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Deep ground fires cause massive above- and below-ground biomass losses in tropical montane cloud forests in Oaxaca, Mexico

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Abstract: Although fire is occurring at greater frequencies and spatial scales in the moist tropics, few studies have examined the ecological impacts of fire in tropical montane cloud forest (TMCF). This study, conducted in the Chimalapas region of Oaxaca, Mexico, documents changes in live tree biomass, live fine-root biomass, and fallen and standing dead wood 4 y following deep ground fires occurring in TMCF during the 1997–98 El Niño Southern Oscillation event. Forests growing on two different substrates (metamorphic and sedimentary) and having three different statures (mean canopy heights: 20–30 m, 15–20 m and 4–6 m) were assessed within six paired plots established on adjacent burned and unburned forest sites. Total live tree biomass was 82% and 88% lower for burned TMCF growing on metamorphic and sedimentary substrates, respectively, compared with unburned TMCF. Nearly 100% of the living biomass was killed in elfin TMCF located on exposed sedimentary limestone at the highest elevations. Live fine-root biomass in the upper organic soil horizon of burned TMCF sites was 49% lower on metamorphic substrates and 77% lower on sedimentary substrates compared with unburned sites. The amount of total dead wood was 3- to 14-fold greater in burned forests compared with unburned forests. These results suggest that first-time fires in relatively undisturbed TMCF can cause dramatic changes in live above- and below-ground biomass at levels greatly exceeding values reported for most lowland tropical rain forests. These patterns may be attributed to the slower decomposition rates and thick organic soils typical of TMCF, combined with the relatively fast drainage associated with steep topography and, in some locations, sedimentary limestone-derived substrates.

Key Words: Chimalapas, disturbance dynamics, ecosystem recovery, fire, Mexico, Oaxaca, root biomass, tropical montane cloud forest, woody biomass

INTRODUCTION

While humans have influenced the occurrence of fire in most terrestrial ecosystems on Earth, including tropical moist forests (Carcaillet *et al.* 2002, Goldammer 1990, Whitmore & Burslem 1998), only recently has the historical significance of interactions between humans and forest fires in the moist tropics been widely documented and recognized (Meggers 1994, Saldarriaga & West 1986, Sanford *et al.* 1985). Most studies on contemporary dynamics of fire in moist tropical ecosystems have focused on lowland evergreen rain forests. These studies have documented increases in the frequency and magnitude of fires in recent decades, largely associated with human land-use activities, particularly slash-and-burn agriculture (Malmer *et al.* in press), logging (Holdsworth & Uhl 1997), pasture conversion (Uhl & Kauffman 1990), road building (Nepstad *et al.* 2001), and habitat fragmentation (Cochrane 2001, Laurance & Williamson 2001, Román-Cuesta *et al.* 2003). Although initial fires in these ecosystems are generally low-intensity surface fires, the effects may be particularly severe because of the high vulnerability of tropical biota to fire (Barlow *et al.* 2003, Laurance 2003), together with increased flammability and susceptibility to repeated fires due to altered microclimate and available fuel conditions (Cochrane *et al.* 1999, Nepstad *et al.* 1999, Uhl & Kauffman 1990).

The occurrence of fire in tropical montane cloud forests (TMCF) has only recently been documented (Anta & Plancarte 2001, Hemp & Bayreuth 2001, Jardel 1991,

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Ramírez-Marcial *et al.* 2001, Sarmiento & Frolich 2002). Although TMCF has a limited distribution on a global scale – representing only about 2.5% of the total area supporting tropical forests (Bubb *et al.* 2004), these ecosystems also harbour exceptional levels of biodiversity and endemism and have high conservation priority on a global basis (Challenger 1998, Wendt 1993). Further, TMCFs also play a critical role in hydrologic cycling by increasing total water inputs through canopy interception of cloud water and regulating the supply of water to downstream areas (Bruijnzeel & Proctor 1995, Cavelier *et al.* 1996a). Consequently, destruction of TMCF may have dramatic impacts on both biodiversity and the ecohydrological functioning of watersheds that support TMCF. However, despite indications that the occurrence of fires in TMCF may be increasing, few studies have assessed the ecological impacts and recovery processes associated with these fires (Asbjornsen & Gallardo-Hernández 2004).

