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A Review of Above Ground Necromass in Tropical Forests

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1. Introduction

Tropical forests are marked by high biological diversity and complex vegetation dynamics that result in a spatially diverse array of forest stand structures (Richards 1952, Denslow 1987, Salati and Vose 1984, Terborgh 1992, Ozanne et al. 2003). Knowledge of the forest structure is vital for estimation of carbon stocks and fluxes (Houghton et al. 2000, 2001), habitat and faunal distributions (Schwarzkopt and Rylands 1989), and interactions between the biosphere and atmosphere (Keller et al. 2004a). With deforestation and land use change occurring throughout the tropics, improved understanding of these dynamic and complex forests are vital for the development of regional and global carbon budgets (Nobre et al. 1991, Werth and Avissar 2002, Houghton et al. 2001, Davidson and Artaxo 2004).

The death and subsequent decomposition of trees is an important component in the forest ecosystem carbon cycling and directly tied to the forest structure (Denslow, 1987; Harmon and Franklin, 1989). The dead portions of trees and branches, termed coarse woody debris (CWD) or above ground coarse necromass (here after termed necromass for this chapter), are an important component in the carbon cycle of forests accounting for 20-40% of carbon storage and 12% of the total above ground respiration (Harmon and Sexton 1996, Brown 1997, Palace et al. 2007). Necromass is also important in nutrient cycling and provides habitat for many organisms (MacNally et al. 2001, Norden and Paltto, 2001).

The dynamics of necromass production and loss through disturbance and decay are poorly understood and quantified in tropical forests (Martius and Banderia 1998, Eaton and Lawrence 2006). The slow process of decomposition is dependent upon the chemical and structural complexity of wood as well as the influence of a multitude of organisms involved with decomposition. Decomposition rates depend upon physical climate properties that vary over time. The production of necromass through the death of whole trees or portions of trees is episodic ranging greatly over temporal and spatial scales (Wessman 1992). This range in scale makes necromass measurement difficult, requiring large plots or long

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transects to catch rare large tree falls, as well as long periods of study to estimate both necromass production and decomposition (Harmon et al. 1986, Palace et al. 2008).

In this paper, we review necromass studies conducted in tropical forested ecosystems. We describe and define important terms and components in necromass research. In conjunction with this discussion, we examined various methodologies designed to measure these components and current literature involved with field based estimates of necromass. A simple model was developed to examine pool and decay estimates throughout these forested regions where literature estimates were unavailable. General relationships between necromass components were explored such as proportion of necromass to biomass and fallen to standing dead necromass.

2. Methods

We reviewed literature that dealt with field measurements of above ground coarse woody necromass stocks, production of dead wood, and decomposition of necromass. We gathered sources on necromass, with a focus on tropical forests through library searches, references cited in seminal ecological articles, peer suggestion, Web of Science© (http:/apps.isiknowledge.com) and an Yahoo© newsgroup focusing on dead wood (http://groups.yahoo.com/group/dead_wood). We avoided the abundant studies focused on fine litter dynamics or soil respiration, although these aspects of carbon cycling would be important for comprehensive review and site comparison of carbon budgets. This study did not examine remote sensing or modeling literature with regard to necromass, although these two approaches may provide fruitful means for estimation and understanding of necromass production and cycling (Frolking et al. 2009).

More than 100 papers were examined for necromass stock, production and decay information and field estimated values. Data relevant to tropical forests is presented in Table 1 and 2. Data in Table 1 presents measured necromass components and information about the site location. Table 2 includes site information along with measured and estimated values of production and decomposition rates. Methodology is presented in a discussion about each necromass component. We recorded stocks of necromass, production of dead wood, and decomposition rates when available. We also attempted to gather biomass estimates from other papers at a site when biomass was not presented originally in the necromass literature and in some cases we were able to contact authors directly for biomass information (personal communications, Simon Grove and Michael Liddell, Keller et al. 2001, Asner et al. 2002, Baker et al. 2004). In each of the following three sections, necromass stocks, production of necromass, and decomposition of necromass, we review the component, present methodologies, and review the literature pertaining to the tropical forests.

2.1 Coarse woody debris stocks

Necromass is defined as the mass of all dead material and usually in reference to dead plant material. Necromass stocks aboveground include fine litter and coarse woody debris (CWD) where CWD has generally been defined as necromass with a diameter greater than 2 cm (Harmon et al. 1986). Necromass, is often divided into two categories: (1) fallen or downed necromass, and (2) standing dead wood (snags) (Harmon et al., 1986). For this review we will use the term necromass to refer to coarse woody debris. Similar stocks for coarse and

fine material are found below ground. Below ground necromass is not treated in this review, but can be a significant portion of total dead material in a forested and savanna ecotone. Necromass stocks or pools have further been divided into groups dependent upon whether the material has fallen to the ground or whether it remains standing. The diameter of necromass and the degree of decomposition (decay class) have been used to further refine necromass categories (Harmon et al. 1986).

Measurement of fallen necromass is done primarily by one of two methods, line intercept or plot sampling (Harmon et al. 1986). Another method, relascope sampling (Gove et al. 2002) has not been used in tropical field studies and is not discussed here. Line intercept sampling (also termed planar intercept sampling) uses a straight line where all pieces of necromass that intersect the line are measured (Image 1).



Image 1. Line intercept sampling in a selectively logged forest in the Tapajos, National Forest, Brazil.

Volume (V) (m^3 ha^{-1}) of necromass for an individual transect is calculated using the following equation:

$$V = \frac{\pi^2 \Sigma \left(d_n\right)^2}{\left(8 * L\right)}$$

where d_n is the diameter of a piece of necromass at the line intercept and L is the length of the transect used in sampling (De Vries, 1986).

In plot based sampling a fixed area is determined and all pieces of necromass are measured in that area. Plot measurements of necromass require more work, but retain spatial information that can be compared with other biometric or other environmental variables. Plot estimates of fallen and standing necromass use a variety of methods to estimate the volume. These include the assumption that a piece of necromass is a cylinder, a frustum, or the use of multiple measurements along the length of the log to calculate the volume. Taper functions have been used to calculate the volume of fallen and standing dead (Rice et al. 2004; Palace et al. 2007, 2008).

Fallen necromass has been divided into diameter size classes. Depending on the sampling methodology, diameter can have different meanings. In line intercept sampling, the fallen necromass diameter is only measured at the point in which the two-dimensional plane is intersected by the piece of necromass (Brown 1974). For plot level sampling, diameter often refers to the average diameter of the entire log, along which multiple diameters have been measured (Harmon et al. 1986). Small diameter fallen necromass is often grouped for to tallies to save labor (Brown 1974). Many studies have used a diameter of 2 cm as a low-end cutoff for sampling although there are a few exceptions.

Plot and line intercept sampling provide measurements of volume. An exception to this is when all pieces of necromass are weighed in a plot. Five studies in our review, published prior to 1980, weighed all pieces of necromass (Table 1). In order to quantify necromass from volume estimates, measurements of the densities of necromass pieces are required. More highly decayed logs theoretically should have less mass (Harmon et al. 1995). A common approach to quantification of mass is the stratification of necromass into decay classes and the application of decay-class-wide densities to the volume quantified by decay class. Other approaches to the estimation of necromass density include application of average density of live trees (Gerwing 2002, Nascimento and Laurence 2002), application of guesses (Gerwing 2002), and use of values from other sites (Rice et al. 2004). One study did not mention how mass was derived from volume estimates (Uhl and Kauffman 1990). Another used measured values for classes of necromass, such as trunks, prop roots, branches, and twigs (Robertson and Daniel 1989).

Decay classes are easily determined by the data collector and allow for a stratification of necromass sampling. Densities are measured for a sample of all coarse dead wood. Measurement approaches for density include weighing entire pieces of coarse dead wood, disks cut out of a log, and smaller plugs or samples across a cut disk (Harmon et al. 1986, Chambers et al. 2000, Keller et al. 2004b) (Image 2 and 3). In all cases, samples must be dried to a constant weight. Keller et al. (2004b) used a constant 60 degrees C. Large void spaces, created by organisms like termites or beetles, are often not considered in necromass density estimates. Larger samples used in density estimate include these void spaces, but smaller

samples need to account for this. Keller et al. (2004b) used digitized images of disks cut through large pieces of fallen necromass in order to measure void spaces adjust density estimates accordingly (Image 4). This methods has been adopted by other studies (Palace et al. 2007, Baker et al. 2007, Chao et al. 2008)

Reference	Location	Type of Site	Forest Type	Total Necromass (Mg ha^{-1})	AG Biomass (Mg ha^{-1})	Fallen CWD (Mg ha^{-1})	Standing Dead (Mg ha^{-1})	Necro Biomass Ratio
Baker et al. 2007, Baker et al. 2004	Southern Peru	UF	TRF	17.7	234.1	13.5	4.2	
Bernhard-Reversat et al. 1978	Yapo, Ivory Coast	LD	TRF	3.6	429.4			0.01
Bernhard-Reversat et al. 1978	Banco, Ivory Coast	UF	TRF	3.8	538.3			0.01
Brown et al.,1992	Acre, Brazil	2nd	TMF	13.0	95.0			0.14
Brown et al.,1992	Acre, Brazil	UF	TMF	43.0	320.0			0.13
Brown et al. 1995	Rondonia, Brazil	UF	TMF	40.0	285.0			0.14
Buxton 1981	Tsavo National Park, Kenya	2nd	TMF	3.2				
Carey et al. 1994	Venezuela	UF	TMF		326.0			0.00
Carey et al. 1994	Venezuela	UF	LMMF		397.0			0.00
Chambers et al. 2000, 2001	Manaus, Brazil	UF	LEF	21.0				
Chao et al. 2008	Northern Peru	UF-flooded	TRF	10.3	214.8			
Chao et al. 2008	Northern Peru	UF-white sand	TRF	45.8	226.1			
Chao et al. 2008	Northern Peru	UF-clay	TRF	30.9	261.4			
Chao et al. 2009a	NE Amazonia	UF	TMF	74.5	434.5	58.7	15.8	
Chao et al. 2009a	NE Amazonia	UF	TMF	62.8	229.7	54.1	8.7	
Chao et al. 2009a	NE Amazonia	UF	TMF	38.4	347.8	20.5	17.9	
Chao et al. 2009a	NW Amazonia	UF	TRF	31.4	254.7	27.1	4.3	
Chao et al. 2009a	NW Amazonia	UF	TRF	41.1	235.3	24.0	17.1	
Chao et al. 2009a	NW Amazonia	UF	TRF	21.5	251.0	17.9	3.6	
Chao et al. 2009a	NW Amazonia	UF	TRF	27.4	251.1	24.9	2.5	
Chao et al. 2009a	NW Amazonia	UF	TRF	25.5	260.0	17.8	7.7	
Chao et al. 2009a	NW Amazonia	UF	TRF	37.9	253.3	28.1	9.8	
Chao et al. 2009a	NW Amazonia	UF	TRF	15.4	263.0	12.4	3.0	
Chao et al. 2009a	NW Amazonia	UF	TRF	18.6	260.4	12.2	6.4	
Clark et al., 2002	La Selva, Costa Rica	UF	TRF	52.8	155.8	46.3	6.5	0.34
Cochrane et al. 1999	Tailandia, Para, Brazil	DF-first burn	TMF	50.0	220.0			0.23
Cochrane et al. 1999	Tailandia, Para, Brazil	DF-second burn	TMF	71.0	129.0			0.55
Cochrane et al. 1999	Tailandia, Para, Brazil	DF-third burn	TMF	116.0	47.0			2.47
Cochrane et al. 1999	Tailandia, Para, Brazil	UF	TMF	53.0	242.0			0.22

