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Coarse woody debris carbon storage across a mean annual temperature gradient in tropical montane wet forest

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ABSTRACT

Coarse woody debris (CWD; defined here as fallen and standing dead trees and tree ferns) is a critical structural and functional component of forest ecosystems that typically comprises a large proportion of total aboveground carbon (C) storage. However, CWD estimates for the tropics are uncommon, and little is known about how C storage in CWD will respond to climate change. Given the predominant role that tropical forests play in global C cycling, this information gap compromises efforts to forecast climate change impacts on terrestrial C balance. The primary objectives of this study were to: (i) quantify CWD C storage in a tropical montane wet forest; and (ii) determine if CWD C storage varies with mean annual temperature (MAT). Coarse woody debris C was quantified with line-intercept sampling techniques in nine permanent plots located across a highly constrained 5.2 °C MAT gradient spanning 800 m elevation on the eastern slope of Mauna Kea Volcano, Island of Hawaii. Forests across this tropical montane MAT gradient contained large quantities of CWD C (44.3 ± 11.2 Mg ha^{-1}; Mean ± 1 SE), which accounted for an estimated 17% of total aboveground C storage. Across the entire gradient, CWD C was found primarily as: moderately decayed CWD (Decay Class 2); tree CWD; fallen CWD; and small diameter CWD (2–10 cm). Tree ferns accounted for an average of ~20% of total CWD C, but are rarely included in tropical CWD estimates. Overall, total CWD C ranged from 12.2 to 104.6 Mg ha^{-1} across the MAT gradient, and decreased with increasing MAT. The negative relationship between CWD and MAT was driven by large accumulations of standing tree CWD at cooler MATs, as fallen CWD did not vary with MAT. The results presented here are in line with limited evidence from tropical studies showing that CWD can make up a large fraction of total aboveground C storage. In addition, these data suggest that CWD could become a net C source to the atmosphere in tropical forests with future warming. A decrease in tropical montane CWD C storage would have important implications for global C dynamics and atmospheric CO_2 levels.

1. Introduction

Coarse woody debris (CWD), defined here as fallen and standing dead trees and tree ferns, is a critical structural and functional component of all unmanaged forest ecosystems (Maser and Trappe, 1984; Harmon et al., 1986; Franklin et al., 1987; McComb and Lindenmayer, 1999). Coarse woody debris plays several important ecological roles including the regulation of nutrient cycling (Holub et al., 2001; Brais et al., 2006; Kuehne et al., 2008) and hydrologic processes (McComb and Lindenmayer, 1999; Lindenmayer and Noss, 2006), as well as the provision of habitat for a wide diversity of organisms (Maser et al., 1979; Harmon et al., 1986; Stevens, 1997), including tree seedlings (Harmon and Franklin, 1989; Gray and Spies, 1997; Sanchez et al., 2009). The role of CWD in ecosystem carbon (C) storage has received increasing attention because climate change could alter terrestrial C balance by reducing C storage in this important detrital pool (Chambers et al., 2000; Jomura et al., 2007; Woodall and Liknes, 2008b; Weedon et al., 2009). In tropical forests, which store ~59% of the C in global forest vegetation (Dixon et al., 1994), CWD has been estimated to account for 19–33% of total aboveground C storage, but few tropical forest studies have quantified CWD C storage (Delaney et al., 1998; Clark et al., 2002; Rice et al., 2004; Baker et al., 2007; Palace et al., 2007). Given the substantial amount of C stored in CWD, credible forecasts of ecosystem responses to rising mean annual temperature (MAT) will require a detailed understanding of how climate change impacts CWD C storage.

Mean annual temperature for tropical regions is projected to increase by ~4 °C by 2099 (IPCC, 2007), and C stocks in tropical forests are generally believed to be sensitive to changes in MAT

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(Malhi and Phillips, 2004; Larjavaara and Muller-Landau, 2012). Despite the importance of CWD to forest C budgets, very few studies have examined responses of CWD to rising temperature (Raich et al., 2006). Thus, it is unknown how CWD will affect overall C balance in tropical forests as MAT rises. Tropical montane wet forests (MWFs), in particular, are thought to be highly susceptible to climate-induced alterations in C cycling due to amplified warming now occurring at higher elevations (Pounds et al., 1999; Nair et al., 2008). Hawaiian tropical MWFs are no exception, and are already experiencing accelerated warming at elevations >800 m.a.s.l (Giambelluca et al., 2008; Diaz et al., 2011).

Tree ferns are an important but commonly overlooked component of many tropical and temperate MWFs (Becker, 1976; Bystriakova et al., 2011). In Hawaii, tree ferns (*Cibotium* spp.) typically dominate the understory and midstory of tropical MWFs. However, tree fern CWD is typically ignored in C budget studies, even those that estimate tree CWD. Importantly, we know of no estimates from any tropical forest of the importance of tree ferns to CWD or aboveground C storage. Consequently, the effect of global climate change on tree fern CWD is completely unknown.

The primary objectives of this study were to: (i) quantify CWD C pools in a tropical MWF; and (ii) determine if tropical montane CWD C storage varies with MAT. We hypothesized that CWD would contain similar quantities of C and would comprise a similar proportion of total aboveground C storage as that found previously in other tropical forests (Raich et al., 2006; Baker et al., 2007). We also hypothesized that CWD C storage would not vary with MAT because any increase in CWD production in response to rising temperatures would be offset by a similar increase in CWD decomposition rates (Chambers et al., 2000). To test these hypotheses, we quantified CWD C pools in nine permanent plots arrayed across a highly constrained 5.2 °C MAT gradient in tropical MWF on the Island of Hawaii (Litton et al., 2011).