This study examines the ecological effects of extensive deep ground fires occurring in TMCF in south-eastern Mexico during the 1997–8 El Niño Southern Oscillation (ENSO) event. We estimated above-ground live tree biomass, below-ground live fine-root biomass, and fallen and standing dead wood 4 y after the fires in TMCF growing on two different geologic substrates (metamorphic and sedimentary) and having different statures (indexed by maximum tree canopy height). This study represents the first assessment of the magnitude of change in these biomass parameters in TMCF following fire.

SITE DESCRIPTION

The Chimalapas region, located in the state of Oaxaca, south-eastern Mexico and comprising a total of 590 993 ha, supports one of the largest remaining areas of tropical montane cloud forest in Mexico and Central America, encompassing an estimated 79 784 ha (Salas-Morales *et al.* 2001). The region is characterized by mountainous topography, with elevation ranging between 500–2500 m asl. Climate is Aw2 (warm subhumid) to Cw2 (temperate subhumid). TMCFs are distributed between 1600 and 2300 m asl, with elfin cloud forests occurring on the highest peaks and ridges.

Fires set to prepare agricultural and grazing lands at lower elevations are usually extinguished when they reach intact TMCF because of the high moisture levels of the forest understorey. An important exception occurred in 1997–8, when the region experienced a severe and prolonged drought associated with the El Niño Southern Oscillation (ENSO) event. The drought provoked deciduous behaviour in evergreen trees, which increased penetration of solar radiation through the canopy, and led to drying of the organic soil, litter and vegetation layers in the understorey, all of which increased the flammability of these forests (Anta & Plancarte 2001). During the months of April and May 1998, approximately 210 000 ha in the Chimalapas region burned, of which an estimated 38 000 ha occurred in TMCF (i.e. 60% of its original extent). Most of the fires originated from escaped anthropogenic fires.

The study area was delineated into three different biophysical zones according to geological substrate, soil type and forest stature. The first zone (1600–1725 m asl) was characterized by deep mineral soils (Ultisols) derived from metamorphic substrate, and supported TMCF with tall stature (canopy height 20–30 m). The second zone (1640–1740 m asl) occurred on sedimentary substrate forming a karst topography with relatively shallow soils (Typic Ustropepts and Lithic Troporthents), and supported TMCF with intermediate stature (canopy height 15–20 m). The third zone (1780 m asl) was characterized by karst topography with frequent outcroppings of bedrock and extremely shallow organic soils (Lithic Troporthents), and supported elfin cloud forests with low stature (canopy height 4–6 m). Classification of fire behaviour and severity within each zone was obtained from maps produced from remote sensing data, aerial photos, helicopter fly-overs, and ground surveys (SEMARNAP–MPS–SERBO 1998). According to these assessments, fires affecting the first two areas (metamorphic and sedimentary substrates) were primarily deep ground fires with occasional crown fires, while elfin forest at the highest elevations (karst topography) were primarily affected by crown fires.

METHODS

Experimental design

A paired-plot research design appropriate for after-only studies (where no pre-disturbance data are available), using carefully matched treatment (burned) and control (unburned) sites, was used to reduce the possibility of errors caused by temporal and spatial correlation (Wiens & Parker 1995). Each pair consisted of adjacent burned and unburned sites where pre-treatment conditions were assumed to have been similar, with a minimum of 30 m between treatment and control plots. A total of six 30 × 30-m paired plots were established: three on metamorphic substrate with tall stature TMCF, and three on sedimentary substrate with intermediate stature TMCF. Visual observations combined with data collected from one 30 × 30-m plot established in the elfin cloud forests confirmed that tree mortality was nearly total (i.e. 100%). No unburned sites suitable as controls could be located for elfin forest; therefore paired plots were not established.

Table 1. Live tree dry-weight biomass (Mg ha^{-1}) estimated according to the equation: $\log_e T = -1.71 + 1.16 \log_e BA$ (T = total tree biomass, kg; BA = basal area; Tanner 1980); amount of fallen, standing, and total dead wood in unburned and burned TMCF growing on metamorphic and sedimentary substrates. Values presented as mean ± SE. Lower case letters indicate significant differences between columns, i.e. unburned forest and burned forest.