Reference	Location	Type of Site	Forest Type	Total Necromass (Mg ha^{-1})	AG Biomass (Mg ha^{-1})	Fallen CWD (Mg ha^{-1})	Standing Dead (Mg ha^{-1})	Necro Biomass Ratio
Collins 1981	Nigeria	DF-fires	S	2.5		1.4	1.1	
Cummings et al. 2002	Rondônia, Brazil	OF	DF	32.4	270.3			
Cummings et al. 2002	Rondônia, Brazil	UDF	TMF	30.5	337.8			
Cummings et al. 2002	Rondônia, Brazil	SE	SE	20.8	319.9			
Delaney et al. 1998	Venezuela	UF	TTW	2.4	13.1	1.0	1.4	0.18
Delaney et al. 1998	Venezuela	UF	TDF	4.8	141.2	1.9	2.9	0.03
Delaney et al. 1998	Venezuela	UF	TMDF	6.6	330.0	3.8	2.8	0.02
Delaney et al. 1998	Venezuela	UF	TMF	33.3	346.9	18.5	14.8	0.10
Delaney et al. 1998	Venezuela	UF	LMMF	42.3	341.1	21.0	21.3	0.12
Delaney et al. 1998	Venezuela	UF	MWF	34.5	325.5	8.2	26.3	0.11
Eaton & Lawrence 2006	Southern Mexico	cleared	DTF	51.6		51.6		
Eaton & Lawrence 2006	Southern Mexico	2nd-1-5 y	DTF	19.9		19.9		
Eaton & Lawrence 2006	Southern Mexico	2nd-6-12 y	DTF	11.4		11.4		
Eaton & Lawrence 2006	Southern Mexico	2nd-12-16 y	DTF	15.0		15.0		
Eaton & Lawrence 2006	Southern Mexico	Montana	DTF	37.5	147.0	37.5		0.25
Edwards & Grubb 1977	New Guinea	UF	LMMF	10.9	490.0			0.02
Gerwing 2002	Paragominas, Brazil	MD-L	TMF	76.0	245.0	68.0	8.0	0.31
Gerwing 2002	Paragominas, Brazil	HD-L	TMF	149.0	168.0	140.0	9.0	0.89
Gerwing 2002	Paragominas, Brazil	LD-fire	TMF	101.0	177.0	70.0	31.0	0.57
Gerwing 2002	Paragominas, Brazil	HD-fire	TMF	152.0	50.0	128.0	24.0	3.04
Gerwing 2002	Paragominas, Brazil	UF	TMF	55.0	309.0	33.0	22.0	0.18
Golley et al. 1973, 1969	Darien, Panama	UF	TMF	17.6	370.5			0.05
Golley et al. 1973, 1969	Darien, Panama	UF	TMF	6.2	263.5			0.02
Golley et al. 1973, 1969	Darien, Panama	UF	TMF	4.8	271.4			0.02
Golley et al. 1973, 1969	Darien, Panama	UF	TMF	19.1	176.6			0.11
Golley et al. 1973, 1969	Darien, Panama	UF	TMF	102.1	279.2			0.37
Golley et al. 1975	Darien, Panama	UF	TMF	14.6	377.8			0.04
Golley et al. 1975	Darien, Panama	UF	RF	4.9	284.1			0.02
Greenland & Kowal 1960	Kade, Ghana	2nd- 50 y	MTF	71.8	213.7			0.34

Reference	Location	Type of Site	Forest Type	Total Necromass (Mg ha^{-1})	AG Biomass (Mg ha^{-1})	Fallen CWD (Mg ha^{-1})	Standing Dead (Mg ha^{-1})	Necro Biomass Ratio
Greenland & Kowal 1960	Yangambi, Belgian Congo	2nd- 18 y	MTF	17.4	128.7			0.14
Grove 2001, biomass Liddell personal	Australia	Logged	TRF	7.3				
Grove 2001, biomass Liddell personal	Australia	2nd	TRF	5.1				
Grove 2001, biomass Liddell personal	Australia	UF	TRF	9.3	270.0			0.03
Harmon et al. 1995	Quintana Roo, Mexico	MD-H	TDF	48.5	112.0	45.7	2.8	0.43
Harmon et al. 1995	Quintana Roo, Mexico	MD-F	TDF	128.2	112.0	72.4	55.8	1.14
Harmon et al. 1995	Quintana Roo, Mexico	MD-H	TDF	60.8	133.0	47.3	13.5	0.46
Harmon et al. 1995	Quintana Roo, Mexico	MD-F	TDF	122.5	133.0	1.6	120.9	0.92
Harmon et al. 1995	Quintana Roo, Mexico	HD-H	TDF	28.0	94.0	21.2	6.8	0.30
Harmon et al. 1995	Quintana Roo, Mexico	HD-fire	TDF	118.6	94.0	25.8	92.8	1.26
Harmon et al. 1995	Quintana Roo, Mexico	UF	TDF	38.0	209.0	24.8	13.2	0.18
Hughes et al. 2000	Tuxtlas, Mexico	UF	TEF	14.0	382.5	14.0		0.04
Kauffman et al. 1988	Rio Negro, Venezuela	DF	TRF	48.5	47.5			1.02
Kauffman et al. 1988	Rio Negro, Venezuela	DF	TRF	26.9	80.1			0.34
Kauffman et al. 1988	Rio Negro, Venezuela	UF	TRF	1.6	11.4			0.14
Kauffman et al. 1988	Rio Negro, Venezuela	UF	TRF	5.3	38.7			0.14
Kauffman et al. 1988	Rio Negro, Venezuela	UF	TRF	42.4	20.6			2.06
Kauffman et al. 1988	Rio Negro, Venezuela	UF	TRF	12.9	51.1			0.25
Kauffman et al. 1988	Rio Negro, Venezuela	UF	TRF	14.4	238.6			0.06
Kauffman et al. 1988	Pernambuco, Brazil	2nd pre-fire	TDF		72.0	63.1		
Kauffman et al. 1988	Pernambuco, Brazil	2nd-post fire	TDF		72.0	11.9		
Keller et al. 2004b, Asner et al. 2002	Cauaxi, Brazil	RIL	TMF	89.6	203.0	74.7		0.44
Keller et al. 2004b, Asner et al. 2002	Cauaxi, Brazil	CL	TMF	129.4	203.0	107.8		0.64
Keller et al. 2004b, Asner et al. 2002	Cauaxi, Brazil	UF	TMF	66.2	203.0	55.2		0.33
Keller et al. 2004b, Keller et al. 2001	Tapajos, Brazil	RIL	TMF	91.4	282.0	76.2		0.32

Reference	Location	Type of Site	Forest Type	Total Necromass (Mg ha^{-1})	AG Biomass (Mg ha^{-1})	Fallen CWD (Mg ha^{-1})	Standing Dead (Mg ha^{-1})	Necro Biomass Ratio
Keller et al. 2004b, Keller et al. 2001	Tapajos, Brazil	UF	TMF	60.8	282.0	50.7		0.22
Kira 1978	West Malaysia	UF	TRF	50.9	421.3			0.12
Kira 1978	West Malaysia	UF	TRF		374.2			
Kira 1978	West Malaysia	UF	TRF		379.8			
Klinge 1973	Central Amazon, Brazil	UF	TRF	18.0	731.7	18.0		0.02
Lang & Knight 1979	Barro Colorado, Panama	UF	TRF					
Lang & Knight 1983	Panama	2nd-60 yr	TMF					
Martius 1997	Central Amazon, Brazil	UF	RF	11.4				
Martius & Bandeira 1998	Manaus, Brazil	UF	TMF	9.5		9.5		
Nascimento & Laurence 2002	Mauaus, Brazil	UF	TMF	31.0	356.2	24.8	6.14	0.09
Odum 1970	El Verde, Puerto Rica	UF	TRF					
Palace et al. 2007	Mato Grosso, Brazil	RIL	TMF	67.0	263.0	67.0	8.8	0.29
Palace et al. 2007	Mato Grosso, Brazil	UF	TMF	44.9	281.0	44.9	5.3	0.18
Palace et al. 2008, Keller et al. 2001, 2004b	Tapajos, Brazil	UF	TMF	50.7	282.0	50.7	7.7	0.21
Palace et al. 2008, Keller et al. 2001, 2004b	Tapajos, Brazil	RIL	TMF	72.6	282.0	72.6	12.9	0.30
Rice et al. 2004	Tapajos, Brazil	UF	TMF	70.0	298.1			0.23
Rice et al. 2004	Tapajos, Brazil	UF	TRF	99.6	298.1			0.33
Roberston & Daniel 1989	Australia	UF	Yman	1.8	387.0	1.0	0.8	0.00
Roberston & Daniel 1989	Australia	UF	Oman	14.3	465.0	4.8	9.4	0.03
Saldarriaga et al. 1988	Columbia and Venezeula	2nd-14 yr	TRF	15.2	60.8			0.25
Saldarriaga et al. 1988	Columbia and Venezeula	2nd- 20 yr	TRF	0.7	100.0			0.01
Saldarriaga et al. 1988	Columbia and Venezeula	2nd- 20 yr	TRF	1.6	73.4			0.02
Saldarriaga et al. 1988	Columbia and Venezeula	2nd- 20 yr	TRF	0.8	79.8			0.01
Saldarriaga et al. 1988	Columbia and Venezeula	2nd- 20 yr	TRF	1.0	116.0			0.01
Saldarriaga et al. 1988	Columbia and Venezeula	2nd- 20 yr	TRF	9.0	61.9			0.15
Saldarriaga et al. 1988	Columbia and Venezeula	2nd- 30 yr	TRF	8.5	130.0			0.07

