Forest Ecology and Management 296 (2013) 81–89

Contents lists available at SciVerse ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Carbon stocks in primary and secondary tropical forests in Singapore

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ARTICLE INFO

Article history:
Received 2 August 2012
Received in revised form 27 January 2013
Accepted 7 February 2013

Keywords:
Aboveground and belowground biomass
Carbon pools
Coastal hill dipterocarp forest
Ecosystem carbon
Necromass
Tropical rain forest

ABSTRACT

Tropical forests contain large reserves of carbon that are vulnerable to perturbation linked to human activities, including deforestation and climate change. Accurate estimates of forest carbon are therefore required urgently to support efforts to conserve tropical forests. We quantified carbon stocks in primary and 60-year-old secondary forest plots located on infertile Ultisols in Bukit Timah Nature Reserve, one of the few remaining areas of forest in Singapore. We used tree census data for 24.2 ha of primary forest and 23 ha of secondary forest, together with allometric equations, to estimate aboveground and coarse root biomass. Coarse woody debris stocks were censused along 2.44 km and 2.12 km of transects in primary and secondary forest, respectively. Soil carbon and fine root carbon stocks were assessed from soil samples taken to 3 m depth in a 2-ha secondary forest plot and a 2-ha primary forest plot, combined with bulk density measured in a nearby soil profile pit. Total estimated carbon stock in the primary forest, which was located on the hilltop and upper slopes (80–115 m elevation), was 337 Mg C ha^{-1}, of which 50% was aboveground biomass, 33% in soil, 12% in coarse roots, 4.6% in coarse woody debris, and 0.8% in fine roots. In the secondary forest, located on lower slopes and valley (50–85 m elevation), the total carbon stock was 274 Mg C ha^{-1} and the relative importance of aboveground biomass and soil were reversed, with 38% in aboveground biomass, 52% in soil, 6.9% in coarse roots, 1.5% in coarse woody debris, and 1.3% in fine roots. Including carbon in deep subsoil (i.e. to 3 m) increased soil carbon stocks by ~40% compared to 1 m depth. Overall, the 60-year-old secondary forest contained 60% as much biomass as the primary forest, while the primary forest had lower carbon stocks than other primary forests in the region.

1. Introduction

Tropical forests play an important role in the global carbon cycle. They contain about 40% of global terrestrial carbon, account for more than half of global gross primary productivity, and sequester large amounts of CO_2 from the atmosphere (Beer et al., 2010; Grace, 2004; Pan et al., 2011). Slightly more than half of the carbon in tropical forests is in the neotropics, with the remainder in Asian and African forests (Dixon et al., 1994).

Carbon is stored in forests predominantly in live biomass and in soils, with smaller amounts in coarse woody debris (Malhi et al., 2009; Sierra et al., 2007). In tropical forests worldwide, about 50% of the total carbon is stored in aboveground biomass and 50% is stored in the top 1 m of the soil (Dixon et al., 1994). However, there are marked differences among sites. For example, an African moist tropical forest had more than three times as much carbon in aboveground biomass as in soil to 1 m depth (Djomo et al., 2011), while a Peruvian montane forest had twice as much carbon in soil as in aboveground biomass (Gibbon et al., 2010). In Asia, a tropical seasonal forest in China (Lü et al., 2010) and a selectively-logged lowland dipterocarp forest in Sabah, Malaysia (Saner et al., 2012), both contained twice as much carbon in biomass as in soil, while a secondary forest in the Philippines contained 50% more carbon aboveground than in soil (Lasco et al., 2004).

The differences in carbon storage among tropical forests reflect variation in a number of factors, including tree community composition, disturbance history, successional stage, climate, and soil fertility. Secondary forests are of particular significance, given that the proportion of tropical forests that are secondary is projected to continue to increase due to increasing anthropogenic pressure and the movement of populations towards urban centers (Thomlinson et al., 1996; Wright, 2005). Thus, carbon stocks and uptake in secondary forests are an increasingly important part of global tropical

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http://dx.doi.org/10.1016/j.foreco.2013.02.004

forest carbon budgets. As more forests come under threat from deforestation and degradation, additional information on carbon stocks and pools in tropical forests worldwide is required to understand controls on carbon stocks and cycling, to calibrate global carbon cycle models, and to support regulatory frameworks such as the United Nations REDD program (Reducing Emissions from Deforestation and Forest Degradation in Developing Countries).

In Singapore, more than 95% of the original forest has been cleared, most of it prior to the 1870s (Corlett, 1992). Much of the remaining forest cover is secondary, although a few small patches of protected primary forest remain. Here we report carbon stocks in long-term forest dynamics plots in primary and secondary forests in Bukit Timah Nature Reserve, one of the few areas of protected forest on the island of Singapore. The site supports dipterocarp forest growing on infertile soils developed on granite bedrock (Burslem et al., 1994). We estimate carbon stored in living trees, coarse woody debris, and soil. Importantly, we estimated soil carbon to 3 m depth; most studies only sample to 1 m, but tropical forest soils, including those at Bukit Timah, can be very deep (e.g. >5 m in Bukit Timah; see Supplementary material) and previous studies may therefore have underestimated soil carbon stocks.

