74.00°W	7.2	5000	146	326	54,55,56
	San Pablo de Tregua, Andes, Chile	*Nothofagus dombeyi, Laureliopsis philippiana, Saxegothaea conspicua*	39.63°S	72.08°W	9.7	2400	439	571	57
	San Pablo de Tregua, Andes, Chile	*Laureliopsis philippiana, Saxegothaea conspicua, Dassyphyllum diacanthoides*	39.63°S	72.08°W	9.7	2400	332	428	57
Australasia	Central South Island NZ	*Nothofagus solandri*	43.25°S	172.00°E	8.0	1447	123	150	58
	Central Highlands, Vict., Aust.	*Eucalyptus regnans*	37.62°S	145.79°E	9.4	1668	501	1141	D. Lindenmayer
	southern Tasmania, Aust.	*E. obliqua*	43.21°S	146.70°E	9.8	1722	444	673	H. Keith

Region	Site	Species	Latitude	Longitude	Mean annual temperature, °C	Mean annual precipitation, mm	Aboveground living biomass carbon, tC·ha^{-1}	Total living + dead biomass carbon, tC·ha^{-1}	Ref.
	southern Tasmania, Aust.	*E. regnans*	42.83°S	146.57°E	8.6	1503	752	1302	59
	southern Tasmania, Aust.	*E. obliqua*	43.09°S	146.70°E	9.9	1490	668	956	59
Cool temperate dry									
North America	Eastern Oregon	*Pinus ponderosa-Pinus contorta*	43.70°N	121.60°W	6.2	497	85	157	49
	Wisconsin	*Tsuga canadensis: Pinus strobus*	45.50°N	89.33°W	5.3	800	286	476	60
	Oregon, Waldo Lake	*Tsuga mertensiana, Pinus contorta, Pinus monticola*	43.50°N	122.00°W	4.6	404	158	202	61
Cool temperate montane									
Asia	Changbai, China	*Acer mono, Betula costata,Pinus koraiensis, Tilia amurensis*	41.00°N	127.00°E	3.9	782	147	153	62
Boreal forest									
Boreal moist									
North America	Minnesota, USA	*Picea marina*	47.50°N	93.50°W	4.1	690	34		63
	Alberta, Canada	*Pinus contorta, Populus tremulous, Picea glauca*	54.25°N	117.00°W	2.6	500	50	79	64
	Thompson, Manitoba, Canada	*Picea marina* - dry	55.80°N	97.87°W	0.1	536	72	116	65
	Thompson, Manitoba, Canada	*Picea marina* - wet	55.80°N	97.87°W	0.1	536	31	53	65
	Manitoba, Canada, BOREAS NSA	*Picea marina*	55.99°N	98.99°W	-4.6	536	57	74	66,67
	Manitoba, Canada, BOREAS NSA	*Pinus banksiana*	55.99°N	98.99°W	-4.6	536	29	50	66,67
	Manitoba, Canada, BOREAS NSA	*Populus tremuloides*	55.99°N	98.99°W	-4.6	536	57	92	66,67
	Canada - Atlantic Maritime		46 °N	66 °W	5.0	1200	87		68
	Canada - Mixedwood Plains		45 °N	77 °W	6.5	860	113		68
	Canada - Pacific Maritime		51 °N	125 °W	6.7	2250	80		68
	Canada - Montane Cordillera		52 °N	118 °W	4.0	1000	107		68
	Canada - Hudson Plains		56 °N	94 °W	-3.0	600	34		68
	Canada - Eastern Boreal Shield		51 °N	82 °W	5.5	1000	67		68
Siberia	Zotino	*Pinus sylvestris*	60.73°N	89.15°E	-3.3	663	75	92	69
	Karelia, Russia	*Picea abies*	62.00°N	34.00°E	2.2	650	38		70
	Tomsk, Russia	*Pinus sylvestris*	58.00°N	83.00°E	-0.8	501	81		71
Europe	Fyedorovskoye, European Russia	*Picea abies*	56.45°N	32.92°E	3.6	714	95		69
	Waldstein, Germany	*Picea abies*	50.15°N	11.87°E	5.8	1100	105		69
	Tampere, southern Finland	*Pinus sylvestris, Picea abies, Betula pendula, B. pubescens*	61.28°N	23.44°E	4.0	548	102	153	72
	Rovaniemi, northern Finland	*Pinus sylvestris, Picea abies, Betula pendula, B. pubescens*	66.34°N	25.50°E	0.5	591	77	116	72
	Kangasvaara, eastern Finland	*Picea abies, Pinus sylvestis, Betula pubescens, Populus tremula*	63.85°N	28.97°E	1.2	709	82	123	73
	Central Finland	*Pinus sylvestris*	64.72°N	26.02°E	2.0	500	34	67	74
	Southern Finland	*Pinus sylvestris*	61.65°N	29.28°E	4.0	550	28	64	74
	Lithuania	*Pinus sylvestris*	55.42°N	26.02°E	6.0	760	75	133	74
	southern Poland	*Pinus sylvestris*	50.47°N	22.98°E	8.0	600	68	143	74
	Llomantsi, Finland	*Picea abies, Pinus sylvestis, Betula pubescens*	62.85°N	30.88°E	1.7	640	25		75
	Jädraås, Sweden	*Pinus sylvestris*	60.82°N	16.50°E	3.0	731	29		76,77
	Oulu, Finland	*Picea excels*	66.37°N	29.00°E	0.0	500	51		78
Boreal dry									
North America	Alaska, USA	*Picea glauca, P. marina, Populus/Alnus, Betula papyrifera*	64.75°N	148.25°W	-3.5	269	61		79
	Alaska, USA	*Picea marina*	64.00°N	148.00°W	-3.4	275	43		80
	Saskatchewan, Canada, BOREAS-SSA	*Picea marina*	53.99°N	104.99°W	-1.1	405	49	66	66,67
	Saskatchewan, Canada, BOREAS SSA	*Pinus banksiana*	53.99°N	104.99°W	-1.1	405	35	63	66,67