Reference	Location	Type of Site	Forest Type	Total Necromass (Mg ha^{-1})	AG Biomass (Mg ha^{-1})	Fallen CWD (Mg ha^{-1})	Standing Dead (Mg ha^{-1})	Necro Biomass Ratio
Saldarriaga et al. 1988	Columbia and Venezeula	2nd- 35 yr	TRF	1.0	129.0			0.01
Saldarriaga et al. 1988	Columbia and Venezeula	2nd- 40 yr	TRF	5.7	186.0			0.03
Saldarriaga et al. 1988	Columbia and Venezeula	2nd- 60 yr	TRF	32.4	133.0			0.24
Saldarriaga et al. 1988	Columbia and Venezeula	2nd- 60 yr	TRF	2.7	244.0			0.01
Saldarriaga et al. 1988	Columbia and Venezeula	2nd- 60 yr	TRF	34.2	169.0			0.20
Saldarriaga et al. 1988	Columbia and Venezeula	2nd- 80 yr	TRF	8.2	160.0			0.05
Saldarriaga et al. 1988	Columbia and Venezeula	2nd- 80 yr	TRF	7.6	213.0			0.04
Saldarriaga et al. 1988	Columbia and Venezeula	2nd- 80 yr	TRF	40.4	173.0			0.23
Saldarriaga et al. 1988	Columbia and Venezeula	2nd- 80 yr	TRF	10.0	170.0			0.06
Saldarriaga et al. 1988	Columbia and Venezeula	UF	TRF	22.3	268.0			0.08
Saldarriaga et al. 1988	Columbia and Venezeula	UF	TRF	53.0	322.0			0.16
Saldarriaga et al. 1988	Columbia and Venezeula	UF	TRF	15.1	326.0			0.05
Saldarriaga et al. 1988	Columbia and Venezeula	UF	TRF	14.6	335.0			0.04
Scott et al. 1992	Roraima, Brazil	UF	LEF	5.1		4.1	1.0	
Summers 1998	Central Amazon, Brazil	DF	TMF	88.8				
Tanner 1980	Jamaica	UF	DTF	7.6	231.0			0.03
Tanner 1980	Jamaica	UF	DTF	12.0	338.0			0.04
Uhl & Kauffman 1990, Kauffman & Uhl 1990	Paragominas, Brazil	P	TMF	40.0		51.5		
Uhl & Kauffman 1990, Kauffman & Uhl 1990	Paragominas, Brazil	LF	TMF	178.8		178.8		
Uhl & Kauffman 1990, Kauffman & Uhl 1990	Paragominas, Brazil	2nd	TMF	23.0	28.0	27.7		0.82
Uhl & Kauffman 1990, Kauffman & Uhl 1990	Paragominas, Brazil	UF	TMF	51.0	250.0	55.6		0.20
Uhl et al. 1988	Paragominas, Brazil	LD-young	TMF	78.3	29.4			2.66
Uhl et al., 1988	Paragominas, Brazil	LD-old	TMF	87.8	86.1			1.02
Uhl et al. 1988	Paragominas, Brazil	LD-old	TMF	49.9	88.9			0.56

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Uhl et al. 1988	Paragominas, Brazil	MD-young	TMF	16.3	5.8			2.81
Uhl et al. 1988	Paragominas, Brazil	MD-young	TMF	21.6	8.3			2.60
Uhl et al. 1988	Paragominas, Brazil	MD-young	TMF	47.4	16.8			2.82
Uhl et al. 1988	Paragominas, Brazil	MD-young	TMF	11.2	17.0			0.66
Uhl et al. 1988	Paragominas, Brazil	MD-old	TMF	20.3	37.0			0.55
Uhl et al. 1988	Paragominas, Brazil	MD-old	TMF	20.4	32.8			0.62
Uhl et al. 1988	Paragominas, Brazil	HD-young	TMF	10.4	7.6			1.37
Uhl et al. 1988	Paragominas, Brazil	HD-young	TMF	8.6	15.5			0.55
Uhl et al. 1988	Paragominas, Brazil	HD-old	TMF	5.7	4.7			1.21
Uhl et al. 1988	Paragominas, Brazil	UF	TMF	41.9	300.0			0.14
Uhl et al. 1988	Paragominas, Brazil	UF	TMF	35.6	327.6			0.11
Uhl et al. 1988	Paragominas, Brazil	UF	TMF	48.1	284.7			0.17
Wilcke et al. 2005	Andes, Ecuador	UF	MWF	9.1		7.6	1.5	
Yoda & Kira 1982	Pasoh, Malaysia	UF	TRF	46.7				
Yoneda et al. 1977	Pasoh, Malaysia	UF	TRF					
Yoneda et al. 1990	Sumatra, Indonesia	UF	TMF	55.0	408.0	39.0	16.0	0.13

Forest types are: TRF – tropical rain forest, TMF – tropical moist forest, LMMF – lower montane moist forest, S – Savanna, SE – Savanna Edge, TTW –tropical thorn woodland, TDF – tropical dry forest, TMDF – tropical moist dry forest, MWF – tropical montane wet forest, RF – riverine forest, YMan – young mangrove, Oman – old mangrove.
Type of site definitions: UF – undisturbed, LD – low disturbance, 2nd – secondary forest (type or year of regrowth), OF – open forest, UDF – undisturbed dense forest, SE – savanna edge, Montana – cleared, MD-L(H, F) – moderate disturbance from logging (hurricane, fire), HD-L(H) heavy disturbance from logging (hurricane, fire), CL – conventional selective logging, RIL – reduced impact logging, LD – light disturbance.
Blank spaces indicate no data available from source. AG – above ground biomass, CWD – coarse woody debris.

Table 1. Reviewed literature for tropical forest necromass stocks.

Decay classes are usually described in two or more categories (Harmon et al. 1986, Chambers et al. 2000). These decay classes range from newly fallen necromass to highly decayed material that can be broken apart by hand (Harmon et al., 1995; Keller et al., 2004b) (Image 5). For a good description of a five decay class description, please refer to Keller et al. (2004). Chao et al. (2008) compared a three and five decay class system and found

comparable patterns between the two systems and concluded that a three class system is preferable because of the higher sample sizes obtained by grouping classes is statistically advantageous.



Image 2. Density measurements using a plug and tenon extractor attached to a hand-held power drill. Section of necromass sampled along a line intercept with section of fallen necromass being chain sawn into section for extraction.



Image 3. Multiple samples extracted from a section of fallen necromass using the tenon extractor.



Image 4. Example of void space in a section of fallen necromass.



Image 5. Example of the variation in decay classes, a sound piece of necromass to the left and a highly decayed and friable piece of necromass to the right.

Reference	Location	Type of Site	Forest Type	Production Measured (Mg ha^{-1} y^{-1})	Decay (k) Measured (y-1)	Production Est. (biomass * 0.02) (Mg ha^{-1} y^{-1})	Estimated Decay (k) (y-1)	Production Est. (necromass * 0.15) Mg ha^{-1} y^{-1})
Baker et al. 2007, Baker et al. 2004	Southern Peru	UF	TRF	3.8	0.21	4.68	0.26	2.66
Bernhard-Reversat et al. 1978	Yapo, Ivory Coast	LD	TRF			8.59	2.39	0.54
Bernhard-Reversat et al. 1978	Banco, Ivory Coast	UF	TRF			10.77	2.83	0.57
Brown et al.,1992	Acre, Brazil	2nd	TMF			1.9	0.15	1.95
Brown et al.,1992	Acre, Brazil	UF	TMF			6.4	0.15	6.45
Brown et al. 1995	Rondonia, Brazil	UF	TMF			5.7	0.14	6
Buxton 1981	Tsavo National Park, Kenya	2nd	TMF	0.31	0.07			0.48
Carey et al. 1994	Venezuela	UF	TMF	8.8		6.52		
Carey et al. 1994	Venezuela	UF	LMMF	9.53		7.94		
Chambers et al. 2000, 2001	Manaus, Brazil	UF	LEF	4.2	0.13, 0.17			3.15
Chao et al. 2008	Northern Peru	UF-flooded	TRF			4.3	0.42	1.55
Chao et al. 2008	Northern Peru	UF-white sand	TRF			4.52	0.1	6.87
Chao et al. 2008	Northern Peru	UF-clay	TRF			5.23	0.17	4.64
Chao et al. 2009	NE Amazonia	UF	TMF	6.7		8.69	0.12	11.18
Chao et al. 2009	NE Amazonia	UF	TMF	8.6		4.59	0.07	9.42
Chao et al. 2009	NE Amazonia	UF	TMF	6.3		6.96	0.18	5.76
Chao et al. 2009	NW Amazonia	UF	TRF	2.5		5.09	0.16	4.71
Chao et al. 2009	NW Amazonia	UF	TRF	7.9		4.71	0.11	6.17
Chao et al. 2009	NW Amazonia	UF	TRF	5.9		5.02	0.23	3.23
Chao et al. 2009	NW Amazonia	UF	TRF	4.4		5.02	0.18	4.11
Chao et al. 2009	NW Amazonia	UF	TRF	5.5		5.2	0.2	3.83
Chao et al. 2009	NW Amazonia	UF	TRF	4.8		5.07	0.13	5.69
Chao et al. 2009	NW Amazonia	UF	TRF	4.8		5.26	0.34	2.31
Chao et al. 2009	NW Amazonia	UF	TRF	4.1		5.21	0.28	2.79
Clark et al., 2002	La Selva, Costa Rica	UF	TRF	4.9	0.09	3.12	0.06	7.92
Cochrane et al. 1999	Tailandia, Para, Brazil	DF-first burn	TMF			4.4	0.09	7.5

Reference	Location	Type of Site	Forest Type	Production Measured (Mg ha^{-1} y^{-1})	Decay (k) Measured (y-1)	Production Est. (biomass * 0.02) (Mg ha^{-1} y^{-1})	Estimated Decay (k) (y-1)	Production Est. (necromass * 0.15) Mg ha^{-1} y^{-1})
Cochrane et al. 1999	Tailandia, Para, Brazil	DF-second burn	TMF			2.58	0.04	10.65
Cochrane et al. 1999	Tailandia, Para, Brazil	DF-third burn	TMF			0.94	0.01	17.4
Cochrane et al. 1999	Tailandia, Para, Brazil	UF	TMF			4.84	0.09	7.95
Collins 1981	Nigeria	DF-fires	S	1.27	0.51			0.37
Cummings et al. 2002	Rondônia, Brazil	OF	DF			5.41	0.17	4.86
Cummings et al. 2002	Rondônia, Brazil	UDF	TMF			6.76	0.22	4.58
Cummings et al. 2002	Rondônia, Brazil	SE	SE			6.4	0.31	3.12
Delaney et al. 1998	Venezuela	UF	TTW		0.06	0.26	0.11	0.36
Delaney et al. 1998	Venezuela	UF	TDF		0.2	2.82	0.59	0.72
Delaney et al. 1998	Venezuela	UF	TMDF		0.52	6.6	1	0.99
Delaney et al. 1998	Venezuela	UF	TMF		0.03	6.94	0.21	5
Delaney et al. 1998	Venezuela	UF	LMMF		0.13	6.82	0.16	6.35
Delaney et al. 1998	Venezuela	UF	MWF		0.11	6.51	0.19	5.18
Eaton & Lawrence 2006	Southern Mexico	cleared	DTF	0.11	0.38			7.74
Eaton & Lawrence 2006	Southern Mexico	2nd-1-5 y	DTF	0.11	0.38			2.98
Eaton & Lawrence 2006	Southern Mexico	2nd-6-12 y	DTF	0.11	0.38			1.71
Eaton & Lawrence 2006	Southern Mexico	2nd-12-16 y	DTF	0.91	0.38			2.25
Eaton & Lawrence 2006	Southern Mexico	Montana	DTF		0.38	2.94	0.08	5.62
Edwards & Grubb 1977	New Guinea	UF	LMMF			9.8	0.9	1.64
Gerwing 2002	Paragominas, Brazil	MD-L	TMF			4.9	0.06	11.4
Gerwing 2002	Paragominas, Brazil	HD-L	TMF			3.36	0.02	22.35
Gerwing 2002	Paragominas, Brazil	LD-fire	TMF			3.54	0.04	15.15
Gerwing 2002	Paragominas, Brazil	HD-fire	TMF			1	0.01	22.8
Gerwing 2002	Paragominas, Brazil	UF	TMF			6.18	0.11	8.25
Golley et al. 1973, 1969	Darien, Panama	UF	TMF			7.41	0.42	2.64
Golley et al. 1973, 1969	Darien, Panama	UF	TMF			5.27	0.85	0.93
Golley et al. 1973, 1969	Darien, Panama	UF	TMF			5.43	1.13	0.72
Golley et al. 1973, 1969	Darien, Panama	UF	TMF			3.53	0.18	2.87
Golley et al. 1973, 1969	Darien, Panama	UF	TMF			5.58	0.05	15.32
Golley et al. 1975	Darien, Panama	UF	TMF			7.56	0.52	2.19
Golley et al. 1975	Darien, Panama	UF	RF			5.68	1.16	0.74
Greenland & Kowal 1960	Kade, Ghana	2nd- 50 y	MTF			4.27	0.06	10.77
Greenland & Kowal 1960	Yangambi, Belgian Congo	2nd- 18 y	MTF			2.57	0.15	2.61
Grove 2001, biomass Liddell personal								1.09
Grove 2001, biomass Liddell personal								0.76
Grove 2001, biomass Liddell personal						5.4	0.58	1.4
Harmon et al. 1995	Quintana Roo, Mexico	MD-H	TDF			2.24	0.05	7.28
Harmon et al. 1995	Quintana Roo, Mexico	MD-F	TDF			2.24	0.02	19.23
Harmon et al. 1995	Quintana Roo, Mexico	MD-H	TDF			2.66	0.04	9.12
Harmon et al. 1995	Quintana Roo, Mexico	MD-F	TDF			2.66	0.02	18.38
Harmon et al. 1995	Quintana Roo, Mexico	HD-H	TDF			1.88	0.07	4.2
Harmon et al. 1995	Quintana Roo, Mexico	HD-fire	TDF			1.88	0.02	17.79