2. Methods

2.1. Study site

Bukit Timah Nature Reserve (BTNR) is a 164-ha forest reserve in central Singapore that contains the island's largest remaining patch of primary forest (LaFrankie et al., 2005). The reserve is naturally dominated by coastal hill dipterocarp forest and contains Singapore's highest natural point (164 m above sea level). The core area of BTNR is a 70-ha block of mainly primary forest dominated by *Shorea curtisii* Dyer ex King, a hill forest species usually found at higher elevation in Peninsular Malaysia (Symington et al., 2004). The remainder of the reserve includes secondary forest regrowth on agricultural land abandoned since the 1950s (Lau and Noor, pers. comm.) and former cattle pasture dominated by the exotic African tulip tree (*Spathodea campanulata*).

Climate is aseasonal, with an average temperature of 27.0 °C between 1929 and 2011. Mean annual rainfall is 2342 mm with all months receiving more than 100 mm on average (National Environment Agency, 2012). Soils in BTNR are Typic Paleudults of the Rengam series formed on Bukit Timah Granite (Ives, 1977), although this differs from the classification of a pedon adjacent to the primary forest plot studied here (see below). The soils are very acidic and infertile (Burslem et al., 1994; Grubb et al., 1994), with a particularly strong response of tree seedlings to phosphorus addition (Burslem et al., 1994).

2.2. Field data collection

Data from three different censuses were used to estimate tree biomass: 2008 censuses of all trees ⩾1 cm dbh in a 2-ha primary forest plot (LaFrankie et al., 2005) and in 1.74 ha of a 2-ha secondary forest plot (the excluded area includes some primary forest), and a 2005 "Big Tree" survey that measured trees ⩾30 cm dbh in the whole 164-ha reserve (Fig. 1). Trees were tagged, mapped and identified to species. Trunk diameters were measured at 1.3 m or above buttresses, and are henceforth referred to as dbh (diameter at breast height), even if measurement height was not at 1.3 m. Within the "Big Tree" survey, a 22.2-ha area of primary forest and a 23-ha area of secondary forest were chosen for analysis based on an analysis of species composition (unpublished data).

Coarse woody debris (CWD) was censused between September 2009 and February 2010, largely following the protocols established by Larjavaara and Muller-Landau (2009a, 2009b, 2010, 2011). The CWD census was done along transects using line-intersect methods (Warren and Olsen, 1964), with a little over half the sampling effort concentrated in the 2-ha plots. Nine 40 × 40 m subplots from the 2-ha primary forest plot and seven from the 2-ha secondary forest plot were sampled, with 160 m of transects within each subplot (Larjavaara and Muller-Landau, 2009a). Ten 200 m transects were spread out regularly in the wider reserve for sampling (Larjavaara and Muller-Landau, 2009b), five in primary and five in secondary forest. Standing woody debris ⩾20 cm dbh was censused in the 2-ha plots only, and necromass of individual stems was estimated from diameter using the equations above. Where stumps were shorter than dbh, diameter was measured at the midpoint of the stump (Larjavaara and Muller-Landau, 2009a). Because destructive sampling was not allowed in BTNR, woody debris wood density was estimated from penetrometer penetration using a relationship fitted for data from Barro Colorado Island, Panama (Larjavaara and Muller-Landau, 2010).

Soils were sampled between April and June 2008 in the 2-ha plots only. Cores were taken systematically from alternate 20 × 20 m quadrats, giving a total of 26 sample locations in each 2 ha plot. In each plot, we used a 6 cm diameter constant volume corer to take samples from 0 to 10 cm (26 cores per plot) and 10–20 cm (18 cores per plot) and then a 7.5 cm diameter auger to take samples from 20 to 50 cm and 50 to 100 cm (10 cores for each depth) and 100–300 cm (2 cores taken in 50 cm increments). Samples were air-dried and roots and stones were removed by hand. Fine roots (<2 mm diameter) were separated by hand, dried at 60 °C, and weighed. The soils were then sieved (<2 mm) and a subsample ground for analysis. Soil carbon concentration was determined by combustion and gas chromatography using a Thermo Flash EA 1112 Elemental Analyzer (CE Elantech, Lakewood, NJ).

Bulk density was determined for surface soils (0–10 cm and 10–20 cm) using a constant volume corer as described above (i.e., a bulk density value was calculated for every sample). Total sample weight was measured and corrected for oven-dried weight of fine earth by determining moisture content on a subsample (105 °C, 24 h) and correcting for root biomass (>2 mm). Bulk density was determined for deeper samples (>50 cm) by digging a 2 m deep soil profile pit close to the primary forest plot and taking bulk density samples by the compliant cavity method every 10 cm. Information on the profile, including profile description and analytical data, is presented in Supplementary material.