2. Materials and methods

2.1. Study site

The study was conducted in native, canopy-intact tropical MWF in the Hawaii Experimental Tropical Forest (HETF; 19°56′41.3″N, 155°15′44.2″W) and the Hakalau Forest National Wildlife Refuge (Hakalau; 19°50′31.3″N, 155°17′35.2″W) on the windward slope of Mauna Kea, Island of Hawaii. The HETF and Hakalau contain large areas of intact, mixed *Metrosideros polymorpha* – *Acacia koa* forest. In 2009, nine 20 m × 20 m permanent plots were established across a 5.2 °C (13.0–18.2 °C) MAT gradient (Fig. 1), which is located across an elevation gradient spanning 800–1600 m.a.s.l. Mean annual temperature for each plot was determined from a 30 year climate record (1961–1990) at the Hilo International Airport (8 m.a.s.l.) and the environmental lapse rate (6.49 °C 1000 m^{-1}) (Litton et al., 2011). Air temperature at 1 m height in the understory of each plot quantified since June 2009 is positively and linearly related to long-term estimated MAT (r^2 = 0.96).

All plots have a similar disturbance history, and are located in mature, moderately aggrading forest (Kellner and Asner, 2009). To achieve constant disturbance history, plots in the HETF were selected such that they were located within 10% of the maximum aboveground biomass at each target MAT using airborne light detection and ranging (LiDAR) measurements of forest structure from the entire HETF (Asner et al., 2009). The two plots in Hakalau were selected using ground-based surveys since LiDAR data were not available (see Litton et al., 2011). Vegetation in all plots is dominated in the upper canopy by *M. polymorpha* Gaudich. and in the mid-canopy by *Cheirodendron trigynum* (Gaudich.) Heller and three *Cibotium* spp. (Sm.) Hook. and Arn. tree fern species, of which *Cibotium glaucum* and *Cibotium menziesii* are the most common. Across all plots, *M. polymorpha* and *C. trigynum* account for >84% of stand tree basal area, and stand basal area increases with MAT while stand density decreases with MAT (Litton et al., 2011). Substrate in all plots is weathered volcanic tephra developed on a single lava flow estimated to be 14–65 ky (Soil Survey Staff, 2010). It is impossible to determine if soil development began at the same time across all nine plots, but soils are well constrained across the entire gradient. All soils are classified as moderately to well-drained Acrudoxic Hydrudands of the very closely related Akaka, Honokaa, Maile, and Piihonua soil series (Litton et al., 2011). Mean annual precipitation varies from ~3200 mm at the coolest MAT plot to ~4200 mm at the warmest MAT plot (Giambelluca et al., 1986). However, because higher MAP is associated with higher MAT and, therefore, higher evapotranspiration rates, soil water balance is high and constant across the entire MAT gradient (Litton et al., 2011). While no ecological gradient that uses elevation as a substitute for MAT is ideal, we propose that our elevation gradient is a significant advancement in that it holds the biotic and abiotic characteristics that influence ecological processes in addition to MAT more constant than prior gradients.

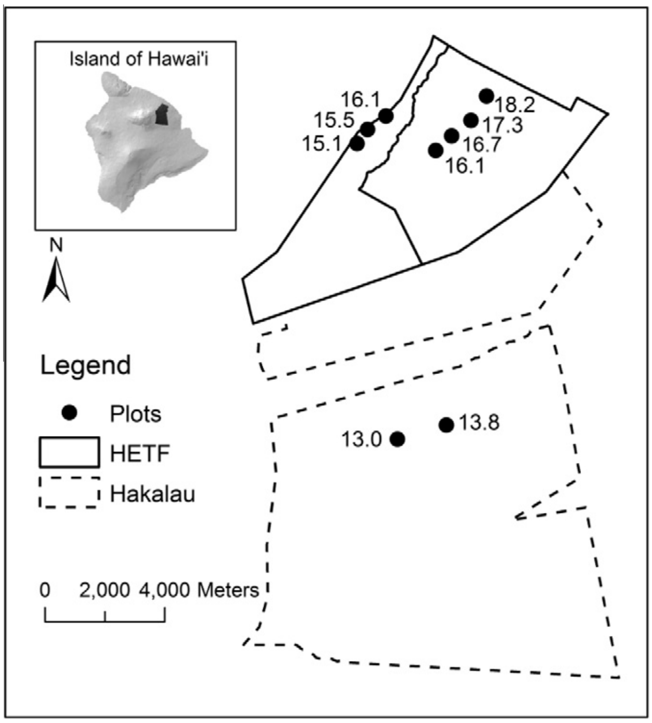

Fig. 1. Experimental plots located across a 13–18.2 °C mean annual temperature gradient on the eastern slope of Mauna Kea Volcano, Island of Hawaii. Seven plots are located in the Hawaii Experimental Tropical Forest (HETF) and two in the Hakalau Forest National Wildlife Refuge (Hakalau). Mean annual temperature (°C) is indicated next to each plot.