Reference	Location	Type of Site	Forest Type	Production Measured (Mg ha^{-1} y^{-1})	Decay (k) Measured (y-1)	Production Est. (biomass * 0.02) (Mg ha^{-1} y^{-1})	Estimated Decay (k) (y-1)	Production Est. (necromass * 0.15) Mg ha^{-1} y^{-1})
Harmon et al. 1995	Quintana Roo, Mexico	UF	TDF			4.18	0.11	5.7
Hughes et al. 2000	Tuxtlas, Mexico	UF	TEF			7.65	0.55	2.1
Kauffman et al. 1988	Rio Negro, Venezuela	DF	TRF			0.95	0.02	7.28
Kauffman et al. 1988	Rio Negro, Venezuela	DF	TRF			1.6	0.06	4.04
Kauffman et al. 1988	Rio Negro, Venezuela	UF	TRF			0.23	0.14	0.24
Kauffman et al. 1988	Rio Negro, Venezuela	UF	TRF			0.77	0.15	0.8
Kauffman et al. 1988	Rio Negro, Venezuela	UF	TRF			0.41	0.01	6.36
Kauffman et al. 1988	Rio Negro, Venezuela	UF	TRF			1.02	0.08	1.94
Kauffman et al. 1988	Rio Negro, Venezuela	UF	TRF			4.77	0.33	2.16
Kauffman et al. 1988	Pernambuco, Brazil	2nd pre-fire	TDF			1.44		
Kauffman et al. 1988	Pernambuco, Brazil	2nd-post fire	TDF			1.44		
Keller et al. 2004b, Asner et al. 2002						4.06	0.05	13.45
Keller et al. 2004b, Asner et al. 2002						4.06	0.03	19.4
Keller et al. 2004b, Asner et al. 2002						4.06	0.06	9.94
Keller et al. 2004b, Keller et al. 2001						5.64	0.06	13.72
Keller et al. 2004b, Keller et al. 2001						5.64	0.09	9.13
Kira 1978	West Malaysia	UF	TRF	3.3	0.3	8.43	0.17	7.64
Kira 1978	West Malaysia	UF	TRF			7.48		
Kira 1978	West Malaysia	UF	TRF			7.6		
Klinge 1973	Central Amazon, Brazil	UF	TRF			14.63	0.81	2.7
Lang & Knight 1979	Barro Colorado, Panama	UF	TRF		0.46			
Lang & Knight 1983	Panama	2nd-60 yr	TMF					
Martius 1997	Central Amazon, Brazil	UF	RF	6	0.33			1.71
Martius & Bandeira 1998	Manaus, Brazil	UF	TMF					1.43
Nascimento & Laurence 2002	Mauaus, Brazil	UF	TMF			7.124	0.23	4.64
Odum 1970	El Verde, Puerto Rica	UF	TRF		0.11			
Palace et al. 2007	Mato Grosso, Brazil	RIL	TMF			5.26	0.07	10.05
Palace et al. 2007	Mato Grosso, Brazil	UF	TMF			5.62	0.11	6.74
Palace et al. 2008, Keller et al. 2001, 2004						5.64	0.1	7.61
Palace et al. 2008, Keller et al. 2001, 2004						5.64	0.07	10.89
Rice et al. 2004	Tapajos, Brazil	UF	TMF	5	0.17	5.96	0.09	10.5
Rice et al. 2004	Tapajos, Brazil	UF	TRF	5	0.12	5.96	0.06	14.94

Reference	Location	Type of Site	Forest Type	Production Measured (Mg ha^{-1} y^{-1})	Decay (k) Measured (y-1)	Production Est. (biomass * 0.02) (Mg ha^{-1} y^{-1})	Estimated Decay (k) (y-1)	Production Est. (necromass * 0.15) Mg ha^{-1} y^{-1})
Roberston & Daniel 1989	Australia	UF	Yman	0.1	0.06	7.74	4.27	0.27
Roberston & Daniel 1989	Australia	UF	Oman	0.97	2	9.3	0.65	2.14
Saldarriaga et al. 1988	Columbia and Venezeula	2nd-14 yr	TRF			1.22	0.08	2.28
Saldarriaga et al. 1988	Columbia and Venezeula	2nd- 20 yr	TRF			2	2.86	0.11
Saldarriaga et al. 1988	Columbia and Venezeula	2nd- 20 yr	TRF			1.47	0.92	0.24
Saldarriaga et al. 1988	Columbia and Venezeula	2nd- 20 yr	TRF			1.6	2	0.12
Saldarriaga et al. 1988	Columbia and Venezeula	2nd- 20 yr	TRF			2.32	2.32	0.15
Saldarriaga et al. 1988	Columbia and Venezeula	2nd- 20 yr	TRF			1.24	0.14	0.15
Saldarriaga et al. 1988	Columbia and Venezeula	2nd- 30 yr	TRF			2.6	0.31	1.35
Saldarriaga et al. 1988	Columbia and Venezeula	2nd- 35 yr	TRF			2.58	2.58	1.28
Saldarriaga et al. 1988	Columbia and Venezeula	2nd- 40 yr	TRF			3.72	0.65	0.15
Saldarriaga et al. 1988	Columbia and Venezeula	2nd- 60 yr	TRF			2.66	0.08	0.86
Saldarriaga et al. 1988	Columbia and Venezeula	2nd- 60 yr	TRF			4.88	1.81	4.86
Saldarriaga et al. 1988	Columbia and Venezeula	2nd- 60 yr	TRF			3.38	0.1	0.41
Saldarriaga et al. 1988	Columbia and Venezeula	2nd- 80 yr	TRF			3.2	0.39	5.13
Saldarriaga et al. 1988	Columbia and Venezeula	2nd- 80 yr	TRF			4.26	0.56	1.23
Saldarriaga et al. 1988	Columbia and Venezeula	2nd- 80 yr	TRF			3.46	0.09	1.14
Saldarriaga et al. 1988	Columbia and Venezeula	2nd- 80 yr	TRF			3.4	0.34	6.06
Saldarriaga et al. 1988	Columbia and Venezeula	UF	TRF			5.36	0.24	1.5
Saldarriaga et al. 1988	Columbia and Venezeula	UF	TRF			6.44	0.12	3.35
Saldarriaga et al. 1988	Columbia and Venezeula	UF	TRF			6.52	0.43	7.95
Saldarriaga et al. 1988	Columbia and Venezeula	UF	TRF			6.7	0.46	2.27
Scott et al. 1992	Roraima, Brazil	UF	LEF					0.76
Summers 1998	Central Amazon, Brazil	DF	TMF					13.32
Tanner 1980	Jamaica	UF	DTF	2	0.26	4.62	0.61	1.14
Tanner 1980	Jamaica	UF	DTF	2	0.17	6.76	0.56	1.8
Uhl & Kauffman 1990, Kauffman & Uhl 1990								6
Uhl & Kauffman 1990, Kauffman & Uhl 1990								25.95
Uhl & Kauffman 1990, Kauffman & Uhl 1990						0.56	0.02	3.45

Reference	Location	Type of Site	Forest Type	Production Measured (Mg ha^{-1} y^{-1})	Decay (k) Measured (y-1)	Production Est. (biomass * 0.02) (Mg ha^{-1} y^{-1})	Estimated Decay (k) (y-1)	Production Est. (necromass * 0.15) Mg ha^{-1} y^{-1})
Uhl & Kauffman 1990, Kauffman & Uhl 1990						5	0.1	7.65
Uhl et al. 1988	Paragominas, Brazil	LD-young	TMF			0.59	0.01	11.75
Uhl et al., 1988	Paragominas, Brazil	LD-old	TMF			1.72	0.02	13.17
Uhl et al. 1988	Paragominas, Brazil	LD-old	TMF			1.78	0.04	7.49
Uhl et al. 1988	Paragominas, Brazil	MD-young	TMF			0.12	0.01	2.45
Uhl et al. 1988	Paragominas, Brazil	MD-young	TMF			0.17	0.01	3.24
Uhl et al. 1988	Paragominas, Brazil	MD-young	TMF			0.34	0.01	7.11
Uhl et al. 1988	Paragominas, Brazil	MD-young	TMF			0.34	0.03	1.68
Uhl et al. 1988	Paragominas, Brazil	MD-old	TMF			0.74	0.04	3.05
Uhl et al. 1988	Paragominas, Brazil	MD-old	TMF			0.66	0.03	3.06
Uhl et al. 1988	Paragominas, Brazil	HD-young	TMF			0.15	0.01	1.56
Uhl et al. 1988	Paragominas, Brazil	HD-young	TMF			0.31	0.04	1.29
Uhl et al. 1988	Paragominas, Brazil	HD-old	TMF			0.09	0.02	0.86
Uhl et al. 1988	Paragominas, Brazil	UF	TMF			6	0.14	6.28
Uhl et al. 1988	Paragominas, Brazil	UF	TMF			6.55	0.18	5.34
Uhl et al. 1988	Paragominas, Brazil	UF	TMF			5.69	0.12	7.22
Wilcke et al. 2005	Andes, Ecuador	UF	MWF	0.82	0.09			1.37
Yoda & Kira 1982	Pasoh, Malaysia	UF	TRF					7.01
Yoneda et al. 1977	Pasoh, Malaysia	UF	TRF		0.32			
Yoneda et al. 1990	Sumatra, Indonesia	UF	TMF	3.8	0.11	5.69	0.12	8.25

Forest types are: TRF – tropical rain forest, TMF – tropical moist forest, LMMF – lower montane moist forest, S – Savanna, SE – Savanna Edge, TTW –tropical thorn woodland, TDF – tropical dry forest, TMDF – tropical moist dry forest, MWF – tropical montane wet forest, RF – riverine forest, YMan – young mangrove, Oman – old mangrove.
Type of site definitions: UF – undisturbed, LD – low disturbance, 2nd – secondary forest (type or year of regrowth), OF – open forest, UDF – undisturbed dense forest, SE – savanna edge, Montana – cleared, MD-L(H, F) – moderate disturbance from logging (hurricane, fire), HD-L(H) heavy disturbance from logging (hurricane, fire), CL – conventional selective logging, RIL – reduced impact logging, LD – light disturbance.
Blank spaces indicate no data available from source

Table 2. Reviewed literature for tropical necromass production and decomposition rates compared with estimated production and decomposition rates.