2.3. Calculations

Aboveground biomass (AGB) of each tree stem was estimated using the allometric equation for moist tropical forest from Chave et al. (2005):

$$\mathrm{AGB} = \rho \times \exp(-1.499 + 2.148\ln(\mathrm{dbh}) + 0.207(\ln(\mathrm{dbh}))^2 - 0.0281(\ln(\mathrm{dbh}))^3)$$

where ρ is wood specific gravity, dbh is in cm, and AGB is in kg dry mass. The generic moist tropical forest equation was used because site-specific equations were not available, and because the annual precipitation of BTNR falls within the interval 1500–3500 mm. Aboveground biomass was calculated for trees of 1–30 cm dbh in the 2-ha plots, and for the ⩾30 cm dbh size class from the 2-ha plots and the Big Tree survey. Data from the 2008 census for the 2-ha plots were used in this analysis. Each species was assigned a wood specific gravity value obtained from a worldwide database (Chave et al., 2005), with species level values used for 274 species, genus level for 200 species and family level for 21 species. Belowground biomass in coarse roots was estimated using allometric equations developed in Malaysia. The equation to estimate coarse

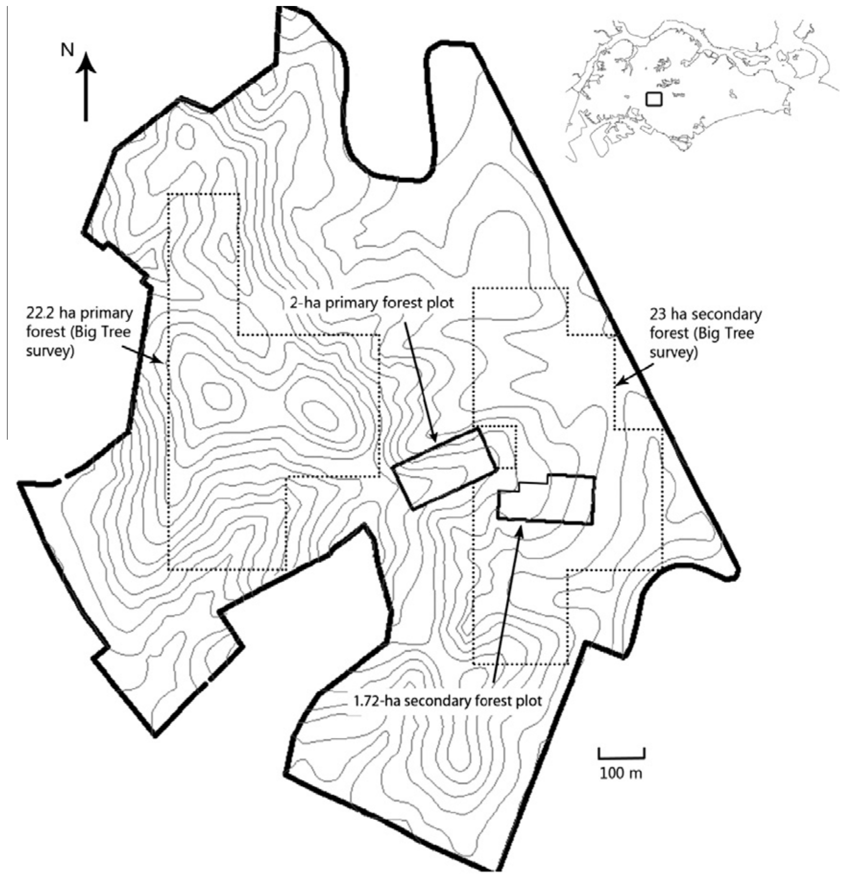

Fig. 1. Map of the Bukit Timah Nature Reserve, Singapore, showing the locations of the primary and secondary forest plots.

root biomass from dbh was taken from Niiyama et al. (2010) for primary forest (R^2 = 0.98) and Kenzo et al. (2009) for secondary forest (R^2 = 0.94). We calculated confidence intervals for both AGB and coarse root biomass using 1000 bootstraps over 20 × 20 m quadrats, thus providing information on uncertainty related to spatial variation in biomass within the study area.

Woody debris volume per area was calculated from transect data using $V = \frac{\pi^2}{8L}\sum d_i^2$, where V is the volume per area (m^3/m^2), L is the total length of the transect (m) and d the diameter (m) of the ith piece of woody debris encountered. Total mass of woody debris was calculated using $M = \frac{\pi}{2L}\sum c_i$ where M is total mass per area (kg m^{-2}), L is total transect length and c is cross-section mass (kg m^{-1}), i.e., dry mass per unit length of the fallen log (Larjavaara and Muller-Landau, 2011). Mean woody debris values were calculated by treating 20 m sections of all transects as replicates. Confidence intervals were calculated by 1000 bootstraps over 20 m sections.

Soil carbon and fine root biomass per unit volume, and per unit ground area, were calculated for each sample using bulk density values.

To convert aboveground biomass, coarse root, fine root, and coarse woody debris dry mass values to carbon stocks, we assumed that 50% of the dry mass was carbon. Studies at nearby sites in Malaysia having similar species composition have found average carbon content close to 50% (Kenzo et al., 2010; Kenzo, pers. comm.).

3. Results

3.1. Aboveground biomass

There was significantly higher AGB in the primary forest than in the secondary forest (Table 1). Trees ⩾30 cm dbh contained 77% and 55% of the AGB in the primary and secondary forests, respectively. There was significantly higher AGB in the 1–10 cm and ⩾30 cm dbh size classes in the primary forest, while the secondary forest had significantly higher AGB in the 10–30 cm size class.