	Metamorphic		Sedimentary	
	Unburned	Burned	Unburned	Burned
Live tree biomass	299.2 ± 90.1a	53.6 ± 17.1b	196.4 ± 41.6a	24.4 ± 11.9b
Standing dead wood	6.0 ± 0b	204.5 ± 37.2a	25.0 ± 5.1b	82.0 ± 8.8a
Fallen dead wood	11.0 ± 3.3b	32.6 ± 3.4a	17.2 ± 3.8b	42.2 ± 10.7a
Total dead wood (standing and fallen)	17.0	237.1	42.2	124.2
Total woody biomass (live and dead)	316.2	290.7	238.6	148.6
% of total dead wood in fallen wood	64.7	13.7	40.8	34.0
% of total above-ground biomass in dead wood	5.4	81.6	17.7	83.6

Data collection

Data were collected between March and June of 2002. Diameter at breast height (dbh = 1.3 m) or directly above the buttress was measured for all live and dead trees (dbh > 10 cm) located within each plot. Individual tree dry-weight biomass was calculated separately for live trees and dead standing trees according to the allometric formula developed by Tanner (1980) for montane cloud forests in Jamaica: $\log_e T = -1.71 + 1.16 \log_e \mathrm{BA}$ (T = total dry-weight tree biomass in kg; BA = basal area). Total tree biomass per plot was calculated as the accumulated total of all values. Although there are methodological problems associated with using only dbh to estimate total biomass (Fearnside 1997, Haugaasen *et al.* 2003), this approach was used due to the lack of available allometric equations derived specifically for TMCF at the study site.

Biomass of fallen dead wood (i.e. coarse woody debris) was estimated using a modification of the line intersection method (Brown 1974, Delaney *et al.* 1998). Assessments were conducted along two 30-m transects established within each plot 10 m apart. Fallen dead wood was separated into four diameter classes (Burgan & Rothermel 1984): (I) < 0.6 cm, (II) > 0.6 and < 2.6 cm, (III) > 2.6 cm and < 12 cm, and (IV) > 12 cm. Pieces of fallen dead wood less than 12 cm in diameter were tallied for the first 5 m along each transect in burned plots, and for the first 10 m along each transect in control plots. Pieces of fallen dead wood greater than 12 cm diameter were tallied along the entire 30-m transect for both treatment and control plots. Decomposition state (solid, partially decomposed, fully decomposed) was noted for each piece of fallen dead wood. Density values presented by Clark *et al.* (2002) for fallen dead wood associated with each of the three decomposition states from moist tropical forests in Costa Rica were used for the mass calculations according to the equation presented in Brown (1974).

To estimate fine-root biomass, five root cores were collected from each plot at arbitrary locations, using PVC tubes with 5 cm diameter. Each tube was inserted into the soil to a depth of 30 cm, extracted with the soil intact, and sealed on both ends with parafilm. In the laboratory, each root sample was separated by horizon (O, A and B), and fine roots (< 2 mm diameter) extracted using a 2-mm sieve. Each root sample was then separated into live and dead roots, dried for 48 h at 110 °C, and weighed. As April is generally one of the driest months of the year, constraints on plant growth were expectedly near their peak, thereby allowing for one-time comparisons of below-ground ecosystem response to maximum levels of stress among treatments (Vogt *et al.* 1993).

Depth of the humus layer was measured at 10 randomly located sampling points within each plot in order to estimate depth of combustion in the organic soil layer as an indicator of burn severity. Depth of the litter layer was measured at the same sampling points as an indicator of change in ecosystem productivity.

Data analysis

All above- and below-ground biomass values were converted to a per hectare basis. Student's t-tests were used to examine differences between measured parameters within treatment and control sites (SAS Inc. 2000). The data were determined to be normally distributed and therefore left untransformed.

RESULTS

Average live tree dry biomass in the unburned forests was 196 Mg ha^{-1} for TMCF with intermediate stature growing on sedimentary substrates and 299 Mg ha^{-1} for TMCF with tall stature growing on metamorphic substrates (Table 1). Burned forests had significantly lower live tree dry biomass compared with the unburned forests ($P < 0.0001$), estimated at 24 Mg ha^{-1} on sedimentary substrates and 54 Mg ha^{-1} on metamorphic substrates. These values for live tree biomass are 88% and 82% lower in burned TMCF growing on sedimentary and metamorphic substrates, respectively, compared with unburned TMCF.