Decay class estimates of density were used in 23 studies, five studies weighed all material, and 11 did not use decay class density estimates, but density site averages or were unclear as to their methodology. Fifteen studies reported their decay class density estimates in detail (Table 3). Decay classes and density measurements for such decay classes were similar across many studies (Table 3). Harmon et al. (1995), Eaton and Lawrence (2006), Keller et al. (2004b), and Palace et al. (2007), all used five decay classes in their studies. Although Palace et al. (2007) and Keller et al. (2004b) conducted field work in the same biome, moist tropical forest, Eaton and Lawrence (2006) worked in a dry tropical forest. Eaton and Lawrence (2006) found consistent decay class density estimates between biomes suggesting that the apparently arbitrary classification is robust. Clearly, site specific density measurements should be most accurate approach. However, Palace et al. (2007) suggested, that coarse dead wood density measurements may be applied across broad areas provided that the decay classes are defined uniformly across the sites.

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Table 3. Density and decay class estimates for tropical forest. Blank spaces indicate no data available from source.

Location and Reference	Forest Type	Group	Decay Groups or Classes			
Southern Peru			DC1	DC2	DC3	DC4
Baker et al. 2007	TRF	Density Adjusted for Void	0.54	0.53	0.40	0.37
Northern Peru		Three Classes	DC1	DC2	DC3	
Chao et al. 2008	TRF	Plug Density	0.57	0.42	0.30	
Chao et al. 2008	TRF	Void Density	0.03	0.03	0.03	
Chao et al. 2008	TRF	Density Adjusted for Void	0.55	0.41	0.23	
Northern Peru		Five Classes	DC1	DC2	DC3	DC4
Chao et al. 2008	TRF	Plug Density	-	0.55	0.42	0.30
Chao et al. 2008	TRF	Void Density	-	0.03	0.04	0.04
Chao et al. 2008	TRF	Density Adjusted for Void	-	0.53	0.41	0.28
Manaus, Brazil			Heavy Wood	Light Wood		
Chambers et al., 2000	LEF		0.85	0.45		
La Selva, Costa Rica			Sound	Partial Decomp.	Full Decomp	
Clark et al., 2002	TRF		0.45	0.35	0.25	
Venezuela			Sound	Intermed.	Rotten	small 2.5-4.99
Delaney et al., 1998	TTW		NW	0.69	NW	0.29
Delaney et al., 1998	TDF		NW	0.59	0.40	0.29
Delaney et al., 1998	TMDF		0.42	0.37	0.25	0.24
Delaney et al., 1998	TMF		0.58	0.59	0.50	0.29
Delaney et al., 1998	TLMF		0.52	0.39	0.31	0.20
Delaney et al., 1998	TMF		NW	0.48	0.32	0.19
Southern Mexico			DC1	DC2	DC3	DC4
Eaton and Laurence 2006	DTF		None	0.74	0.78	0.62
Australia			DC1	DC2	DC3	DC4
Grove 2001	TRF	Yellow fibrous	0.29	0.23	0.18	0.11
Grove 2001	TRF	Hard	0.35	0.36	0.38	0.35
Grove 2001	TRF	Brown crumbly	0.29	0.23	0.20	0.16
Grove 2001	TRF	Brown fibrous	0.29	0.23	0.20	0.23
Grove 2001	TRF	Red Block	None	0.23	0.19	0.17
Quintana Roo, Mexico		By Species	DC1	DC2	DC3	DC4
Harmon et al., 1995	TDF	Used Range	0.25 - 0.81	0.19 - 0.84	0.06 - 0.81	0.49 - 0.64
Australia			Mod. Decayed	Very Decayed	Extremely Decayed	
Roberston and Daniel 1989	Mangrove	Trunk	0.34	0.34	0.23	
Roberston and Daniel 1989		Prop Roots	0.51	0.28	0.39	
Roberston and Daniel 1989		Branches	0.60	0.43	0.28	
Roberston and Daniel 1989		Twigs	0.63	0.41	0.35	
Reserva Ducke, Manaus, Brazil			Fine Wood	Coarse Wood		
Martius and Bandeira 1998	TMF	Fresh to Dry Mass	0.55	0.46		
Ecuadorian Andes, Ecuador			Intact	Rotten	Full Decomp.	Bark
Wilcke et al. 2005	TMonF		0.38	0.22	0.25	0.37
Tapajos, Brazil			DC1	DC2	DC3	DC4
Keller et al., 2004	TMF	Plug Density	0.61	0.71	0.63	0.58
Keller et al., 2004	TMF	Void Density	0.02	0.02	0.08	0.21
Keller et al., 2004	TMF	Density Adjusted for Void	0.60	0.70	0.58	0.45
Jurueña, Brazil			DC1	DC2	DC3	DC4
Palace et al. 2007	TMF	Plug Density	0.72	0.70	0.66	0.67
Palace et al. 2007	TMF	Void Density	0.01	0.02	0.08	0.12
Palace et al. 2007	TMF	Density Adjusted for Void	0.71	0.69	0.60	0.59
Sumatra, Indonesia			DC0	DC1	DC2	DC3
Yoneda et al. 1990	TMF	Density	0.69	0.58	0.56	0.41

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In our review of the literature, we found a total of 49 papers on tropical necromass, with 24 papers reporting stock. All but five of the 24 papers used a volume sampling method, either plots (20 studies) or line intercepts (seven studies) or both methods (six studies). Fallen necromass was measured using line intercept sampling and standing dead was measured using plots in a few studies (Nascimento and Laurence 2002, Palace et al. 2007). One study used plots except for one area in which dense understory prohibited movement and line intercept sampling was used (Grove 2001). Baker et al. (2007) compared line intercept with plot sampling and found similar values for necromass volume and estimated the fallen mass. In our review, reported values of necromass stock were evenly distributed between disturbed and undisturbed sites. Many studies included both undisturbed and disturbed plots. Standing dead and fallen necromass were both measured in 21 articles, with the ratio of standing dead to total necromass ranging from 6% in a disturbed forest and 98% at a heavily disturbed site (Gerwing 2002, Harmon et al., 1995). In undisturbed forests, standing dead to total fallen necromass stock measurements ranged from 11% to 76% (Palace et al. 2007, Delaney et al., 1998). We do not present averages of necromass stock or other components because this would be misleading; the literature examined do not represent a statistical sample of the necromass or forest types found in the tropics.

Size class criteria differed slightly among studies. Of the 23 studies that reported stock estimates, the majority explained their size class methodology. A cutoff of less than 2 cm was used in seven of 23 studies that reported size class methodology. Six studies used a cutoff of 2.5 cm. Many used a cutoff greater than 10 cm. Six studies used a 10 cm cutoff to define the difference between small and large diameter necromass. Approximately half of all studies used a cutoff of 10 cm for standing dead measurement. We suggest standardization, with the use of three size classes, small diameter (2-5 cm), medium diameter (5-10 cm), and large diameter (greater than 10 cm) for fallen CWD.

Standing dead trees or snags include whole dead trees and portions of dead trees that remain upright (Harmon et al. 1986). In tropical forests, standing dead was measured 65% less frequently than fallen CWD. Many studies use a percentage of total fallen necromass to estimate standing dead necromass (Keller et al. 2004b). The size of standing dead included in tallies differs between studies. Palace et al. (2007) and many others have used a cutoff of 10 cm dbh, while others have measured standing dead down to 2 cm dbh (Edwards and Grubb 1997). The methodology of height measurement also varies among studies. Visual estimates or average heights (Rice et al. 2004) were used when standing dead heights are not measured. For more precise studies, measuring tapes and clinometers or laser range finders have been used (Palace et al. 2007). No studies in tropical forest that we examined included in their methodology specific mention of stumps or standing dead less than 1.3 m in height in estimates of standing dead other than Palace et al. (2007).

The stock of coarse woody debris contributes a large percentage to the total carbon pool in any forest. In tropical forests, fallen necromass was found to range from 1.0 to 178.8 Mg ha^{-1} (Table 1). In dry tropical forests, fallen necromass amounts tended to be lower than moist tropical forests, with dry forests ranging from 2.5 (Collins 1981) to 118.6 Mg ha^{-1} (Harmon et al., 1995) in a heavy logged area. In moist tropical forests necromass ranged from 2.4 (Delaney et al., 1998) to 178.8 Mg ha^{-1} (Uhl and Kauffman 1990, Kauffman and Uhl 1990) (Table 1). In tropical forest areas outside of the Brazilian Amazon researchers found

necromass ranging from 3.8 to 6.0 Mg C ha^{-1} in montane forest in Jamaica (Tanner 1980), 22.4 Mg C ha^{-1} in wet forest in Costa Rica (Clark et al 2002) and 22.5 Mg C ha^{-1} in dipterocarp forests in Malaysia (Yoda and Kira 1982). In the Brazilian Amazon, where much recent work on necromass is concentrated, estimates of fallen necromass in undisturbed moist forests in terra firma included 42.8 Mg C ha^{-1} (Summers 1998) and 48.0 Mg C ha^{-1} (Rice et al. 2004 on the high end and 27.6 Mg C ha^{-1} (Keller et al. 2004), 15 Mg C ha^{-1} (Brown et al 1995), and 16.5 Mg C ha^{-1} (Gerwing 2002) on the low end. Other studies examined necromass in secondary forests and the effects of logging on necromass (Gerwing 2002, Uhl et al 1988, Keller et al. 2004b). The proportion of necromass to total above ground mass can be surprisingly high, 18 to 25% (Keller et al. 2004b; Rice et al. (2004) even in unmanaged forests. These values are for the Tapajos National Forest near Santarem, Brazil where Saleska et al. (2003) hypothesized that the 1997-1998 El Niño drought led to substantial mortality prior to the necromass measurements cited above.

2.2 Production of necromass

Death of whole trees or portions of trees creates necromass. Mechanisms that lead to tree death include forest disturbances at various scales. The spatial scale of disturbances ranges from branch-falls and small gaps to landscape level blowdowns due to microbursts that can cover thousands of hectares (Nelson et al. 1994). Tree mortality in tropical forest plots ranges from 0.001 to 0.07 per year (Carey et al. 1994, Phillips and Gentry 1994). Disturbance in tropical forests include individual tree processes, landscape level processes, and regional and climate influences. These processes and influences function on different temporal and spatial scales and are variable in the impact they have on tropical forests (Chambers et al. 2007, Frolking et al. 2009).