The 10 species contributing the most biomass in the ⩾30 cm size class accounted for about half of the total AGB in the primary forest, but only 28.7% in the secondary forest (Supplementary material Table 1). In contrast, the ten species contributing the most biomass in the 10–30 cm size class accounted for only 7.6% of the total AGB in the primary forest, but 31.7% in the secondary forest (Supplementary material Table 2). Dipterocarpaceae, the dominant tree family, contributed a large proportion of AGB in the primary forest. *S. curtisii* and *Dipterocarpus caudatus* made up 24% and 7.1% of AGB in the ⩾30 cm size class (Supplementary material Table 1). For the 10–30 cm size class, *S. curtisii* again accounted for the highest percentage of AGB, followed by *Streblus elongatus* (Moraceae) and *Timonius wallichianus* (Rubiaceae) (Supplementary material Table 2), both of which are common species in primary and mature secondary forest. In secondary forest, *Ixonanthes reticulata* (Ixonanthaceae) had the highest AGB in the ⩾30 cm size class, followed by *Campnosperma auriculata* (Anacardiaceae) (Supplementary material Table 1), even though there were far more *C. auriculata* individuals (288) than *I. reticulata* individuals (119).

3.2. Fine and coarse root biomass

The majority of the fine roots in both primary and secondary forest plots were contained in the upper 10 cm of soil; the secondary forest contained more fine roots in this horizon than the primary forest (Table 3). No roots were detected in secondary forest soils below 50 cm, while roots were detected to 3 m depth in the primary forest plot. However, in the upper meter of soil the total fine root biomass was ∼50% greater in the secondary compared

Table 1
Tree aboveground biomass (AGB) and density in primary and secondary forests. Figures in parentheses indicate 95% confidence intervals based on 1000 bootstrap samples over 20 × 20 m subplots.

Tree size class (dbh)	Primary forest		Secondary forest	
	AGB (Mg ha^{-1})	Individuals (ha^{-1})	AGB (Mg ha^{-1})	Individuals (ha^{-1})
1–10 cm	15.37 (14.40–16.34)	5909 (5547–6245)	11.53 (10.42–12.61)	1365 (1133–1614)
10–30 cm	60.96 (53.42–68.93)	336 (305–368)	81.85 (73.57–91.47)	468 (420–522)
⩾30 cm [a]	258.66 (241.39–277.67)	79 (75–83)	115.66 (105.43–126.17)	60 (56–64)
Total	334.98 (315.60–354.37)		209.04 (195.80–223.04)	

[a] Stocks for trees ⩾30 cm were averaged over the entire study area, while stocks for trees <30 cm were based only on the 2-ha plots.

to the primary forest plot (Table 3). When roots to 3 m depth were considered, the secondary forest contained only around one third more fine root biomass than the primary forest.

Using the equations of Niiyama et al. (2010) and Kenzo et al. (2009), we estimated that coarse roots (i.e., total belowground carbon minus fine root carbon) contributed 40.2 and 18.8 Mg C ha^{-1} biomass in the primary and secondary forests, respectively.

3.3. Coarse woody debris

There was three times more necromass in the primary forest (31.2 Mg ha^{-1}) than in the secondary forest (8.3 Mg ha^{-1}) (Table 2). The majority of the necromass in both forests was standing woody debris, which accounted for 61% and 71% of necromass in the primary and secondary forests, respectively (Table 2). There was considerably more fallen and standing woody debris in the primary compared to the secondary forest, although confidence intervals for the latter were wide and the difference was not statistically significant. This may be due to the small sample size for standing dead wood.

3.4. Soil carbon stocks

The soil profile pit excavated close to the primary forest plot confirmed the soils as Ultisols (Typic Kanhapludult), with clear clay accumulation in the subsoil and a low effective cation exchange capacity (<5 cmol$_c$ kg^{-1}) in the clay enriched horizon (i.e., a kandic horizon) (Soil Survey Staff, 1999). The soil contained very low concentrations of base cations (total exchangeable bases <1 cmol$_c$ kg^{-1} throughout the profile) and most of the cation exchange capacity was aluminum. Total phosphorus was also low (<10 mg P kg^{-1} in subsoil >50 cm deep) and the soils were extremely acidic throughout (pH in deionized water ⩽ 4.0 in the upper meter). Below the kandic horizon the soil contained ∼20% fine gravel, consisting of angular quartz fragments from the granite parent material. A full profile description and analytical information is provided in Supplementary material.

Carbon concentrations in surface soil (0–10 cm) of the primary plot (2.9 ± 0.8%, mean ± standard deviation of 26 samples) were lower than in the secondary plot (4.1 ± 1.4%) (Fig. 2). This was reflected in differences in bulk density (see below), which was greater for the primary plot. Subsoil horizons in the two plots contained similar carbon concentrations, with <0.5% in soils deeper than 50 cm, and <0.2% in soils deeper than 150 cm (Fig. 2). There was little further variation down to >5 m, as revealed by measurements in a soil profile pit adjacent to the primary forest plot (Supplementary material). Soil carbon to nitrogen ratios were in general much higher in the upper 50 cm of soil in the secondary forest (soil C:N 22–31) compared to the primary forest (soil C:N 11–17).