2.2. Coarse woody debris sampling

In 2009, fallen and standing CWD ⩾ 2 cm diameter was sampled within each 20 × 20 m plot across the MAT gradient. In 2010, fallen CWD was also sampled immediately outside of seven of the nine plots using longer transects to compare to within-plot estimates. Coarse woody debris at an angle <45° with the ground was considered fallen and CWD at an angle >45° with the ground was considered standing (Harmon and Sexton, 1996). To estimate the percentage of total aboveground C contained in CWD, we utilized stand-level aboveground tree biomass estimates for the HETF

(Asner et al., 2009) and the assumption that biomass is 48% C. Specifically, we averaged maximum aboveground tree biomass for low and mid-elevation native-dominated forests published in Asner et al. (2009) that are found on the same substrate type and age as the plots used in this study (181.1 Mg ha^{-1} of C). We do not assume that aboveground biomass is constant with MAT. Rather, these more general values are the only estimates of aboveground biomass currently available for this area. Maximum aboveground tree biomass estimates were used because plots in the current study were established in areas within 10% of the maximum aboveground biomass for a given elevation. Total CWD C storage for the seven plots located in the HETF was then divided by the sum of average aboveground tree biomass (which already included standing CWD) and plot-specific fallen CWD to calculate a plot-based percentage of total aboveground C storage in CWD.

2.2.1. Fallen coarse woody debris

Carbon mass (Mg ha^{-1}) of each fallen tree and tree fern CWD piece was calculated as the product of volume, density and C content. Within each plot, the line intersect-method was used to estimate fallen CWD volume across thirteen parallel 20 m transects (260 m total transect length) spaced 1.5 m apart. Volume per unit area (V; m^3 ha^{-1}) of fallen CWD was calculated as $V = \pi^2 \sum d^2/8L$, where d (cm) is the diameter of the CWD piece where it intersects the transect, and L (m) is the length of the transect (Harmon et al., 1986; Palace et al., 2008). Where possible, diameter measurements were made with a DBH tape to account for asymmetry that is common in CWD. When this was not possible (e.g., the CWD was in contact with the ground), calipers were used and asymmetrical pieces were measured following Woldendorp et al. (2004), where two measurements were taken at the maximum and minimum diameters and averaged.

To calculate CWD biomass from volume, each piece of CWD was assigned to one of five decay classes modified from Maser and Trappe (1984) and Keller et al. (2004) (Table 1). Decay classes 1–4 were successively more decomposed tree CWD, and tree fern CWD comprised a fifth decay class. Coarse woody debris biomass was calculated as the product of CWD volume and decay class-specific densities. Densities (dry mass/green volume) for each decay class were quantified on 7–42 representative samples from cross-sections of debris collected *in situ* from random locations across the entire MAT gradient using the water displacement method (Chave et al., 2006) (Table 1). The one exception was for Decay Class 1, which was based on live wood density of *M. polymorpha* (Litton and Kauffman, 2008; Asner et al., 2011). Here, it was assumed that *M. polymorpha* comprised the majority of CWD since it was, on average, >80% of the live tree basal area in each plot (D.K. Iwashita, unpub. data). Void space (Chao et al., 2008) was not quantified and, as a result, CWD C reported here may be overestimated.

To calculate CWD C content from CWD biomass, 6–26 representative samples were taken from randomly chosen pieces of CWD from each decay class across the entire MAT gradient, and finely ground on a ball mill to pass a #40 mesh. A well-homogenized subsample was then analyzed for %C content on a Costech 4010 Elemental Combustion system (Valencia, CA) at the University of Hawaii at Hilo Analytical Lab. The C content of CWD was calculated as the product of CWD biomass and decay class-specific C concentrations.

Longer transect lengths are often recommended for estimating CWD (Woldendorp et al., 2004), and so to determine if the thirteen 20 m transects precisely estimated CWD in each plot, fallen CWD was also quantified in 2010 using longer transects (six 90 m transects for a total of 540 m) spaced 10 m apart immediately outside of seven of the nine permanent plots (13.0 °C, 13.8 °C, 15.1 °C, 15.5 °C, 16.1 °C, 16.7 °C and 17.3 °C). The same methods were used to calculate C mass for the longer transects as were used for the 20 m transects. Fallen CWD C estimates from the thirteen 20 m transects spaced 1.5 m apart versus the six 90 m transects spaced 10 m apart were marginally different for tree CWD ($P = 0.07$), but were not significantly different for tree fern CWD ($P = 0.39$) or for total CWD ($P = 0.12$). Based on the similarity between the CWD estimates from the short versus long transects, the original 2009 data based on thirteen 20 m transects in all plots were used for all analyses in this study. Importantly, utilizing data from the longer transects would have resulted in very small changes in stand level CWD estimates from those presented herein, and no change in patterns in CWD with MAT.

2.2.2. Standing coarse woody debris

Standing CWD (i.e., snags) was sampled within the entirety of each plot (400 m^2). For intact standing coarse woody debris, biomass was estimated with the generalized wet forest allometric equation (Model II.3) from Chave et al. (2005). This equation has been shown to accurately estimate biomass for *M. polymorpha* trees (Litton and Kauffman, 2008). For broken snags >1.3 m tall, height was visually estimated and used to calculate biomass using the generalized wet forest allometric equation (Model I.3) from Chave et al. (2005). For snags <1.3 m height and for all standing dead tree ferns, the top and bottom diameters of each piece were measured, and volume was estimated as the frustum of a cone (Fraver et al., 2007). The same decay classes and densities used for fallen CWD were utilized for standing CWD, and C pools were calculated as the product of biomass and C content (intact snags) or volume, density and C content (broken snags and tree ferns).