Tree mortality in tropical forests is driven on the individual tree level by competition, primarily for nutrients and light (Prance and Lovejoy 1985, Martinez-Ramos et al. 1988, Lieberman et al. 1989). As a tree dies and falls to the forest floor, a gap in the canopy is created (Denslow 1987). These gaps are important in an ecological sense because they are involved with tree regeneration dynamics and species diversity and distribution (Schemske and Browkaw 1981, Denslow 1987, Vitousek and Denslow 1986). Gaps increase light levels in understory, release nutrients, and create structural habitat for some species of flora, fauna, and fungi (Schemske and Browkaw 1981, Denslow 1987, Vitousek and Denslow 1986, Dickinson et al. 2000, Svenning 2000). Blackburn and Milton (1996) examined gap production and progressive enlargement of gaps as natural disturbances instead of catastrophic events. Young and Hubbell (1991) also found that trees were more likely to fall into gaps and suggested that gaps may be more persistent in tropical forests then previously thought. The persistence of gaps also predicts the locations where necromass is likely to collect. This spatial coincidence has not been tested.

Mortality of trees in the tropics is also influenced by fungi, insects and other animals, and the trees themselves (Denslow 1987). Branch fall as a source of necromass has rarely been quantified although it has been recognized as is a major disturbance for seedlings growing in the understory (Lang and Knight 1983, Aide 1987, Clark and Clark 1991, van der Meer and Bongers 1996). The diversity of trees in the mosaic that is a tropical forest landscape makes it rare for a single insect infestation to create denuded canopies and cause the death

of many trees (Janzen 1987). Vines entangling adjacent crowns may cause the death of a single tree to result in tree falls that involve several neighboring trees (personal observation). Some species of *Ficus*, strangler figs, have constricting vines that eventually kill the host tree (Windsor et al. 1988). Epiphytic vegetation load has also been tied to tree mortality (Prance 1985). Trees can also die as a result of genetic programming as is the case for monocarpic trees such as *Tachigalia versicolor* (Kitajima and Augspurger, 1989).

On non-degraded moist and wet forests, fires are rare events that do not propagate easily (Prance 1985). However, this belief is being challenged with studies of forest drying during El Niño events (Nepstad et al. 2002). Fire has also been shown to be an influential disturbance on white-sand forests in the Amazon (Anderson 1981). Fire in the Amazon is strongly influenced by people (Cardoso et al. 2003). Lightning may also cause fires and localized mortality in tropical forests (Magnusson et al. 1996).

Disturbances are also influenced by weather and topography (Bellingham and Tanner 2000). Topography was found to be influential on disturbances and thus was reflected in the local species distributions (Gale 2000). Tropical trees tend to have shallow root mass for nutrient exploitation and buttresses for structural support and have been shown to easily topple (Prance 1985). Disturbances also include larger scale processes such as microbursts, blowdowns, volcanoes, and landslides in the tropics (Nelson et al. 1994, Sanford et al. 1986, Lawton and Putz 1988, Garwood et al. 1979). Hurricanes have been shown to have an influence on the tropical forests in the Caribbean and elsewhere (Lugo and Scatena 1996, Walker et al. 1996). Spatial patterns and recent trends in tree mortality have also been attributed to ENSO events (Condit et al. 1995, Malhi et al. 2004).

Approximately half of the studies we reviewed compared undisturbed forests with forests experiencing disturbance due to anthropogenic factors, such as selective logging. Selective logging is a practice that fells a few trees per hectare (Peireira et al. 2002). This type of logging has been shown to affect substantial areas in the Brazilian Amazon and in tropical Asia (Asner et al. 2005, Curran et al. 2004). Other human influenced disturbances in the literature of tropical necromass included fire, agriculture, conversion to pasture through deforestation, and repeated disturbances due to a combination of fire and agricultural practices (Table 1). The number of sites in our literature review was evenly distributed among the undisturbed and disturbed forests. We excluded a study by Feldpausch et al. (2005) because that study measured the amount of necromass generated by selective logging, but did not measure total necromass stocks in either logged or undisturbed forests.

Few studies have measured the production of necromass in tropical forests. Approaches to the estimation of necromass production include allocating a portion of Net Primary Productivity (NPP), a portion of existing biomass (Palace et al. 2007), or mortality estimates of trees (Rice et al. 2004, Baker et al. 2007). Flaws associated with these methods include the lack of variation over time, lack of spatial influence, lack of size class estimates, and a lack of knowledge of the proportion of necromass that remains standing and an assumption that the system is in a steady state.

Necromass production has been directly measured using repeated surveys on the same plots by marking necromass or removing it at each survey period (Harmon et al. 1986, Clark et al. 2002). Few necromass production studies conducted repeated surveys (Palace et al. 2008, Chao et al. 2008). This lack of repeated sampling limits the understanding of longer

term influences of weather patterns such as El Niño or ability to assess if the forest is at a steady state or if it is recovering from a larger scale disturbance (e.g. Saleska et al. 2003).

Rare events such as blowdowns or even large tree falls complicate sampling design and interpretation of necromass data. For example, a tree fall of diameter 150 cm DBH drastically altered the measured flux of necromass in one sampling interval from a study at the Tapajos National Forest in Brazil (Palace et al. 2008). Trees of this size occur with a frequency of only about 0.079 per ha (Keller et al. 2001) at Tapajos. Assuming adequate sampling of 100 ha blocks, there are only 7.9 trees of this size class per block. Assuming an annual mortality rate of 1.7 (Rice et al. 2004) then the chance of seeing a fall of this size is $(1\text{-}0.983^{7.9})$ or 12.7% per year. In the study of Palace et al. (2008), a much larger sample area would have been required to record a large tree death annually. Larger but less frequent disturbances such as blowdowns (Nelson et al. 1994) require even more extensive sampling designs.

A compilation of studies that directly measured necromass production is present in Table 2. Of the 48 papers reviewed here only 30% made measurement or estimates of necromass production. Eaton and Lawrence (2006) measured production in several disturbed sites and in one undisturbed site in dry tropical forest in southern Mexico. Their estimate removed and measured new necromass four times over a two year period for an undisturbed forest was 0.91 Mg ha^{-1} yr^{-1}. Tanner (1980) estimated necromass production in a Jamaican forest to be 2.0 Mg ha^{-1} yr^{-1} using repeated samples over four years. Other estimates in dry tropical studies include 0.1 and 0.97 Mg ha^{-1} yr^{-1} conducted by Buxton (1981) and Collins (1981) respectively. Kira (1978) directly measured necromass production of 3.3 Mg ha^{-1} yr^{-1} in Pasoh Forest in western Malaysia. Clark et al. (2002) measured influx of necromass to be 4.8 Mg ha^{-1} yr^{-1} using a repeated survey in Costa Rica. In a 4.5 year study in the Brazilian Amazon, Palace et al. (2008), measured necromass production to be 6.7 Mg ha^{-1} yr^{-1}. Large size class necromass (>10 cm DBH) production was 4.7 Mg ha^{-1} yr^{-1}. The production of small size class necromass (< 2cm DBH) was 0.8 Mg ha^{-1} yr^{-1} and medium size class necromass (≥2cm and ≤10 cm) was 1.2 Mg ha^{-1} yr^{-1}. Interestingly, Rice et al. (2004) estimated necromass production based on mortality of trees > 10 cm DBH at 4.8 Mg ha^{-1} yr^{-1} for a nearby forest area. This suggests that mortality based approaches will underestimate necromass production.

2.3 Decomposition of necromass

Decomposition of wood is generally a slow process that involves biological, chemical, and physical processes. The sequence that these processes act on dead wood varies over time due to changes in physical climate and the chemical and physical makeup of the wood over its decay life. Each piece of dead wood has a unique chemical and physical makeup (Kaarik 1974). The difference in chemical and physical composition starts with differences in live trees. Differences among trees depend on tree species (wood characteristics), nutrient composition of soil, climate, tree health (including infections by insects, microbes, and fungus), and how the tree died (Harmon et al. 1986, Martius 1997). Differences within trees may also be important due to internal variation in wood density (Noguiera et al. 2005).

Wood decomposition involves unique fauna (Dickinson and Pugh 1974). Decay organism can be grouped into three categories, bacteria, fungi, and macroorganisms (Dickinson and Pugh 1974). The presence of fauna and their own growth efficiencies, nutrient requirements, and temperature and moisture requirements dictate the overall decomposition process. Each

of these categories of organisms acts on wood differently and are important at different time in the temporal sequence of wood decay (Kaarik 1974). In the tropics, wood fragmentation is primarily caused by termites (Buxton 1981). This fragmentation occurs on highly decayed logs or parts of logs. In addition, termites remove the wood to other places (Collins 1981).

The placement of the wood on the ground can dictate the rate of its decay. Logs on hills tend to accumulate more soil on the uphill side, creating a wetter microclimate beneficial for many decomposing soil organisms (Harmon et al. 1986). In the Brazilian *varzea* forest, (a flooded forest type), the season that the wood falls is influential on its immediate and longer term decomposition rate (Martius 1997). Decomposition of smaller litter occurs rapidly, often less than one year, while larger CWD can have a turnover time close to a century (Mackensen et al. 2003).

The estimation of necromass decomposition rates uses two major approaches, chronosequences and time series (Harmon and Sexton 1996). In a time series, individual pieces of wood are followed over time (Harmon and Sexton 1996). In chronosequence studies, varying ages of coarse dead wood are examined at a single point in time (Harmon et al. 1986). Dates of necromass production have been made using disturbance records, living stumps, seedlings, dendrochronology, fall scars, and bent trees (Harmon et al. 1999). Some researchers have conducted a combination of chronosequences and time series (Harmon and Sexton 1996, Chambers et al. 2000).

Within sample chronosequences or time series, decomposition may be studied by mass loss, density change, uniform substrate decomposition, radioisotopes, respiration rates, mineralization, enzyme activity, and selective inhibition experiments (Swift et al. 1979, Harmon and Sexton 1996, Harmon et al. 1999). The majority of studies in the tropics have used mass loss, density change, or chamber systems to measure the respiration.

Measurement of decomposition through mass loss requires multiple measurements of necromass over time (Buxton 1981, Harmon et al. 1995, Chambers et al. 2000). This can only be done accurately if moisture content can be measured accurately and non-destructively. Alternatively, changes in density can be used as a surrogate for mass loss. It is important for density measurements to account for void spaces. Void spaces in logs must be accounted for in density measurements either by using large pieces of necromass (e.g., Chambers et al., 2000, Clark et al., 2002) or by separately quantifying void space (Keller et al., 2004a, Palace et al. 2007). Direct measurements have also been made in the laboratory with CWD removed from the field (Richards 1952, Chambers 2001).

Respiration studies have been conducted on necromass in a number of ways. Essentially all methods depend upon isolating, sections, full pieces, or extracted samples of necromass in a chamber. Chambers may be attached to the surface of necromass or necromass pieces may be inserted into chambers. The chambers are sealed and CO_2 concentration is measured directly by infra-red detection (Chambers et al. 2001) or, in older studies, CO_2 emitted is absorbed in alkali (Swift et al. 1979; Marra and Edmonds 1994). Respiration will underestimate necromass loss because it does not account for dissolution and fragmentation. However, there are indications that for tropical moist forests, respiration is the major pathway for CO_2 loss. Chambers et al. (2004) estimated that 80% of mass loss in necromass resulted for respiration. This was done by using the ratio from a respiration study and a mass loss study (Chambers et al. 2000, 2001)

Substrate decomposition studies have also been conducted (Harmon et al. 1995). In this method, uniform substrates such as Popsicle sticks or wooden dowels are placed in the field and measured over time. These studies provide information on the temporal variability of decomposition and also provide a standard for comparison of decomposition rates across the sites.