Bulk density for the 0–10 cm depth was 0.79 ± 0.17 g cm^{-3} (mean and standard deviation of 26 samples) for the primary plot and 0.71 ± 0.24 g cm^{-3} for the secondary plot. These values were comparable to the value for 0–10 cm depth obtained by the compliant cavity method in a soil profile pit adjacent to the primary forest plot (i.e., bulk density = 0.89 g cm^{-3}). For the 10–20 cm depth, bulk density was 0.97 ± 0.18 g cm^{-3} for the primary plot and 1.12 ± 0.28 g cm^{-3}for the secondary forest plot (n = 18 samples), compared to 1.36 g cm^{-3} in the profile pit. Bulk density measurements in deeper soils taken by the compliant cavity method in the profile pit in the primary forest plot ranged between 0.97 and 1.31 g cm^{-3}, the variation reflecting the relatively large content of coarse fragments in subsoil horizons (see above).

When converted to carbon stocks, more soil carbon was contained in the secondary forest compared to the primary forest. In the upper 1 m, for example, the primary forest contained 77.5 Mg C ha^{-1} while the secondary forest contained 103.9 Mg C ha^{-1}, approximately one third more carbon (Table 3). Including soil to 3 m increased carbon stocks to 110.8 and 143.2 Mg C ha^{-1} for the primary and secondary forests, respectively, an increase of 43% and 38%, respectively, compared to the upper 1 m (Table 3).

3.5. Total carbon stocks in Bukit Timah Nature Reserve

The total carbon stock was greater in primary forest (337 Mg C ha^{-1}) than secondary forest (274 Mg C ha^{-1}) (Table 4). The secondary forest therefore contained 63 Mg C ha^{-1} less carbon than the primary forest, a difference of 19%.

Of the four main compartments measured, the majority of the carbon in both primary and secondary forests was contained within aboveground biomass and soil (Table 4). However, there was marked variation in the proportional contribution of these two main pools between the two forests. The majority of the carbon in primary forest was in aboveground biomass (49.8%), with only

Table 2
Coarse woody debris stocks in primary and secondary forests in Bukit Timah Nature Reserve, Singapore. Values in parentheses indicate 95% confidence intervals based on 1000 bootstrap samples of 20-m transect sections.

	Primary forest		Secondary forest	
	Necromass (Mg ha^{-1})	Volume (m^3 ha^{-1})	Necromass (Mg ha^{-1})	Volume (m^3 ha^{-1})
Fallen	12.31 (8.40–19.37)	47.20 (35.18–77.47)	2.43 (0.61–5.09)	7.55 1.99–16.52)
Standing	18.87 (5.84–23.49)	58.07 (18.10–74.86)	5.88 (0.96–13.81)	16.64 (2.95–37.63)
Total	31.18	105.27	8.31	24.19

Table 3
Soil carbon stocks and fine root biomass in primary and secondary forests in Bukit Timah Nature Reserve, Singapore. Values in parentheses indicate standard errors.

Depth (cm)	Primary forest		Secondary forest	
	Soil C (Mg C ha^{-1})	Fine roots (Mg ha^{-1})	Soil C (Mg C ha^{-1})	Fine roots (Mg ha^{-1})
0–10	22.1 (± 0.8)	2.72 (± 0.31)	28.4 (± 2.4)	5.07 (± 0.50)
10–20	12.2 (± 0.9)	0.60 (± 0.10)	19.4 (± 1.9)	1.33 (± 0.24)
20–50	19.4 (± 0.7)	0.81 (± 0.23)	26.7 (± 2.7)	0.64 (± 0.15)
50–100	23.8 (± 0.8)	0.57 (± 0.50)	29.4 (± 6.8)	0
100–150	13.4 (± 0.6)	0.48 (± 0.04)	15.2 (± 1.8)	0
150–200	8.3 (± 1.0)	0.03 (± 0.03)	8.6 (± 1.1)	0
200–250	6.8 (± 0.4)	0	6.7 (± 0.6)	0
250–300	4.9[a]	0.09[a]	8.8 (± 0.2)	0
Total to 1 m	77.5	4.70	103.9	7.04
Total to 2 m	99.2	5.20	127.7	7.04
Total to 3 m	110.8	5.29	143.2	7.04

[a] Only a single sample collected at this depth.

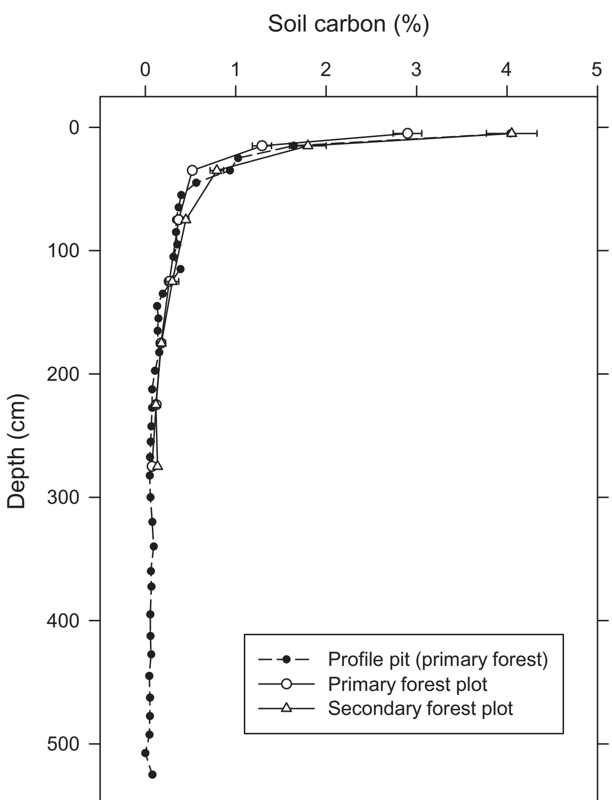

Fig. 2. Soil carbon concentrations in primary and secondary forest plots (to 300 cm depth) and a profile pit (sampled to >500 cm depth) in Bukit Timah Nature Reserve, Singapore. Error bars indicate standard errors.