2.3. Statistical analysis

All statistical analyses were conducted in Minitab 16 (Minitab Inc., State College, PA, USA) and SigmaPlot 11.0 (Systat Software, Inc., San Jose, CA, USA). To compare fallen and standing tree and tree fern CWD, a Kruskal–Wallis test and post hoc Tukey's test were performed. Linear regressions were used to determine if CWD C (total, tree, tree fern) varied with MAT. Response variables

Table 1
Description of coarse woody debris decay classes utilized, with measured mean wood density and mean carbon content, in tropical montane wet forests in Hawaii.

Decay class[a]	Description	Density (g cm^{-3})	(SE)	n	Carbon (%)	(SE)	n
1	Solid, fresh wood with leaves and/or fine twigs attached; bark intact	0.69[b]	–	–	46.3	(0.71)	6
2	Solid or decaying sapwood; heartwood solid; bark sloughing off or absent; round in shape	0.39	(0.02)	42	46.8	(0.26)	26
3	Heartwood and sapwood decayed; broken when stepped on; round to elliptical in shape	0.16	(0.02)	14	47.6	(0.79)	9
4	Rotten and friable; easily broken apart with hands; elliptical in shape; often scattered across forest floor	0.07	(0.00)	7	47.9	(0.77)	7
Tree fern		0.17	(0.02)	8	47.7	(0.85)	8

[a] Modified from Maser and Trappe (1984) and Keller et al. (2004).
[b] Based on live wood density of *Metrosideros polymorpha* (Asner et al., 2011), the dominant tree in all nine plots studied.

were log-transformed if they did not pass homogeneity of variance tests, but all figures display non-transformed data for ease of interpretation.

3. Results

3.1. Coarse woody debris carbon storage

Total CWD C storage ranged from 12.2 to 104.6 Mg ha^{-1} (Table 2), averaging 44.3 (±11.2) Mg ha^{-1} of C across all plots. Total CWD accounted for an estimated mean value of 16.9% of total aboveground C storage, ranging from 6.3% to 50.6%, across the seven plots in the HETF. Approximately 80% of all CWD was of tree origin, and 20% of tree fern origin (Table 3). Total volumes of tree and tree fern CWD were 242.9 (±83.1 S.E.) and 119.4 (±18.7 S.E.) m^3 ha^{-1}, respectively. Mean fallen CWD C pools (tree + tree fern) were ~40% higher than mean standing CWD C pools across all plots (Table 3). Fallen and standing tree CWD C pools were nearly identical, and both exceeded fallen and standing tree fern CWD C, although this difference was only significant for standing CWD C ($P < 0.05$; Fig. 2). The majority of total CWD C (25.9 Mg ha^{-1}; 58.4%) was found in the fallen pool (Table 3). Across decay classes, the largest quantity of CWD C (29.3 Mg ha^{-1}; 66.2%) was found in moderately decayed wood (Class 2; Table 3), where the highest proportion of both fallen and standing CWD pieces was also found (Fig. 3). Less than 0.1% of total CWD C was found in freshly decayed CWD (Class 1), 13.6% of total CWD C was found in advanced decay stages (Classes 3 and 4), and the remaining ~20% of CWD C was found in tree ferns (Table 3). Similar patterns across decay classes were apparent for fallen CWD. For standing CWD, there was a disproportionate amount of C stored in moderately decayed CWD (Class 2; 82%) owing to a few large snags. Tree fern CWD accounted for <1% of standing CWD (Table 3 and Fig. 3).

There were a total of 1355 fallen and 157 standing pieces of CWD quantified in this study. The majority of tree CWD pieces were found in smaller diameter size classes (<10 cm), while the majority of tree fern CWD pieces ranged from 10 to 20 cm diameter (Fig. 4a). The number of CWD pieces per decay class generally decreased as diameter size class increased. In contrast to the distribution of CWD pieces (Fig. 4a), CWD C pools were more evenly distributed across diameter size classes (Fig. 4b). While the vast majority of CWD C pieces (>70%) were <10 cm diameter, this size class accounted for only ~6% of total CWD C storage. Since CWD volume increases geometrically with size (Harmon et al., 1986), a handful of large CWD pieces (snags ⩾ 60 cm diameter) stored a large fraction of total CWD C (Fig. 4b). In contrast, the shape of the tree fern CWD C distribution more closely followed the shape of the tree fern CWD diameter size class distribution, with the exception of relatively low C mass for the 10–20 cm size class.

