Forest Ecology and Management 291 (2013) 336–343

Contents lists available at SciVerse ScienceDirect

Forest Ecology and Management

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

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

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ARTICLE INFO

Article history:
Received 3 October 2012
Received in revised form 23 November 2012
Accepted 26 November 2012
Available online 7 January 2013

Keywords:
Aboveground carbon storage
Climate change
Hawaii
Metrosideros polymorpha
Tree fern

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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http://dx.doi.org/10.1016/j.foreco.2012.11.043

(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).

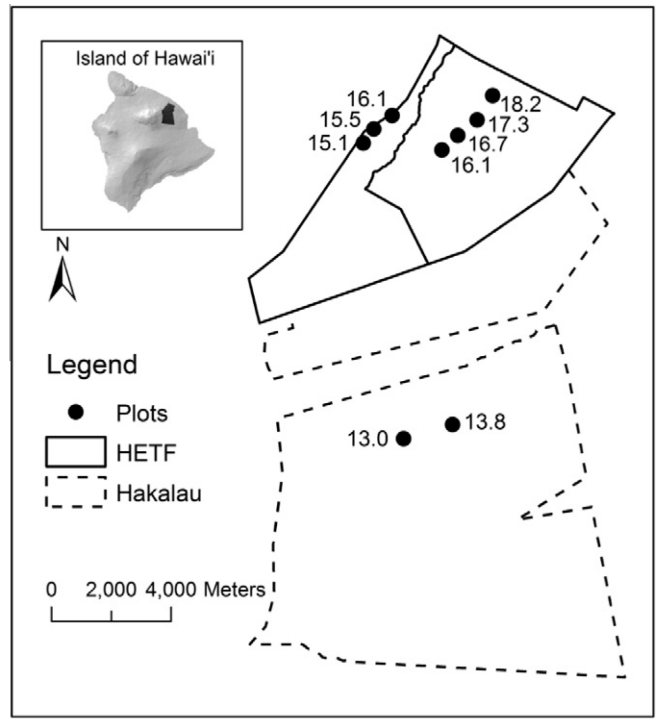

Fig. 1. Experimental plots located across a 13–18.2 °C mean annual temperature gradient on the eastern slope of Mauna Kea Volcano, Island of Hawaii. Seven plots are located in the Hawaii Experimental Tropical Forest (HETF) and two in the Hakalau Forest National Wildlife Refuge (Hakalau). Mean annual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

2. 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.

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