Spring 2012

Coarse Woody Debris in a Tropical Rainforest in North Queensland, Australia: Relationships with Stand Structure and Disturbance

Nadine Rea
SIT Study Abroad

Coarse woody debris in a tropical rainforest in North Queensland, Australia: Relationships with stand structure and disturbance

Nadine Rea
Project Advisor: Matt Bradford, CSIRO Tropical Forest Research Centre
Atherton, Queensland, Australia

Academic Director: Tony Cummings
Home Institution: Hampshire College

Submitted in partial fulfillment of the requirements for Australia: Rainforest, Reef, and Cultural Ecology, SIT Study Abroad, Spring 2012

ABSTRACT

Coarse woody debris (CWD) refers to the woody material on the forest floor, including fallen stems, large branches, coarse roots, wood pieces, and standing dead trees (snags) (Harmon *et al.* 1986). CWD is an essential but often overlooked aspect of ecosystems. It plays many key ecosystem roles and is instrumental in overall ecosystem functionality. While a piece of CWD decomposes, it provides key habitat for many different species, minimizes soil erosion, affects soil development, stores nutrients and water, and influences the global carbon cycle (Harmon and Hua 1991). In some forests, CWD can exist on the forest floor for hundreds of years, and therefore has an enduring influence on the forest comparable to that of living trees (Harmon and Hua 1991). Managed forests have considerably less CWD since most trees are being removed and therefore do not rot on the forest floor after they die (Spies *et al.* 1988). However, research on CWD is scarce. In order to properly address and correct this issue, forest managers need to increase their understanding of the dynamics and structure of CWD in a healthy, productive, and diverse forest.

The objective of this study was to gain knowledge of the CWD in a 25-ha rainforest plot in tropical North Queensland, Australia. This study assessed CWD in two ways: its relationship with stand structure and plant response to the disturbance associated with CWD. CWD was spatially heterogeneous within the 1-ha plot and measured values of CWD volume were relatively high compared to other rainforests in the world and other forests within Australia (Keller *et al.* 2004; Manning *et al.* 2007). CWD was found to generally decrease as number of tree stems and tree basal area increased, but the results were not conclusive. The number of pioneer species in a given area was found to increase as CWD volume increased. While significant relationships between CWD and stand structure are difficult to observe, future studies similar to this should be conducted to further explore the various factors that contribute to the differences observed in CWD volume across the rainforest landscape.

TABLE OF CONTENTS

ABSTRACT **3**

ACKNOWLEDGEMENTS **5**

1 INTRODUCTION **6**

1.1 Definition of Coarse Woody Debris 6
1.2 Ecosystem Roles of Coarse Woody Debris 6
1.2.1 Habitat Role *6*
1.2.2 Geomorphic Function *9*
1.2.3 Nutrient Cycling *9*
1.2.4 Carbon Reservoir *10*
1.3 Recruitment of Coarse Woody Debris 11
1.4 Justification and Aims of Study 12
1.4.1 Hypotheses *13*

2 METHODOLOGY **14**

2.1 Site Description 14
2.2 Field Methods 16
2.2.1 Plot Division *16*
2.2.2 Coarse Woody Debris Measurements *16*
2.2.3 Vascular Plant Measurements *17*
2.2.4 Pioneer Species Survey *18*
2.3 Data Analyses 18
2.3.1 Calculations *18*
2.3.2 Statistical Analyses *19*

3 RESULTS **20**

3.1 CWD Volume 20
3.2 CWD and Stand Structure 20
3.3 CWD and Disturbance 22

4 DISCUSSION **24**

4.1 CWD Volume 24
4.2 CWD and Stand Structure 25
4.3 CWD and Disturbance 25

5 CONCLUSION **27**

5.1 Management Implications 27

REFERENCES **29**

APPENDIX A **32**

ACKNOWLEDGEMENTS

I would like to thank first and foremost my project advisor, Matt Bradford, for his guidance throughout this project. Without his participation, this research would not have been possible. He not only helped me narrow down my research question, but he also gave me a great deal of freedom when designing the project. His assistance with statistical analysis is also greatly appreciated. I would next like to thank CSIRO Tropical Forest Research Centre for providing me with accommodation, data, and a community of friendly people who were eager to pass on knowledge and assist with my project. Thanks are also due to Matt's colleague, Andrew Ford, for helping me gather data on pioneer species in the plot. Special thanks to Jillian Spies for helping me complete the fieldwork portion of this project. Last, but certainly not least, I would like to thank my academic director, Tony Cummings, who is primarily responsible for the incredible learning experience I have had in Australia.