Region	Site	Species	Latitude	Longitude	Mean annual temperature, °C	Mean annual precipitation, mm	Aboveground living biomass carbon, tC·ha^{-1}	Total living + dead biomass carbon, tC·ha^{-1}	Ref.
	Saskatchewan, Canada, BOREAS SSA	*Populus tremuloides*	53.99°N	104.99°W	-1.1	405	93	136	66,67
	Canada - Taiga Plains		58 °N	118 °W	-5.5	350	99		68
	Canada - Western Taiga Shield		59 °N	110 °W	-4.0	350	47		68
	Canada - Western Boreal Shield		51 °N	99 °W	-4.0	400	33		68
	Canada - Boreal Plains		54 °N	115 °W	0.0	462	113		68
Siberia	Yakutsk	*Larix gmellinii*	60.85°N	128.27°E	-10.0	213	55		69
	Central Siberia	*Pinus sylvestris, lichen*	60.75°N	89.41°E	-3.7	493	62		81
	Central Siberia	*Pinus sylvestris, Vaccinium* mosses	60.73°N	89.32°E	-3.7	493	149		81
	Central Siberia, Yenisei River	*Pinus sylvestris, lichen*	60.72°N	89.13°E	-3.7	493	65	88	82
	Central Siberia, Yenisei River	*Pinus sylvestris, Vaccinium* mosses	60.72°N	89.13°E	-3.7	493	121	152	82
	Koinas, Russia	*Picea abies*	64.67°N	47.50°E	-1.2	499	66		80
	Irkutsk	*Pinus sylvestris*	53.00°N	103.00°E	-1.2	470	71		83
	Yakutsk	*Larix gmelinii*	60.85°N	128.27°E	-9.6	213	18		83
	Tura	*Larix gmelinii*	64.32°N	100.22°E	-9.5	322	11		84
Europe	northern Finland	*Pinus sylvestris*	69.73°N	27.02°E	-1.0	450	14	54	74
Asia	China, Daxing'anling	*Larix gmelinii*	50.83°N	121.50°E	-5.4	500	26		85
	China, Daxing'anling	*Larix gmelinii*	50.68°N	121.84°E	-4.0	425	31		86
	China, Daxing'anling	*Larix gmelinii-Ledum*	52.73°N	123.83°E	-3.0	425	28	54	87
	China, Daxing'anling	*Larix gmelinii-grass*	52.73°N	123.83°E	-3.0	425	30	40	87
	China, Daxing'anling	*Larix gmelinii-Rhododendron*	52.73°N	123.83°E	-3.0	425	93	101	87

Canadian sites from ref. 59 are average values from plots within a region, where the individual plot data were not provided in the reference.

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