Radioisotopes have been used as tagging agents for materials to estimate leaching and soil organic matter formation (Wedin et al. 1995, Carvalho et al. 2003). Studies have been done by injecting isotopes into litter, but for necromass this is difficult (Harmon et al. 1999).

A compilation of field measured decay rates and estimated decay rates based on a mortality estimate of 0.02 yr^{-1} are presented in Table 2. Of the 46 papers we reviewed only 35% made measurement of necromass decomposition. Estimates of necromass decomposition rates in the Brazilian Amazon are rare. Chambers et al. (2000) used two different methods (closed chamber using an infra-red analyzer and measured mass loss) for estimates of 0.13 y^{-1} and 0.17 y^{-1} for each method. Palace et al. (2008) estimated decomposition rates using a steady state model. Their estimate of decay for all pieces of wood is 0.17 y^{-1} for large (>10 cm diameter), 0.21 y^{-1} for medium (5-10 cm diameter), and 0.47 y^{-1} for small size (2-5 cm diameter) class necromass. No other study that we know of has data for these smaller size classes and their production decomposition rates for tropical forests. Other tropical forest necromass decomposition rates range from 0.03 y^{-1} (Delaney et al. 1998) to 0.51 yr^{-1} (Collins 1981). An extremely high decay rate of 2.0 y^{-1} was estimated in a tropical mangrove forest by Robertson and Daniel (1989). We found only two studies that estimated decomposition rates for standing dead with estimates being 0.461 y^{-1} (Lang and Knight 1979) and 0.115 y^{-1} (Odum 1970). Palace et al. (2008) estimated the movement of standing dead through the pool to be 0.24 y^{-1}.

2.4 A simple model to expand and compare literature results

When production or decomposition rates were lacking in the literature that we reviewed, estimates were generated using the following methods and rationale. A production estimate of necromass was generated using the biomass value and a mortality rate of 0.02 y^{-1}. We used a mortality rate at the upper end of the range for old-growth tropical forests (Philips and Gentry, 1994) but feel that this is a reasonable estimate, since most biomass studies do not include smaller diameter trees and lianas. In addition, mortality rates we used to estimate necromass production often underestimate necromass production because, branch fall is not included (Palace et al. 2007).

Using the production estimate divided by the stock measured values, we calculated decomposition rates. If no biomass estimate was available, we estimated necromass production to be 0.15 y^{-1} of the total necromass stock. Though these estimates of decay and production amounts are prone to error and hypothetical in nature, they allow us to attempt to compare sites and biomes in tropical forests. Comparison of field data and model estimates also allow us to evaluate the assumption of steady state for a variety of sites.

3. Discussion

3.1 Methodology

Methodology was comparable among sites with similarity in decay classes and size classes used. Although there are some discrepancies among papers, we believe that stock estimates

are broadly comparable. Biomass estimates were not done at all sites and we suggest that biomass be measured whenever necromass is examined. Production and decomposition measurements were both lacking at many sites and the existing measurements lacked consistency. We suggest longer temporal studies, allowing for a better understanding of the dynamics of these fluxes and their relation to meteorological parameters.

Different methods for fallen necromass quantification may be used depending upon the question being asked by the researcher, such as fuel load amount (Uhl and Kauffman 1990) or biometry and respiration estimates (Chambers et al. 2000, Keller et al. 2004b). In concert with previous evaluations for other regions, we find that line intercept sampling is generally easier to adapt to field conditions where sufficient area is available for sampling. For example, Grove (2001) switched from plot based work to line intercept sampling when confronted with dense understory. Baker et al. (2007) compared line intercept sampling with plot based sampling measuring similar amounts of fallen necromass. Palace et al. (2007) conducted line intercept sampling at the same site as Rice et al. (2004) and had similar estimates with similar uncertainties. Palace et al. (2007) suggest that line intercept sampling was six times as efficient and took about one third the amount of time and with half the field crew. Plot estimates require more movement than line intercept sampling and become especially difficult in logged sites or in sites with dense under-story.

Fallen necromass stock was almost 1.5 times more frequently measured than standing dead. This is likely due to difficulty measuring the height of standing dead in a complex and dense forest canopies common in many tropical sites. We believe that stock estimates tend to be the easiest and most accurate necromass component to measure when compared to decomposition and production rates, which require multiple samples over time.

Methodology for decay classes was similar among studies. Much of the recent literature cites Harmon et al. (1995) in regard to decay classification. It is likely that this paper has set the standard for decay classes used. Implementation of the decay classification may vary across the sites in necromass studies. We do not know of tests for field classification differences across the sites in tropical forests. A number of studies we examined had similar decay class definitions (Harmon et al. 1995, Eaton and Lawrence 2006, Keller et al. 2004b, Palace et al. 2007). In addition, some studies had similar decay class density measurements (Table 3). Chao et al. (2008) compared a three and five decay classification and suggest using a three class system because of less interpretation issues and higher sample numbers in each category. A wider range of decaying logs in a class may increase the variability within a class, though Chao et al. (2008) did not find this to be true.

Decomposition and production estimates of dead wood both have unique difficulties. Decomposition is a complex process; however estimates for decomposition rates based on a variety of methods often give similar results (Palace et al. 2007, Chambers et al. 2001). Production estimates need to cover a large enough area to capture the rare episodic tree fall events. While trading space for time is helpful for quantifying necromass productions, long term studies that could link necromass to weather changes and other aspects of interannual variability would help us better understand variability in carbon dynamics.

Tropical forests contain a large number of tree species and this creates difficulty when measuring decomposition rates (Chambers et al. 2000). Decomposition rate measurements maybe be misleading when only a few species of trees or a few trees are only examined for a

short period of time. Chambers et al. (2000) developed a regression for decay that incorporates temperature, moisture, and necromass diameter. An exponential relationship has been shown between microbial activity and temperature, until temperature is so high that proteins are damaged and enzymes denature (Mackensen et al. 2003).

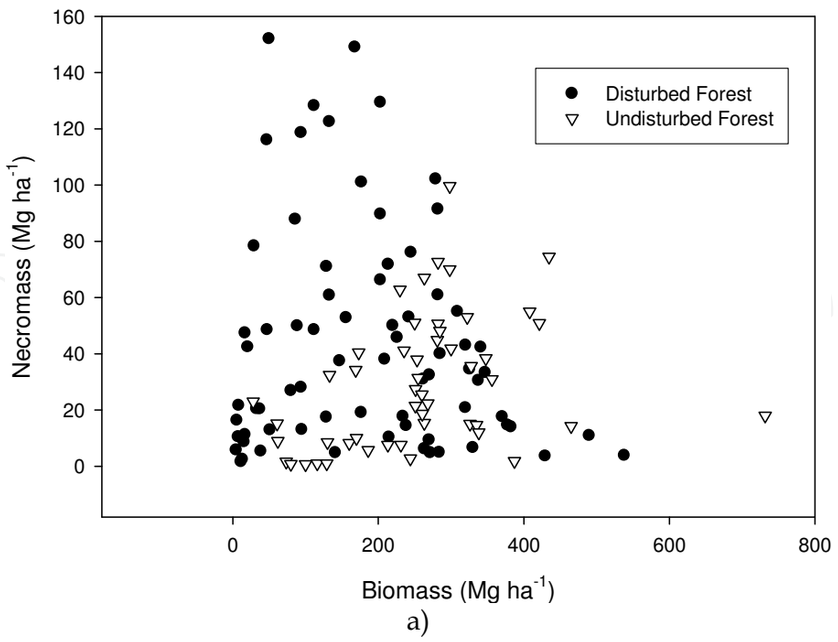
Many of the studies (38%) only examined one component of necromass dynamics. A combination of methods and components measured is preferable, allowing for the comparison of production and decomposition rates with stock estimates at the beginning and end of the study. Comparison to other measurable ecological parameters, such as NPP, woody increment, and mortality rates proves helpful in better understanding necromass dynamics. Necromass and biomass estimates should be done in conjunction at research sites. Finally, studies using the same methodology are beneficial to necromass research (Palace et al. 2007).

3.2 Comparison among sites

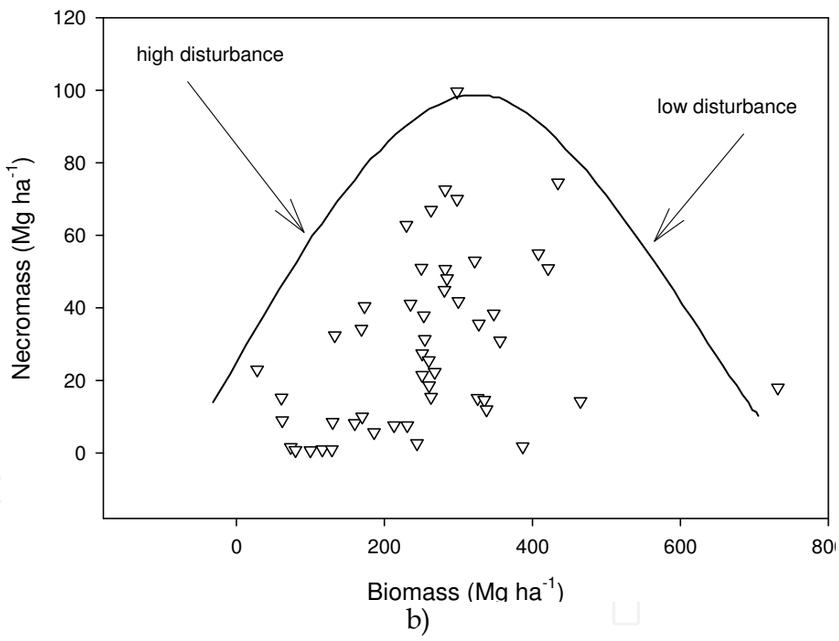
Necromass studies in tropical forests are few in number and concentrated in Central American dry forests and areas of the Eastern Amazon, especially in the State of Pará, Brazil. Many of the sites were highly disturbed due to logging activity, agriculture, fire, and in African, one case elephants (Buxton 1981, Uhl et al. 1988, Eaton and Lawrence 2006). We estimated production and decay estimates for these areas, but admit that our steady state approach is ill-suited to these sites.

The proportion of necromass to biomass is highly variable among among sites (Figure 1a) ranging from 0.01 in an undisturbed site in the Ivory Coast (Bernhard-Reversat et al., 1978) to 3.04 (Gerwing, 2002) in a heavy logged and burned site in Paragominas, Brazil. In undisturbed forests there appears to be a peak in the necromass with middle values of the biomass distribution (Figure 1b). Beyond that peak as biomass increases the proportion of necromass decreases. The highest biomass sites may have been undisturbed for long periods resulting in low necromass. We drew a hypothetical limit to illustrate such a relationship. High biomass and low necromass sites were often from studies that used small plots that do not reflect the landscape spatial distribution of biomass and necromass. Small plots may be chosen with the "majestic forest bias" that tends toward high biomass and little recent disturbance (Keller et al. 2001, Chave et al. 2001). Disturbed sites filled in are of the lower portion of biomass and higher necromass in Figure 1b. Chao et al. (2009a) found a significant but weak relation between biomass and necromass in a study across Amazonia (r^2=0.12). There work showed a stronger relation between living wood density and necromass, indicating that denser woods decay more slowly, with an additional insight as to differences in turnover time between Eastern and Western Amazonia. Use of living wood density is probably the best indicator of necromass at sites.