Table 4
Carbon stock estimates for primary and secondary forests in Bukit Timah Nature Reserve, Singapore. Biomass was assumed to contain 50% carbon.

Component	Primary forest		Secondary forest	
	Mg C ha^{-1}	% of total	Mg C ha^{-1}	% of total
Aboveground biomass	167.5	49.8	104.5	38.1
Coarse roots	40.2	11.9	18.8	6.9
Fine roots	2.6	0.8	3.5	1.3
Soil (to 3 m)	110.8	32.9	143.2	52.2
Coarse woody debris	15.6	4.6	4.2	1.5
Total	336.7	100.0	274.2	100.0

32.9% in soil. In contrast, the majority of the carbon in the secondary forest was in soil (52.2%), with only 38.1% contained in aboveground biomass (Table 4).

Of the remaining pools, coarse woody debris was of much greater quantitative importance in the primary forest (4.6% of total carbon) compared to the secondary forest (1.5%), while the opposite was true for fine roots (Table 4), although the latter made only a small contribution to total carbon stocks (~1%). The contribution of coarse roots was greater in primary forest (11.9%) compared to secondary forest (6.9%).

4. Discussion

The majority of the carbon in our study area at BTNR was stored in aboveground biomass and soil. The contribution of these pools to the total carbon stocks varied markedly between the primary and secondary forests. Specifically, in primary forest the dominant pool was aboveground biomass (~50% of carbon) and soil made a smaller contribution (33%), while the opposite was true in the secondary forest. It is important to note that our primary forest area is largely on hill or ridge top, while our secondary forest area is on lower slopes and valleys, and that these topographic differences are thus confounded with forest age in our analyses. However, our study plots are reasonably representative of primary and secondary forests in the BTNR in general, and indeed, they encompass a full 29% of the total forest area in the BTNR.

The much greater aboveground biomass in the primary forest compared to the secondary forest was due in large part to a difference in the number of large trees. The top 10 species ⩾30 cm dbh made up 46.3% of total aboveground biomass in the primary forest. In contrast, trees 10–30 cm dbh in the primary forest contained far less biomass than in secondary forest, both in absolute and proportional terms (18% vs. 39% of total aboveground biomass; 15.7 m^2 vs. 17.0 m^2 basal area). This is closely related to the species composition of the secondary forest, because most of the canopy species in the secondary forest are pioneers that rarely grow beyond 30 cm dbh.

Primary forest aboveground biomass at our study site in BTNR is comparable to most forests in the neotropics, while relatively low compared to other sites in tropical Asia (Fig. 3). In general, neotropical primary forests contain less aboveground biomass than Asian and African primary forests (Fig. 3). The canopies of Asian forests are dominated by members of the Dipterocarpaceae, with significant contributions from the Fabaceae. Both families are usually wind dispersed (Ng and Whitmore, 1989; Symington et al., 2004), which might have pre-disposed them to grow taller for more effective dispersal of their seeds instead of widening their crowns (Slik et al., 2010). The 60-year-old secondary forest had AGB stocks 63% as large as those of the primary forest. This value is consistent with rates of successional biomass accumulation seen in other secondary tropical forests (Brown and Lugo, 1990; Mascaro et al., 2012).

The confidence intervals on woody debris stocks in primary forest at BTNR overlap the range of those previously observed in the region (Table 5). The mean estimates for BTNR suggest that this site has relatively low stocks of fallen coarse woody debris, and relatively high stocks in standing woody debris. However, confidence intervals are high, especially for standing stocks. Further, differences in sampling methods may lead to discrepancies in total woody debris, because plot-based methods tend to produce lower values than those measured by the line-intersect method (e.g., Chao et al., 2008). Nonetheless, we speculate that the apparent abundance of standing dead trees at BTNR may be caused by lightning strikes, due to the higher elevation of the 2-ha primary forest plot.

Soil carbon to 3 m depth in primary forest at BTNR constituted around one third of the total carbon stock, and more than half the carbon stock in the secondary forest. Soils are typically only assessed to 1 m depth (e.g., Dixon et al., 1994) and the IPCC recommendation is to sample to a minimum of 0.3 m (IPCC, 2006). Accounting for soil carbon to 3 m depth in the BTNR plot increased the soil carbon pool by approximately 40% relative to 1 m depth, albeit our estimates of deep carbon have considerable uncertainty as they are based on only two sample points per forest plot. Deep soil carbon can be unstable (Fontaine et al., 2007) and might therefore be susceptible to climate-induced perturbation, particularly if increasing tropical forest productivity promotes allocation of carbon below-ground, as appears to be the case in temperate forests (e.g., Alberton et al., 2005). It is therefore important to include subsoil carbon in assessments of carbon stocks in tropical forests. Considering just the top 1 m of soil, soil carbon in primary forest at BTNR appears to be within the range of other primary forests (Fig. 4). Neotropical forests in general appear to have a higher proportion of their carbon in soil than in aboveground biomass (Malhi et al., 2009; Sierra et al., 2007), although additional studies are required to confirm this pattern.