3.2. Coarse woody debris and mean annual temperature

Total CWD C storage decreased as MAT increased ($R^2 = 0.45$; $P < 0.05$; Total CWD C = 261.5–13.8∗MAT; Fig. 5a). This negative relationship was driven exclusively by tree CWD ($R^2 = 0.55$; $P = 0.02$; Tree CWD = 280.2–15.6∗MAT; Fig. 5a), since tree fern CWD C increased marginally with MAT ($R^2 = 0.37$; $P = 0.08$; Fig. 5a). Fallen tree fern CWD C increased with MAT ($R^2 = 0.48$; $P = 0.04$; Fallen Tree Fern CWD = −25.2 + 2.1∗MAT; Fig. 5b). However, standing tree fern CWD C decreased as MAT increased ($R^2 = 0.60$; $P = 0.014$; Standing Tree Fern CWD = 6.5–0.36∗MAT; Fig. 5c), as did standing tree CWD C ($R^2 = 0.51$; $P = 0.03$; log Standing Tree CWD = 7.7–0.47∗MAT; Fig. 5c). As a result, standing CWD C also decreased as MAT increased ($R^2 = 0.58$; $P = 0.02$; log Total Standing CWD = 7.3–0.43∗MAT; Fig. 5c). Standing tree CWD C also had a substantial influence on the overall negative relationship between total CWD C and MAT, where standing tree CWD C was much greater at lower MATs owing to a small number of large snags at those sites. As a result, there was an abrupt shift in the distribution of tree CWD C at 15.5 °C (Fig. 5), whereas tree fern CWD C was more evenly distributed across the MAT gradient.

4. Discussion

4.1. Coarse woody debris carbon storage

The quantity of CWD C found in this study (mean of 44.3 Mg ha^{-1} across all plots) is higher than what has been previously reported for tropical forests, in contrast to our first hypothesis. In undisturbed, old-growth moist tropical forests, CWD C storage has been estimated to range between 14.7 and 25.4 Mg ha^{-1} (Clark et al., 2002; Raich et al., 2006). Assuming that biomass is ~48% C, CWD C storage in tropical MWFs (16.6 Mg ha^{-1} [Delaney et al., 1998]) falls at the lower end of the range across all moist tropical forests. The high tree CWD volume estimated in the current study (242.9 m^3 ha^{-1}) is, however, very similar to the CWD volume (237.5 m^3 ha^{-1}) estimated in a native tropical MWF on Maui (Santiago, 2000), suggesting that Hawaiian wet forests can contain large quantities of CWD relative to other tropical locations.

The large CWD C stocks observed here may result from overall greater net primary productivity and aboveground C storage in Hawaiian forests and, hence, greater CWD inputs, compared with other tropical forests. As such, the percent of total aboveground C in CWD provides a better indication of the importance of CWD to ecosystem C storage, and a better means of comparing CWD C across forests. Based on total aboveground biomass estimates for similar forests in the HETF (Asner et al., 2009) and the assumption that CWD is 48% C, CWD C pools quantified in this study constitute, on average, 16.9% of total aboveground C storage. This value is on

Table 2
Total, fallen, and standing coarse woody debris (CWD) carbon pools across a 5.2 °C mean annual temperature gradient in tropical montane wet forests in Hawaii.

Plot & Elev. (m.a.s.l.)	MAT[a] (°C)	MAP[b] (mm)	Total CWD C (Mg ha^{-1})	Fallen CWD C (Mg ha^{-1})			Standing CWD C (Mg ha^{-1})		
				Total	Tree	Tree fern	Total	Tree	Tree fern
HAK 1600	13.0	3195	70.1	23.9	23.3	0.6	46.1	68.0	1.4
HAK 1468	13.8	3488	85.0	51.3	49.4	1.9	33.7	81.0	2.1
WPL 1274	15.1	3448	104.6	25.5	11.9	13.5	79.2	89.4	1.7
WPL 1204	15.5	3521	14.9	13.2	5.0	8.2	1.6	6.0	0.7
WPL 1116	16.1	3714	35.1	33.1	19.9	13.2	2.0	21.9	0.0
SPE 1116	16.1	3988	12.2	11.4	5.1	6.3	0.9	5.2	0.8
SPE 1024	16.7	4043	31.3	31.1	25.7	5.4	0.2	25.9	0.0
SPE 934	17.3	4133	23.1	22.4	12.8	9.6	0.7	13.2	0.3
SPE 800	18.2	4204	22.6	20.9	6.6	14.3	1.7	7.8	0.4

[a] From Litton et al. (2011), calculated from 1961 to 1990 at the Hilo International Airport (8 m.a.s.l.) and the environmental lapse rate (6.49 °C/1000 m).
[b] Mean annual precipitation (MAP) from Giambelluca et al. (1986).

Table 3
Total, fallen, and standing tree and tree fern coarse woody debris carbon pools (Mean ± 1 S.E.) by decay class in tropical montane wet forest in Hawaii (n = 9).

Decay class	Total CWD C (Mg ha^{-1})		Fallen CWD C (Mg ha^{-1})		Standing CWD C (Mg ha^{-1})	
1	0.01	(0.01)	0.01	(0.01)	0.0	(0.0)
2	29.3	(9.7)	14.2	(4.2)	15.1	(8.7)
3	5.9	(3.5)	3.4	(1.4)	2.5	(2.2)
4	0.1	(0.1)	0.1	(0.1)	0.0	(0.0)
Tree fern	8.9	(1.6)	8.1	(1.7)	0.8	(0.3)
Total	44.3	(11.2)	25.9	(4.7)	18.5	(9.5)