Table 2. Live fine root dry-weight biomass (< 2 mm diameter; g m^{-2}) for three soil horizons (O, A and B) to a depth of 30 cm for unburned and burned TMCF growing on metamorphic and sedimentary substrates. All values presented as mean ± SE and per cent change. Lower case letters indicate significant differences between columns, i.e. unburned forest and burned forest.

	Metamorphic		Sedimentary	
	Unburned	Burned	Unburned	Burned
Soil Horizon O	628.2 ± 172.3a	145.4 ± 76.2a	419.9 ± 141.4a	214.3 ± 30.2a
Soil Horizon A	189.0 ± 48.5a	166.8 ± 20.2a	166.8 ± 47.7a	119.2 ± 6.8a
Soil Horizon B	129.1 ± 77.8a	151.6 ± 115.1a	152.3 ± 91.7a	49.8 ± 24.7a
Total	946.2 ± 101.9a	463.8 ± 70.5b	739.0 ± 93.6a	383.3 ± 20.6b

Table 3. Depth of leaf litter and humus layers (cm) for burned and unburned forests growing on metamorphic and sedimentary substrates. All values presented as mean ± SE and per cent change. Lower case letters indicate significant differences between columns, i.e. unburned forest and burned forest.

	Metamorphic			Sedimentary		
	Unburned	Burned	% Change	Unburned	Burned	% Change
Leaf litter (cm)	2.2 ± 0.3a	1.1 ± 0.3b	50.0	3.3 ± 0.3a	2.8 ± 0.3a	15.2
Humus (cm)	8.7 ± 1.7a	1.0 ± 0.2b	88.5	4.7 ± 0.5a	2.1 ± 0.2b	55.3

The amount of fallen dead wood and total dead wood (i.e. fallen and standing combined) in unburned forests was 11.0 and 17.0 Mg ha^{-1}, respectively, for forests growing on metamorphic substrates, and 17.2 and 42.2 Mg ha^{-1}, respectively, for forests growing on sedimentary substrates (Table 1). The amount of fallen dead wood recorded in burned TMCF located on metamorphic and sedimentary substrates was 2.9-fold and 2.5-fold higher, respectively, compared with values recorded for unburned forests. The amount of total dead wood was 3- to 14-fold greater for TMCF impacted by fire and growing on sedimentary and metamorphic substrates, respectively. The estimated proportion of total above-ground biomass occurring as dead wood for TMCF on metamorphic and sedimentary substrates ranged 5.4–17.7% for unburned forests, and 81.6–83.6% for burned forests, respectively.

Measures of fine-root biomass for unburned and burned TMCF located on the two substrate types were not significantly different, potentially due to the small sample size and the high degree of within-plot spatial variability in fine-root biomass (Table 2); however, general trends can be discerned from the data. In burned forests, live fine-root biomass in the organic (O) horizon was 76.9% (metamorphic substrates) and 49% (sedimentary substrates) lower compared with live fine-root biomass recorded for unburned forests. For the deeper horizons (A and B), differences in live fine-root biomasses between the unburned and burned forests were not as pronounced, varying between 11.7% and 28.5%, with the exception of the B horizon on the sedimentary substrate, for which fine root biomass was 67.3% lower in the burned forests.

Average depth of the humus layer for TMCF growing on metamorphic and sedimentary substrates was 8.7 cm and 4.7 cm in unburned sites and 1.0 and 2.1 cm in burned sites, respectively, representing a change in the humus layer depth of 57–89% (Table 3). Average depth of the litter layer for sedimentary and metamorphic substrates was 15–50% lower, respectively, for burned compared with unburned TMCF.