We found higher soil carbon in the secondary forest than in primary forests, contrary to the dominant pattern reported in the literature (de Camargo et al., 1999; Sierra et al., 2007). Powers et al. (2011) showed that soil carbon stocks may increase or decrease

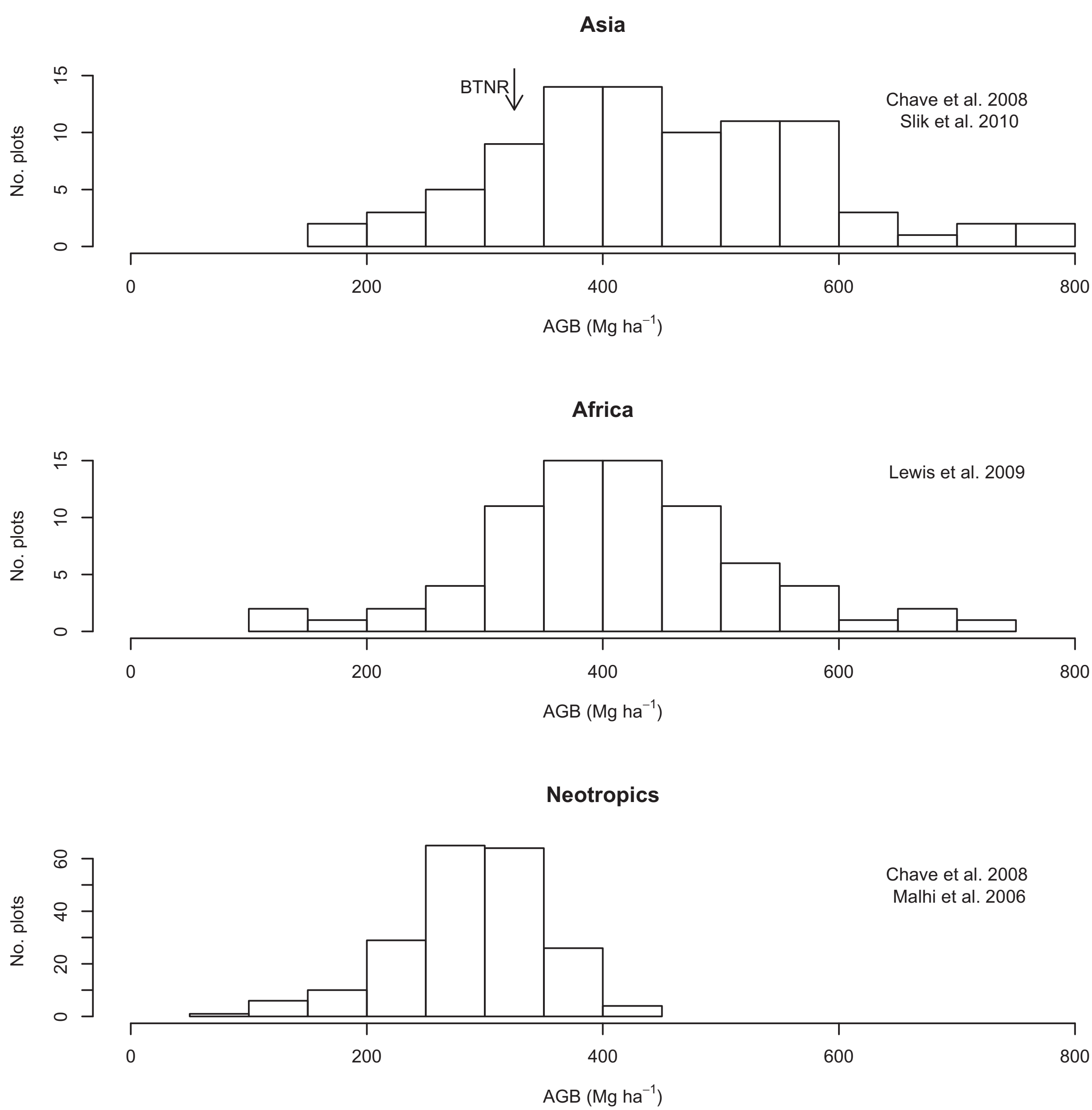

Fig. 3. Aboveground biomass of tropical forests in Asia, Africa, and the neotropics. The arrow represents the Bukit Timah Nature Reserve. Data are from the references beside each graph. (See above-mentioned references for further information.)

Table 5
Comparison of coarse woody debris in primary tropical forests in Asia and neotropics. Values in parentheses indicate 95% confidence intervals based on 1000 bootstrap samples (see Table 2).