1 INTRODUCTION

1.1 Definition of Coarse Woody Debris

Coarse woody debris (CWD) refers to the woody material on the forest floor, including fallen stems, large branches, coarse roots, wood pieces, and standing dead trees (snags) (Harmon *et al.* 1986). CWD is separate from litter, which is composed of the finer portion of debris (Woldendorp *et al.* 2002). CWD can be various sizes, but for the purpose of this study, it includes only pieces with diameters greater than or equal to 10cm.

1.2 Ecosystem Roles of Coarse Woody Debris

CWD is an essential but often overlooked aspect of ecosystems. It plays many key ecosystem roles and is instrumental in overall ecosystem functionality. In some forests, CWD can exist on the forest floor for hundreds of years, and therefore has an enduring influence on the forest comparable to that of living trees (Harmon and Hua 1991). While a piece of CWD decomposes, it provides habitat for a diverse range of organisms, impacts soil development, contributes to the nutrient cycle and energy flow, and is a long-term carbon reservoir.

1.2.1 Habitat Role

Unless timber is extracted for human use, the fate of all trees is to fall to the ground. Many organisms use CWD as habitat, and therefore depend on the ongoing cycle of tree mortality and decomposition. The different characteristics of CWD, such as size, tree species, decay stage, quantity, and distribution, all determine what organisms can employ it as habitat (Bunnell and Houde 2010). Furthermore, as debris decomposes, it offers a succession of habitat types. As a result, numerous organisms will use a single piece of CWD as it decays (Graham 1925). Larger pieces of CWD take longer to decompose and consequently provide habitat for a longer period of time. Some species require CWD habitat that has already been colonized by a previous species. For example, insects use fungal hyphae as a food source, which means these fungi must inhabit the CWD prior to the insects (Savely 1939).

Plants may rely on CWD for habitat, particularly for seedling establishment (Harmon *et al.* 1986). It has been shown that establishment on CWD assists in the formation of mycorrhizal relationships with fungi (Harvey *et al.* 1987). Mycorrhizal relationships are incredibly beneficial for the plant because the hyphal networks of the fungal symbiont form extensive branching networks with large surface area that have an exceptional capacity for absorption. As a result, hyphae can provide a plant with resources that are beyond the limit of the plant's own root systems. These associations significantly improve the plant's resistance to disease as well as its ability to deal with environmental stresses (Sharmila and Pardha Saradhi 2002).

CWD provides favorable habitat for seedlings because it stores both nutrients and moisture (Hale and Pastor 1998). Christy and Mack (1984) found that 98% of *Tsuga heterophylla* seedlings in forests in the Cascade Range, Oregon were found on logs, despite only 10% of the forest floor being covered by CWD. Since CWD has the ability to retain more water than litter or soil, it is especially beneficial for plants to establish on CWD in forests where water is a seasonally or continuously limited resource (Harmon *et al.* 1986). Also, because of its structure and ability to trap loose soil, CWD offers an ideal substrate for root formation and provides seedlings with protection from being stepped on by animals (DeLong *et al.* 1997; Brown *et al.* 2003). CWD additionally provides substrate for many bryophytes and ferns that prefer the shady forest floor. Forests containing abundant CWD have been found to possess more diverse bryophyte communities (Andersson and Hytteborn 1991).

CWD is particularly necessary for pioneer, light-demanding species in rainforests, where light is a limiting resource in the understory (Shiels *et al.* 2010). In a mature forest, light gaps, and therefore light-demanding species, are uncommon. When a canopy tree falls to the forest floor and becomes CWD, this results in a canopy gap in which sunlight can reach the forest floor. These conditions are ideal for the germination and rapid growth of pioneer species.

CWD provides significant habitat for both vertebrate and invertebrate fauna. Most notably, it is used as shelter from predators and serves as a site to breed and protect young (Bunnell and Houde 2010). It is also a protected place to feed, especially for those animals that eat invertebrates living in the CWD (Bunnell and Houde 2010). CWD is especially important habitat for species like amphibians that cannot endure extreme temperatures and humidity, and require the cooler, moister microclimate provided by the CWD (Brattstrom 1979).

The presence of CWD is particularly essential to many fungi and micro-organisms (Abbott and Crossley 1982). Fungi play a key role in decomposition of CWD and cycling nutrients through the ecosystem. Furthermore, the hyphae of fungi in CWD are a food source for many insects, which are in turn a food source for many other animals (Bunnell and Houde 2010). CWD serves as habitat for many species of microarthropods, which have been found to disperse fungal spores to the CWD. This ultimately influences the decomposition of the CWD and recycling of its nutrients back to the soil.