Standing dead and fallen necromass have been found to be proportionally related, even at disturbed sites (Palace et al. 2007). A regression examining just undisturbed sites was found to be significant (r^2 = 0.22, p=0.003; Figure 2). No such relation was found in our examination of disturbed sites. Nonetheless, standing necromass accounts for a large proportion of the total necromass stock, up to 66% in an undisturbed forest and 98% at a heavily disturbed site, and should be included in future field measurements (Palace et al. 2007, Harmon et al. 1995).



a)



b)

Fig. 1. a) Biomass and Necromass field measured values in undisturbed and disturbed tropical forests. b) Biomass and Necromass field measured values in undisturbed tropical forests showing areas of high and low disturbance.

We did not make comparisons of size classes among sites because few studies separated data by size class. In addition, comparisons among studies for necromass size classes are difficult because of differences in the limits for size classes themselves (Table 3). Still some studies indicate that smaller size classes (generally less than 10 cm diameter) contribute up to 21% of the total CWD stock (Uhl and Kauffman 1990, Palace et al. 2007) and we suggest

that smaller size classes be included in field measurements. Smaller size classes decay more quickly and may contribute more to the overall site respiration budget (Harmon et al. 1986, Palace et al. 2008). Chambers et al. (2000), showed a relation with decomposition rates and necromass diameter. Palace et al. (2007, 2008) using production and stock estimates grouped by size classes were able to estimate decomposition rates for the size classes using a simple model.

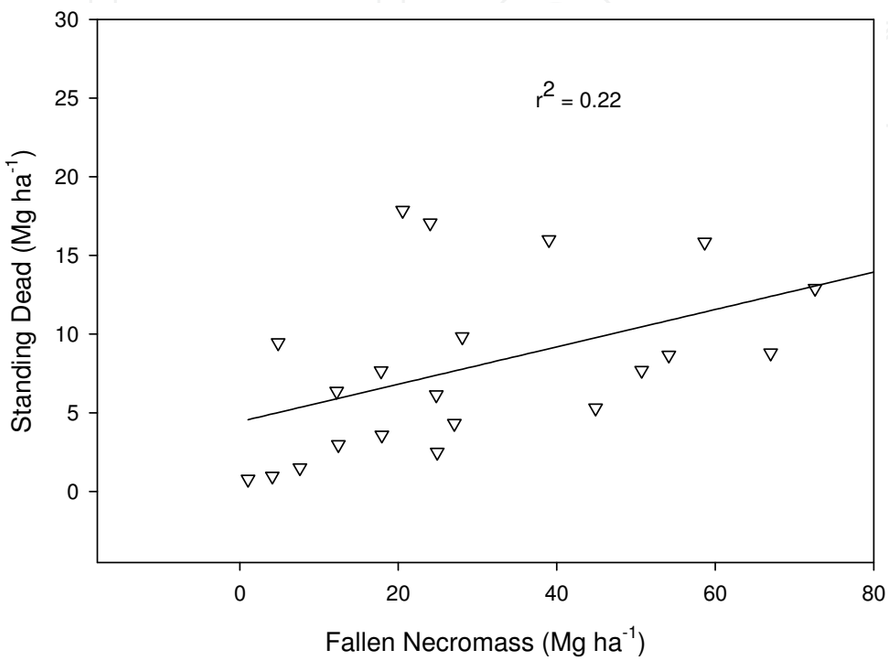


Fig. 2. Fallen necromass and standing dead field measured values in undisturbed tropical forests.

Trees lose branches through several processes that do not lead to whole tree mortality. For example, shaded lower branches may be shed and physical damage may result from crown interactions or animal activity. Mortality estimates used to determine necromass may underestimate production due to branch fall that is not associated with the death of a tree. Determination of the source of necromass would aid in quantifying branchfall. These small and medium classes are likely to include a substantial component from branchfall. Chambers et al. (2001) estimated branch-fall to be 0.9 Mg ha^{-1} y^{-1} based upon a comparison of field measured allometries and an optimized model tree structure based on the hydraulic constraints to tree architecture. Palace et al. (2008) examined the source of necromass by field classification of necromass as either branch, trunk, or unidentifiable. Necromass derived from tree trunks dominated the large size class in both necromass production and in pools. The other size classes were more evenly distributed among sources. Palace et al. (2008) found significant differences between logged and undisturbed forest treatments for the proportions of trunk, branch, and unidentified material within both production and pool necromass. Proportions between groups (production and pool estimates) and within a treatment were also found to be significantly different according to Palace et al. (2008). Chao et al. (2009b) found that trees die differently across Amazonia, with Northwest Amazonian

trees dying more often in blowdowns with multiple deaths, while Northeastern Amazonian trees die as single tree events and die standing.

In our review, we used measured necromass stock and either an estimated production (biomass * 0.02) or decomposition rate (necromass * 0.15) to generate production and decay rates when they were missing from the literature. Using these rates and stocks, we examined if sites were at steady state. No sites were found to be at steady state. Either these sites were not at steady state or the generalized assumptions of production and decomposition rates may not accurately reflect real world values. It is not reasonable to expect all sites to be at steady state. Plots were often too small to represent landscape necromass dynamics.

We compared total necromass with field measured necromass production and found a significant relation, though the r^2 value was low (r^2 = 0.28, p=0.014; Figure 3). Chao et al. (2009a) found a similar relation with mortality mass input and necromass (r^2 = 0.28, p=0.003). Though both of these relations are significant, we are cautious about drawing conclusion with regression with low r^2 values.

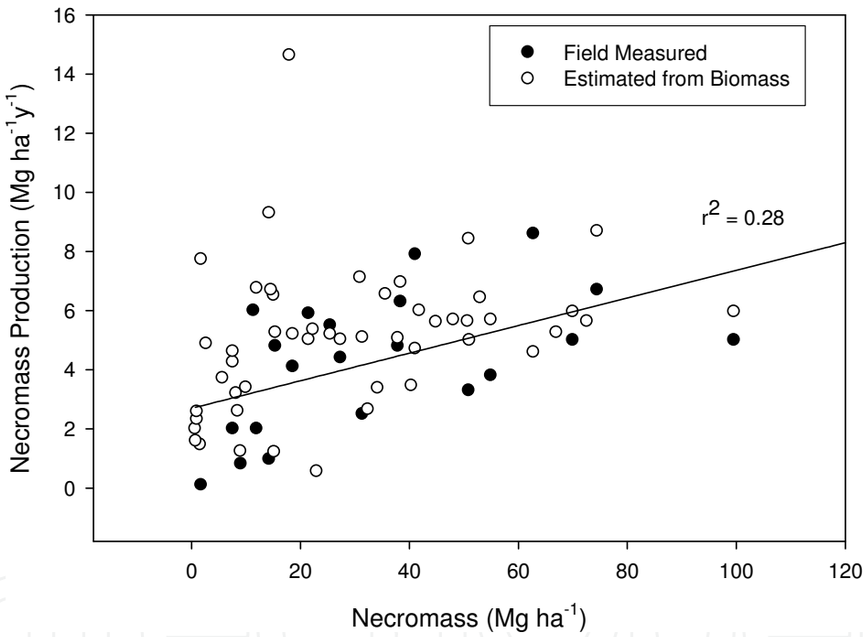


Fig. 3. A comparison of undisturbed forests for field measured necromass production and estimated necromass production from biomass with field measured necromass stocks. Only field measured necromass production is used in our regression.

We found that measured decomposition rates and those estimated by our simple model were similar. Higher decomposition rates associated with lower necromass stocks suggests that decomposition rates are an important control. We caution that this conclusion depends upon our model estimates using necromass production equal to a fixed proportion of biomass (0.02 y^{-1}). Higher decomposition rates may be associated with forests that experience higher disturbance rates as hypothesized by Baker et al. (2004) and Malhi et al. (2004) based upon a comparison between western and eastern Amazon forests. Baker et al. (2004) discussed the variation in wood density and how this determines the biomass in

Amazonian forests. Wood density variation is attributed to nutrient cycling and this influences species assemblages. The syndrome suggested by these two studies is that high-turnover forests have low density wood that in turn decomposes faster.

4. Conclusion

We compiled data from existing studies and compared pools and fluxes of necromass among tropical forest sites. General relationships among necromass components were explored such as necromass to biomass proportions and fallen to standing dead necromass. Methodology was comparable across the literature for necromass production and stock estimates. Fallen stock was 1.5 times more frequently measured than standing dead. We calculated production and decomposition rate estimates through the use of a simple model when these values were not available. General relations and proportions between necromass components were explored and were found to vary greatly. In undisturbed forests, we found weak but significant relations between fallen necromass and standing dead, as well as total necromass and measured necromass production. In undisturbed forests there appears to be a peak in the necromass with middle values of the biomass distribution. Beyond that peak as biomass increases the proportion of necromass decreases. The ratio of necromass to biomass ranged from 0.4 % in an undisturbed forest to 304% in a disturbed forest. Standing dead necromass accounts for a large proportion of the total CWD stock, up to 66% in an undisturbed forest and 98% at a heavily disturbed site, and should be included in further field estimates. We found that localized variability is high and complicates or hinders the development of general relationships of necromass components across the tropics. Many of the studies (37%) only examined only one component of necromass dynamics. We stress the importance of measuring multiple necromass components and ideally conducting these measurements over years or even decades in order to improve our knowledge of necromass dynamics in tropical forests.

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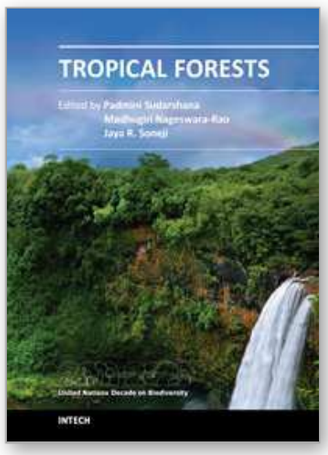
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The astounding richness and biodiversity of tropical forests is rapidly dwindling. This has severely altered the vital biogeochemical cycles of carbon, phosphorus, nitrogen etc. and has led to the change in global climate and pristine natural ecosystems. In this elegant book, we have defined "Tropical Forests" broadly, into five different themes: (1) tropical forest structure, synergy, synthesis, (2) tropical forest fragmentation, (3) impact of anthropogenic pressure, (4) Geographic Information System and remote sensing, and (5) tropical forest protection and process. The cutting-edge synthesis, detailed current reviews, several original data-rich case studies, recent experiments/experiences from leading scientists across the world are presented as unique chapters. Though, the chapters differ noticeably in the geographic focus, diverse ecosystems, time and approach, they share these five important themes and help in understanding, educating, and creating awareness on the role of "Tropical Forests" for the very survival of mankind, climate change, and the diversity of biota across the globe. This book will be of great use to the students, scientists, ecologists, population and conservation biologists, and forest managers across the globe.

How to reference

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