DISCUSSION

The values reported for total live tree biomass in our study of tropical montane cloud forests in Oaxaca, Mexico (196–299 Mg ha^{-1}) are similar to values reported for montane rain forest in the Luquillo Mountains of Puerto Rico (Weaver & Murphy 1990: 180 Mg ha^{-1}) and for montane rain forests in Jamaica (Tanner 1980: 211–341 Mg ha^{-1}) and near the upper range of values reported for old-growth tropical forest sites worldwide (Clark *et al.* 2001). The relatively high losses in live tree biomass following fire reported in this study, ranging 82–88% for TMCF and nearly 100% for elfin cloud forest, is at least partly a reflection of accumulated post-fire mortality, as trees damaged or stressed by the severe disturbance continue to die after the event has passed (Condit *et al.* 1995, Zimmerman *et al.* 1994). Despite the temporal factor, these results document one of the most severe effects of fire in relatively undisturbed tropical moist forests where ecosystem structure, composition, and microclimate had not been significantly impacted by human activities prior to the fires. For example, in a study on the effects of a first burn in Amazonian rain forests with relatively low human disturbance, Barlow *et al.* (2003) reported a 23% loss of living biomass 1 y after the fires occurred, which increased to 49% 3 y after the fires. Biomass losses following fire in more disturbed tropical forests tend to be higher, although they still do not reach the levels reported for TMCF in our study. In a selectively logged evergreen rain forest in the Amazon Basin, first burns were characterized by surface fires that resulted in a 40% reduction in live woody biomass after 1 y (Cochrane *et al.* 1999).

Tree mortality, also related to biomass loss, reflects similar patterns. In the study by Barlow *et al.* (2003), tree mortality increased from 45% the first year after a fire to 52% in the second year, while in the Cochrane *et al.* (1999) study, tree mortality increased from 38% in the first year to 68% in the second year. Working in a selectively logged Amazon rain forest, Holdsworth & Uhl (1997) reported an increase in tree mortality from 38% the first year after a surface fire, to 44% 18 mo after the fire. In a seasonal tropical evergreen forest in Brazil, tree mortality following low-intensity surface fires was 24% almost 2 y after the fires occurred (Ivanauskas *et al.* 2003). Pinard *et al.* (1999) reported 39% tree mortality 1 y following surface fires in selectively logged tropical subhumid forests in Bolivia. At our study site, accumulated tree mortality 4 y after deep ground fires occurring in relatively undisturbed TMCF was 83% (Asbjornsen & Gallardo-Hernández 2004). This suggests that TMCF may be exceptionally vulnerable to fire damage, especially considering that most of the previously cited studies were conducted in disturbed forests presumably more susceptible to intense fires.

Fine-root biomass for intact TMCF reported in our study (420–628 $g\,m^{-2}$) was slightly greater than that reported for tropical montane forest in the Andes of Colombia (346–400 $g\,m^{-2}$; Cavelier *et al.* 1996b), but lower than that reported for mature old-growth tropical montane forests in Costa Rica (1128 $g\,m^{-2}$; Hertel *et al.* 2003). We are aware of no other studies that have considered the impact of fire on fine-root biomass in tropical montane forests. Despite the changes in fine root biomass not being significant, a trend indicating severe reduction (49–77%) in fine-root biomass for the upper A horizon was recorded in this study. This trend suggests a potential long-term effect of fire on the resilience of these ecosystems, especially since these estimates include both surviving and newly regenerating plants. Working in a tropical deciduous forest in Mexico, Castellanos *et al.* (2001) reported a reduction in fine-root biomass of only 11% in the upper 10 cm of soil after fire and conversion to pasture – which may be considered a more severe disturbance than fire alone. The high values reported in our study are probably a result of the deep ground fires that occurred in these TMCF ecosystems and likely penetrated – either directly or through heat conductance – deep into the soil horizon. This is further supported in our study by the data on changes in the depth of the humus layer, in which average humus layer depth was 55–89% (2.6–7.7 cm) lower in burned sites compared with unburned sites. Soils in montane tropical forests tend to have greater organic matter content as a result of slow decomposition processes (Bruijnzeel & Proctor 1995). Under low moisture conditions these deep organic soil horizons provide additional fuel, often sustaining slow-burning smouldering ground fires with potentially severe impacts on the below-ground biological system (Neary *et al.* 1999). The high losses in fine-root biomass may also have contributed to the high mortality levels recorded for trees mentioned above.