1.2.2 Geomorphic Function

CWD affects two main aspects of geomorphology: landforms and transport of storage and sediment. When a stem falls to the forest floor, the uprooting creates microtopographic landforms and mixes soil. On slopes, root-throw is responsible for disturbing 14-48% of the forest floor (Stone 1975). The resulting sediment is transported away from the pit-and-mound topography due to erosion. The initial uprooting and subsequent sediment transport is integral in pedogenesis (Harmon *et al.* 1986). CWD in the form of logs plays another key role on forested slopes, by reducing the downslope transport of water, soil, and litter (Hodge and Peterken 1998).

1.2.3 Nutrient Cycling

CWD significantly contributes to the cycling of nutrients through a forest ecosystem. A considerable percentage of the forest's nutrients are stored in CWD. Fungi are able to feed on CWD by releasing enzymes that breaks down the cellulose, lignin, and other constituents in plant cell walls. Once the material is degraded, the mycelia absorb the freed nutrients, such as nitrogen and phosphorus (Stamets 2000). These nutrients are returned to the soil once the fungi die and decompose, becoming available for use by plants and animals. This nutrient cycling produces a healthy and fertile soil, which is the foundation upon which the entire forest is built upon (Stamets 2005).

The productivity of a forest as a whole is connected to the decomposition of CWD, as it is this process that affects the amount of soil organic matter (Jurgensen *et al.* 1997). This productivity is dependent on the slow but continual release of nutrients from CWD back into the soil. Furthermore, by storing nutrients in CWD and slowly releasing them, there is a lower potential for nutrient loss from the ecosystem (Abbott and Crossley 1982). Logs with larger diameters are able to offer long-term nutrient reservoirs, as these logs take longer to decompose, sometimes hundreds of years (Spetich *et al.* 1999)

1.2.4 Carbon Reservoir

60% of the world's terrestrial carbon stocks are contained in forest and savanna vegetation (Woldendorp *et al.* 2002). In forests, about 50% of vegetative biomass is carbon (Harmon *et al.* 1986). When a tree dies and becomes CWD, that carbon is slowly released back into the atmosphere as carbon dioxide. CWD accounts for 33% of a forest's aboveground carbon stock, but this contribution is often overlooked (Baker *et al.* 2007). CWD decomposes at a slower rate than fine litter, making it a long-term carbon reservoir (Harmon and Hua 1991). Therefore, it has the ability to reduce the carbon dioxide released into the atmosphere if it remains on the forest floor to slowly decaying (Brown *et al.* 1992). In contrast, fire rapidly releases carbon dioxide back into the atmosphere. This particular function of CWD is significant because carbon dioxide, a greenhouse gas, is contributing to climate change as the concentration of carbon dioxide in the atmosphere continues to increase.

1.3 Recruitment of Coarse Woody Debris

CWD is a consequence of trees or parts of trees falling to the forest floor, either by death or disturbance. Thus, tree mortality directly contributes to the amount of CWD in a forest. The time it takes for a snag to fall to the forest floor is related to the cause of death, tree size and species, and whether or not there are advantageous conditions for decomposers (Harmon *et al.* 1986). Factors influencing the creation of CWD can either be natural or human-caused. The former includes wind, fire, disease, insects, earthquake, drought, flood, avalanches, and death resulting from competition or age (Spies et al. 1988). The latter encompasses forest management and harvesting operations.

Since CWD is a consequence of disturbance, the disturbance history of a forest can determine the amount of CWD present. Immediately following a disturbance, the amount of CWD is high as a direct result of the disturbance. As this material decays, the amount of CWD decreases. However, as forests mature, the amount of CWD grows as tree mortality increases (Hely *et al.* 2000). In addition to disturbance history, the tree species, forest productivity, tree size, and climate can all influence the volume of CWD (Harmon *et al.* 1986). Fire also plays a role in CWD recruitment. Fire causes an initial increase in CWD, as burnt trees die and fall. In fact, trees killed by fire fall sooner than snags unaffected by fire, which suggests that fire promotes the formation of CWD (Morrison and Raphael 1993). However, burning debris decreases the CWD on the floor at the time and also reduces the mass of potential CWD material (Spies *et al.* 1988).