Site	Fallen	Standing	Total	Fallen	Standing	Total
	Necromass (Mg ha^{-1})			Volume (m^3 ha^{-1})		
ASIA						
Bukit Timah	12.31 (8.40–19.37)	18.87 (5.84–23.49)	31.2	47.2 (35.18–77.47)	58.1 (18.10–74.86)	105.3
Pasoh, Malaysia[a]	–	–	49.0			
West Sumatra[b]	39.0	16[k]	55.0			
Malua, Malaysia[c,l]	9.0	17.4	26.4			
Belalong, Brunei[d]				66.0	37.7	103.7
Andalau, Brunei[d]				105.0	46.1	151.1
Danum, Malaysia[d]				70.6	25.8	96.4
NEOTROPICS						
Jenaro Herrera, Peru[e]	14.4	5.9	20.3			
Porce, Colombia[f]	–	–	6.1			
Tapajos, Brazil[g]	40.8	8.1	49.0			
La Selva, Costa Rica[h]	46.3	6.5	52.8			
Moist forest, Venezuela[i]	18.5	14.8	33.3			
Madre de Dios, Peru[j]	19.0[m]	4.2	23.2			

[a] Yoneda et al. (1977).
[b] Yoneda et al. (1990)'.
[c] Saner et al. (2012).
[d] Gale (2000).
[e] Chao et al. (2008).
[f] Sierra et al. (2007).
[g] Palace et al. (2008).
[h] Clark et al. (2002).
[i] Delaney et al. (1998).
[j] Baker et al. (2007).
[k] Estimated.
[l] Selectively-logged forest.
[m] Mean of plot-based and transect-based methods.

after land use conversion depending on soil type and precipitation. The increase in the soil carbon stock under secondary forest at BTNR appears to be primarily due to an increase in soil carbon concentrations throughout the upper meter of soil associated with an increase in fine root biomass. This suggests that fine root turnover might contribute to the increase in soil carbon stocks. The soil carbon to nitrogen ratios were also higher in the secondary forest compared to the primary forest, indicating less decomposed organic matter. In assessing the difference in soil carbon between the primary and secondary forest plots it is important to consider landscape position – the primary forest plot is on top of a hill and includes a ridge with steeply sloping soils. A greater rate of erosion might account for the lower carbon concentrations in the topsoil, compared to more enriched sites lower down the slope where the secondary plot is located.

5. Conclusion

This first quantification of carbon stocks in a Singapore forest indicates a marked difference between primary and 60-year-old secondary forests. Total carbon stocks were greater in primary forest than secondary forest, with the majority of carbon in primary forest stored in aboveground biomass, while secondary forest soils held the majority of the carbon. In general, carbon stocks in BTNR forests are lower than other sites in Southeast Asia, but are comparable to many neotropical forests. The importance of accounting for carbon in deep subsoil (>1 m) is emphasized by the approximate 40% increase in soil carbon stocks when including soils to 3 m depth.

Carbon stocks in the 60–70 year old secondary forests in BTNR still lag well behind the adjacent primary forest. In secondary forests, carbon stocks typically increase rapidly during the initial phase of regeneration, and then decelerate over subsequent decades and even centuries as primary forest species gradually colonize the area and grow to maturity. Given that primary forest is in such close proximity to secondary forest in BTNR, the slow dipterocarp recolonization at this site is surprising. This has implications for secondary forest management in Singapore and Southeast Asian forests. Active management, like enrichment planting, might accelerate regeneration and carbon accumulation of secondary forests in BTNR.

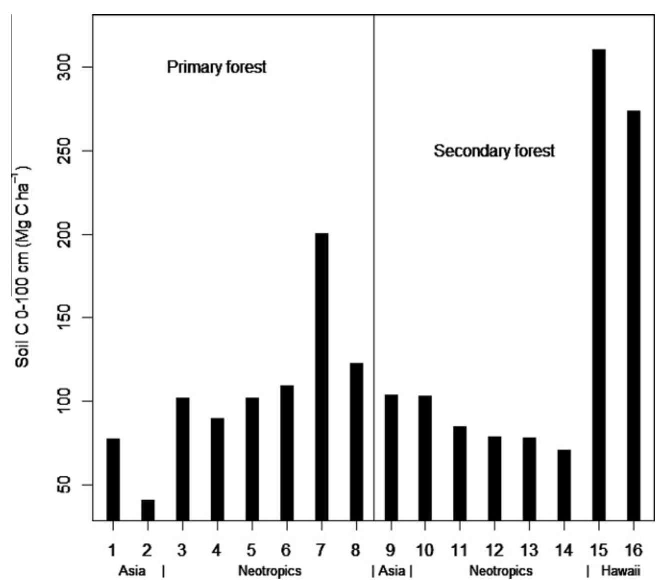

Fig. 4. Comparison of soil carbon for the upper 1 m of soil in a range of tropical forests in Asia, the neotropics, and the Hawaiian Islands. Locations are as follows: 1 = this study, 2 = Yonekura et al. (2010), 3 = de Camargo et al. (1999), 4 = Sommer et al. (2000), 5 = Trumbore et al. (1995), 6 = Marin-Spiotta et al. (2009), 7–8 = Veldkamp et al. (2003), 9 = this study, 10 = de Camargo et al. (1999), 11–14 = Sommer et al. (2000), 15–16 = Osher et al. (2003).

Acknowledgements

We thank Mohamad Fairoz bin Mohamed and other assistants for help in the field, Ryan Chisholm for help with data analysis, and Dayana Agudo for laboratory support. The research was funded by the HSBC Carbon Initiative and a CTFS grant to K.M.N.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2013.02.004.

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