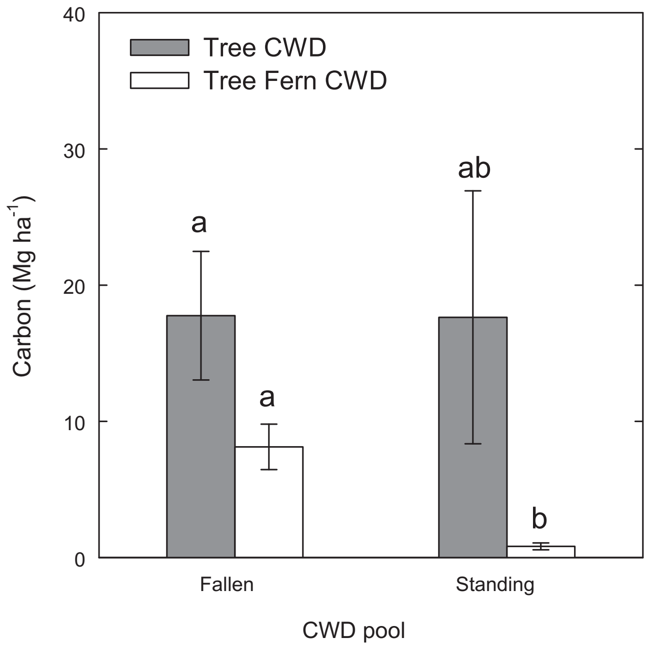

Fig. 2. Fallen and standing tree and tree fern coarse woody debris (CWD) carbon pools (Mg ha^{-1}; Mean ± 1 SE) averaged for nine plots across a 5.2 °C mean annual temperature gradient in tropical montane wet forests in Hawaii. Means sharing the same letters are not significantly different (α = 0.05; one way ANOVA; post hoc Tukey's test).

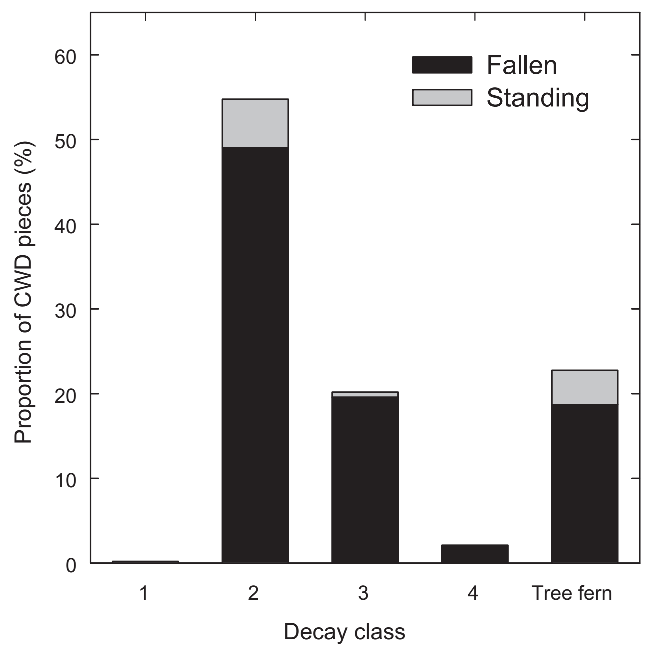

Fig. 3. Proportion of fallen and standing coarse woody debris (CWD) by decay class averaged for nine plots across a 5.2 °C mean annual temperature gradient in tropical montane wet forests in Hawaii.

the low end of, but similar to, estimates of 19–26% for tropical forests in the Amazon and Venezuela (Delaney et al., 1998; Rice et al., 2004; Palace et al., 2007, 2008), in support of our first hypothesis. Thus, the large quantity of CWD C stored in these forests appears to be driven primarily by the relatively large amount of aboveground live biomass contained in these forests compared to other tropical wet forests.

The large quantities of CWD C observed here were not evenly distributed across decay classes. Moderately decayed (Class 2) tree CWD C pools accounted for >80% of fallen and standing tree CWD C. Large quantities of moderately decayed wood may result from a variety of factors, including the successional stage of the forest (Spies et al., 1988) and the long residence time of moderately decayed CWD (Harmon et al., 1986, 2008). Stand dieback of *M. polymorpha* in Hawaiian MWFs, which is thought to occur every ~300–400 years, was proposed to explain the large quantities of highly decayed wood observed in a MWF on Maui (Santiago, 2000). Likewise, stand dieback could also determine the large stock of moderately decayed (Class 2) CWD observed in this study. The missing piece to accurately test this hypothesis is estimates of CWD mean residence times, but CWD decay rates have not been estimated in Hawaiian MWFs.

Tree fern CWD C pools accounted for a substantial proportion of total CWD C (~20%), particularly for fallen CWD (31.4%). While little is known about tree fern dynamics in Hawaiian MWFs or in forests generally where they occur, they represent a large fraction of CWD in the current study and their omission would have resulted in a substantial underestimation of total CWD C storage. It is likely that tree fern CWD C inputs result from some combination of mortality caused by competition, canopy disturbance and successional stage, and disturbance by feral pigs (*Sus scrofa*; wild boar) which are widely distributed in the study area and are known to damage tree ferns (Becker, 1976; Nogueira et al., 2009; Murphy-Winters et al., in preparation).