1.4 Justification and Aims of Study

Despite its integral role in forest ecosystems, CWD is considerably deficient in managed forests because wood is removed before it has the chance to rot on the ground. Harvesting trees by clear-cutting removes 90% of live biomass (Spies *et al.* 1988). The remaining biomass is small, broken pieces that decay rapidly. This removal of live wood significantly decreases the amount of wood that would eventually become CWD. On top of that, forestry operations often incorporate thinning practices to promote desired tree growth. This act removes the competitive pressure that causes tree mortality, which ultimately leads to the input of CWD. Some managed forests directly remove CWD such as fallen logs or snags, often to maintain trails, roads, or infrastructure. However, forest harvesting practices in North Queensland in the 20th century were less invasive (Crome *et al.* 1992)

Following disturbance, both natural and anthropogenic, CWD takes longer to recover than the living portion of the forest, sometimes hundreds of years after live trees (Harmon and Hua 1991). In harvested forests, short rotations of fewer than one hundred years do not provide enough time for CWD to accumulate. One to two rotations in old-growth forests can eliminate all of the preharvest CWD, and further accumulation is slow (Spies *et al.* 1988).

Research demonstrates that managed forests not only have lower volumes of CWD, but the CWD that remains is smaller and in a less decayed state (Bunnell and

Houde 2010). This influences all other aspects of the forest, especially organisms that rely on CWD for habitat. The bigger pieces and more decayed pieces are particularly important because bigger pieces take longer to decompose, thus providing long-lasting habitat and a slow release of nutrients and carbon dioxide (Graham 1925; Spetich *et al.* 1999). More decomposed pieces are necessary for organisms that require the previous habitation of the CWD by a different species, such as insects that will only inhabit logs following fungi (Savely 1939). Many forest species are now considered threatened as a result of forestry practices (Bunnell and House 2010).

In order to properly address and correct this issue, forest managers need to increase their understanding of the dynamics and structure of CWD in a healthy, productive, and diverse forest. The issue is that studies on this topic are scarce (Spies *et al.* 1988). The objective of this study was to gain knowledge of the CWD in a 25-ha rainforest plot in tropical North Queensland, Australia. Much of the research on CWD has occurred in temperate forests, with less taking place in tropical rainforests. Understanding the role of CWD in rainforests is especially important because rainforests boast high levels of biodiversity and biomass, but are being clear-cut at an ever-increasing rate throughout the world.

1.4.1 Hypotheses

This study assessed CWD in two ways: its relationship with stand structure and plant response to the disturbance associated with CWD. The former involved comparing CWD volume to stand basal area and number of live stems ($\geq$10cm diameter). It was hypothesized that subplots with less live basal area will have greater volumes of CWD. This was based on the idea that if more wood is stored in live trees, then less of it is dead in the form of CWD. CWD volume was expected to increase as tree abundance decreased because if fewer trees are still standing, then there are more on the floor as CWD.

In addition, the number of pioneer plant species (<10cm diameter) was compared to the volume of CWD (not including snags). When a tree dies and falls, it opens a gap in the canopy and allows light to reach the forest floor. It was hypothesized that subplots with greater CWD volume will contain more light-demanding pioneer species and individuals. Snags were not included in this comparison because they have not yet fallen and created a canopy gap.

2 METHODOLOGY

2.1 Site Description

This study took place in a 1-ha plot within the Terrestrial Ecosystem Research Network (TERN) Robson Creek 25-ha permanent plot (Figure 1), located approximately 30 km northwest of Atherton, in Queensland, Australia (17^0 01'12"S, 145^0 37'56"E, elevation 700m). The site is situated within Danbulla National Park in the Wet Tropics World Heritage Area. This permanent plot, which is managed locally by CSIRO Tropical Forest Research Centre, was chosen to be a TERN site because it is a representative upland (400-1000m) rainforest with all weather access. Furthermore, the site maintains uniformity of forest type and parent material throughout. The 1-ha plot within the Robson Creek permanent plot was chosen for this study because of its proximity to the road, its heterogeneity of topography within the subplot, and its homogeneity of forest type and structure.