Another important factor that likely had a strong influence on the severity of the fires in the TMCF examined in this study was the interaction between substrate, vegetation and microclimate. The elfin cloud forests growing on karst topography located in high-elevation exposed environments were affected by crown fires that killed nearly all of the living biomass. Drainage of water in karstic substrates is extremely rapid; consequently dry periods often result in extended and more severe droughts compared with non-karstic substrates (Crowther 1986, Kelly *et al.* 1988). These drought-prone conditions would likely favour more severe fires. Further, because the stature of elfin forests is lower, fires can more easily ascend into the forest canopy. Lack of significant differences in the amount of living biomass killed in the taller forests growing on the metamorphic versus sedimentary substrates in our study may be attributed to the relatively small area sampled and high variability in the data. However, it is also possible that the severity of the drought was so great that its effects masked any differences in soil moisture that, under normal rainfall years, may prevail across the two substrates types due to differing drainage and soil water storage capacities. Similar homogenization effects of extreme climatic conditions on microclimate variability have been reported elsewhere (Asbjornsen *et al.* 2004).

The amount of fallen dead wood recorded in our study for unburned TMCF, ranging 11–17 $Mg\,ha^{-1}$, agrees with other studies from montane rain forests, where reported values ranged 8–21 $Mg\,ha^{-1}$ (Delaney *et al.* 1998). The total amount of dead wood in unburned TMCF (17–42 $Mg\,ha^{-1}$) is also similar to values reported elsewhere (Delaney *et al.* 1998: 35–42 $Mg\,ha^{-1}$). In a study by Cochrane & Schulze (1999), in which dead and living woody biomass was assessed for tropical moist forests in the Amazon following multiple burns in logged forests, the increase in dead woody biomass to 31–71% of total biomass (compared to 18% in unburned forests) significantly increased the flammability of these forests. At the Chimalapas site, where fires occurred for the first time in relatively undisturbed TMCF, the total amount of dead wood 4 y after the fires ranged 52–75% of the total woody biomass, compared to only 5–18% in unburned forests, which suggests that under severe drought conditions the vulnerability of these burned TMCF areas to repeated fires would be greatly augmented.

The amount and distribution of dead woody biomass also provide an indication of differences in fire severity on the two study sites. Burned forests on sedimentary substrates had over 40% of the total dead wood occurring as fallen wood, compared to only 14% in burned forests on metamorphic substrates. This pattern may be attributed to more severe fires in the former leading to higher mortality, as well as greater vulnerability of standing dead trees growing on sedimentary substrates to blowdown due to more shallow soils. Further, while differences in total woody biomass between unburned and burned forest were not as great for TMCF growing on metamorphic substrates (8%) compared to that on sedimentary substrates (38%), the change in amount of dead wood was less for sedimentary substrates (3-fold increase) compared to metamorphic substrates (14-fold increase). This suggests that total combustion of woody biomass was higher on sedimentary substrates, possibly due to greater propensity for crown fires and higher burn intensities.

In conclusion, this study suggests that despite relatively few reports in the literature of fire in TMCF to date, relatively undisturbed TMCF can become highly flammable under extreme drought conditions and severity of these fires in TMCF may be exceptionally high. While first burns in tropical moist evergreen forests tend to be low-intensity surface fires that cause minimal damage to large canopy trees (Laurance 2003), first burns in TMCF examined in this study were characterized by slow-burning, deep ground fires that resulted in massive above- and below-ground biomass losses. The recovery of burned TMCF may be much slower relative to burned lowland tropical forests due to the extreme climatic conditions where TMCF occur, and subsequently slow turnover rates of carbon and nutrients and slow establishment and growth rates of regenerating vegetation following severe disturbance (Waide *et al.* 1998). Moreover, unequivocal evidence indicates that once tropical moist forests burn, they become increasingly susceptible to fire (Cochrane *et al.* 1999, Nepstad *et al.* 1999, Uhl & Kauffman 1990), and that repeated fires further retard recovery processes (Cochrane & Schulze 1999). Thus, initiatives aimed at reducing fire occurrence in TMCF need to work closely with local villages to promote appropriate practices that reduce risk of escaped fires, create alternative land use options that are not dependent on fire yet are sustainable and economically viable, and establish effective fire management programmes in which local villagers participate actively as full partners.

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