4.2. Coarse woody debris and mean annual temperature

Tropical elevation gradients, particularly well constrained gradients such as the one used in this study, are valuable natural laboratories for quantifying the impacts of rising MAT on the structure and function of tropical forests (Malhi et al., 2010; Litton et al., 2011). Using our MAT gradient to test hypotheses about rising MAT, we found that, in contrast to our second hypothesis, CWD C storage declined with MAT. Since total basal area, and presumably C storage in live biomass, increase across our MAT gradient (Litton et al., 2011), the decrease in total CWD C as MAT increases suggests that live tree biomass turnover rate must decrease as MAT increases, that CWD decomposition must increase faster than CWD production with MAT, or some combination of the two. Decreasing live tree turnover with increasing MAT is unlikely to explain large quantities of CWD C at lower MATs, since Raich et al. (2006) found that live tree

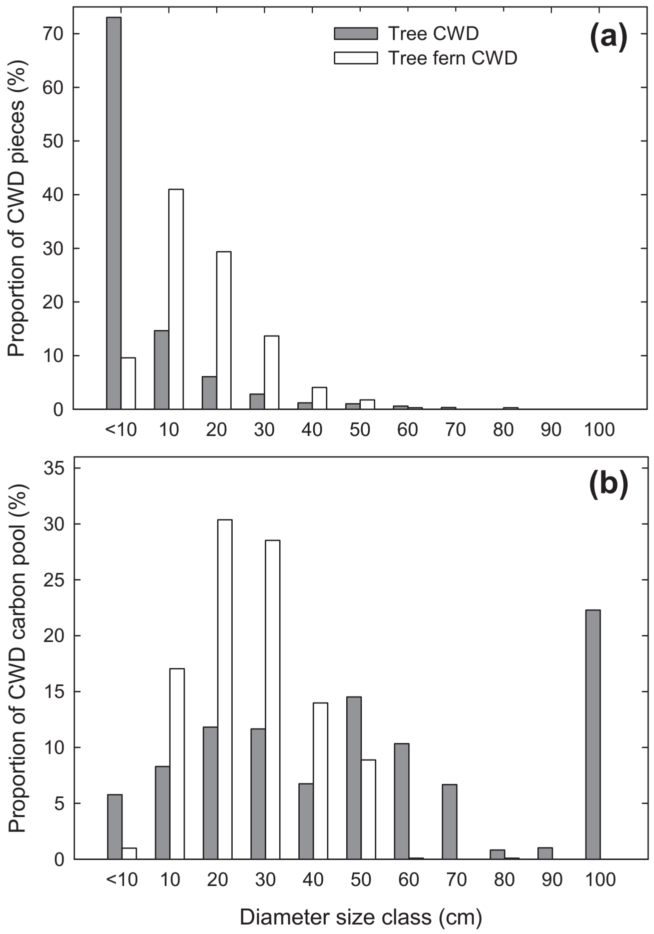

Fig. 4. Diameter size class distributions averaged for nine plots across a 5.2 °C mean annual temperature gradient in tropical montane wet forests in Hawaii: (a) proportion of coarse woody debris (CWD) individual pieces (total 1355 fallen, 157 standing), and (b) proportion of carbon stored in CWD.

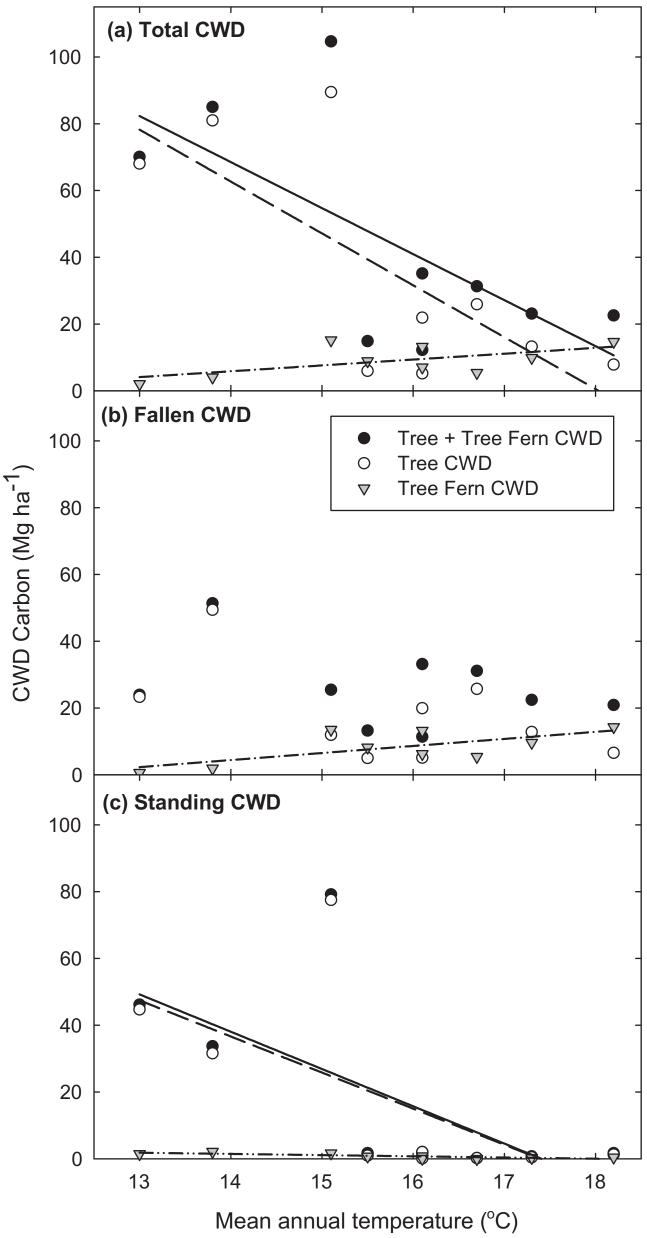

Fig. 5. Relationship between mean annual temperature (MAT) and coarse woody debris (CWD) carbon pools in tropical montane wet forests in Hawaii: (a) total CWD (Total: $R^2 = 0.45$, $P < 0.05$; Tree: $R^2 = 0.55$, $P = 0.02$; Tree fern: $R^2 = 0.37$, $P = 0.08$), (b) fallen CWD (Total: $R^2 = 0.13$, $P = 0.34$; Tree: $R^2 = 0.30$, $P = 0.13$; Tree fern: $R^2 = 0.48$, $P = 0.04$), and (c) standing CWD (Total: $R^2 = 0.58$, $P = 0.02$; Tree: $R^2 = 0.51$, $P = 0.03$; Tree fern: $R^2 = 0.60$, $P = 0.01$). In all panels for all linear regressions, solid lines are for total CWD, dashed lines are for tree CWD, and dash-dot lines are for tree fern CWD.

turnover did not vary with MAT in a larger dataset of moist tropical forests. Increasing decomposition rates with temperature have been observed in tropical forests (Chambers et al., 2000), indicating that one of the major controls on CWD storage could accelerate with warming. However, a meta-analysis of moist tropical forests indicated that CWD C storage does not vary with MAT (Raich et al., 2006), suggesting that either CWD decomposition rates are insensitive to temperature or that increases in CWD decomposition are matched by increases in CWD production. Notably, only nine data points were available in this cross-site tropical analysis and variation was high across studies. In tropical forests that are not moisture limited, net primary productivity (NPP) increases with MAT (Raich et al., 1997; Luyssaert et al., 2007). In line with this finding, our prior work in tropical MWFs in Hawaii showed that tree basal area and soil-surface CO_2 efflux increase across our MAT gradient (Litton et al., 2011), suggesting a similar response in these forests of increasing NPP with rising MAT (Litton et al., 2007). In addition, in temperate forests of the U.S. CWD C storage is negatively correlated with mean daily maximum temperature across a latitudinal (i.e., temperature) gradient (Woodall and Liknes, 2008a,b). Overall, our results and those of other studies suggest that CWD C storage may decrease with global warming, with the net balance of CWD production and decomposition shifting in favor of decomposition. However, more work on this topic is warranted given the very limited number of studies that have examined the response of CWD to rising temperature.

The negative relationship between MAT and CWD C was not consistent between fallen and standing tree CWD, and so it is uncertain whether decomposition rates (which are influenced by contact with the ground, wind, wood-decomposing fungi, moisture, etc.) differ between standing and fallen CWD pools. However, the main difference between fallen and standing tree CWD C pools was the large quantity of standing tree CWD C at cooler MATs. Specifically, large CWD C pools at low MATs drive the negative relationship between CWD C and MAT – there was no relationship between total CWD C and MAT at MATs ⩾15.5 °C. Relatively high accumulations of CWD at cooler MATs have been observed in both tropical and temperate forests (Raich et al., 2006; Woodall and

Liknes, 2008b). The abrupt shift in CWD C pools between cooler and warmer MATs observed here may be a result of increased NPP accompanied by a lag in mortality at warmer MATs, which has been observed in other tropical forests (Lewis et al., 2006). Other climatic factors such as moisture, which is positively correlated with decomposition rates (Gough et al., 2007), and differences in forest dynamics across the MAT gradient are unlikely to explain the relatively large standing CWD C pools at cooler MATs observed in this study since soil water balance and disturbance history were constant across our MAT gradient.

In contrast to tree CWD C, tree fern CWD C was distributed more evenly across the MAT gradient, while fallen tree fern CWD C actually increased with MAT. Taken together, these results suggest that tree fern CWD responds to warming differently than tree CWD, and that plant functional traits or canopy position can drive ecosystem responses to climate change. As with tree CWD, it is unclear why standing and fallen tree fern CWD showed opposite relationships with MAT. Because there is little known about tree ferns in these forests despite their critical role in providing seedling establishment sites (Iwashita, 2012), more research is needed to understand tree fern CWD dynamics and the effects that rising MAT may have on them, along with other driving factors such as feral pigs (Murphy-Winters et al., in preparation).

5. Conclusion

Hawaiian tropical MWFs store large amounts of C in CWD (mean of 44.3 Mg ha^{-1}), higher than in other tropical forests. However, the estimated percentage of total aboveground C stored in CWD in these forests (~17%) is similar to prior estimates from other tropical forests, highlighting the general importance of CWD in tropical forest C budgets. Across this MAT gradient, total CWD C storage decreased with MAT due to large accumulations of standing tree CWD C at cooler MATs. This negative relationship suggests that CWD decomposition increases with MAT faster than CWD production, which may result in net emissions of CO_2 from CWD to the atmosphere as MATs rise. A better understanding of the role of CWD in C storage will become increasingly important, both locally and globally, as MATs rise with global climate change. If rising MAT does decrease tropical CWD pools, this would also influence regeneration and succession patterns since CWD provides important establishment sites for many dominant tree species in tropical forests (Sanchez et al., 2009), including tropical MWFs in Hawaii (Santiago, 2000). Because disturbance regimes and successional dynamics will also likely be impacted by climate change, predicting responses of total CWD and aboveground C storage to rising MATs poses many challenges, particularly where information on CWD stocks and dynamics (e.g., CWD decomposition and production rates) is lacking.

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