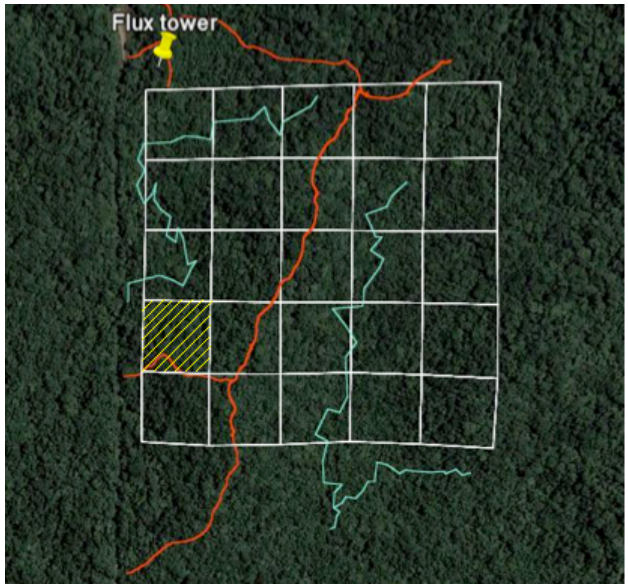


Figure 1. Aerial view of the TERN Robson Creek 25-ha permanent plot. The yellow diagonal lines mark the study site. The blue lines represent creeks and the red lines signify logging roads. The access road, Mount Edith Preservation Road, runs parallel to the western edge of the plot. Photo courtesy of GeoEye and CSIRO.

The climate of the study site is seasonal, with a majority of annual rainfall occurring from January to March. The mean annual rainfall at Danbulla Forestry (4.5km south of the plot) is 1597mm. This forest plot, which is at the western base of the Lamb Range, is classified as a complex mesophyll vine forest. Structurally, the forest is a very tall to extremely tall closed forest, with canopy heights ranging from 23m to 40m. In the past, the site was selectively logged. The most recent logging of this plot occurred between the years of 1960 and 1964. Prior to that, the site was possibly logged one to two times previously. Both of the two severe recent cyclones, cyclone Larry (2006) and cyclone Yasi (2011), resulted in minimal to moderate damage throughout the plot. The disturbance history is relevant to this study because CWD is a product of disturbance.

2.2 Field Methods

2.2.1 Plot Division

The 1-ha plot was divided into twenty-five subplots. Figure 2 summarizes the numbering scheme implemented. Within each 20-by-20m subplot, data was collected on the coarse woody debris and vascular plants present. The plot was divided into these subplots in order to provide twenty-five sample sites. This is necessary in order to make comparisons and find trends within the data.

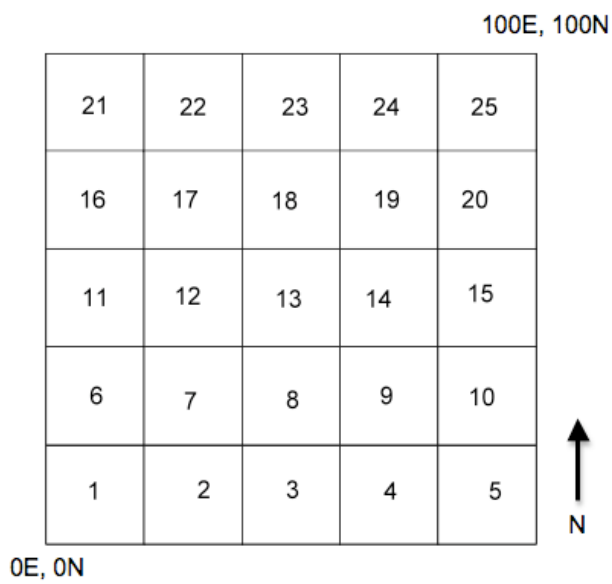


Figure 2. Subplot divisions and numbering pattern within 1-ha plot.

2.2.2 Coarse Woody Debris Measurements

Within each subplot, all CWD pieces with diameter larger than 10cm were measured. This included standing dead trees snags as well as fallen dead trees and branches. The diameter of snags was measured at a height of 1.3m, or directly above buttress roots. The height, measured using a Nikon laser range finder, was measured to the point where the trunk tapered to 10cm. If branches were greater than 10cm in diameter, their dimensions were estimated.

For all pieces of fallen wood, the length and diameter at both ends were measured. Length measurements were made to the edge of the plot. When pieces had only one end larger than 10cm in diameter, measurements were only made to the point where the diameter began to decrease to less than 10cm. If a fallen tree had attached branches greater than 10cm diameter, the branches were measured separately. For fallen trunks with buttresses, measurements were made above the buttress.

2.2.3 Vascular Plant Measurements

All trees, palms, vines, ferns, and strangler figs with diameter greater than 10cm at breast height were included in this study. The diameter was measured usually at 1.3m (breast height) on the uphill side of the tree. If the tree had buttress roots, diameter measurements were made above the buttress. To obtain accurate diameter measurements, vines were pulled away from tree. When this was not possible, the diameter was measured using a caliper.

If there was a deformity in the trunk at breast height, diameter was measured above it, so that later calculations more accurately represented the tree. In the occasion of a forked trunk, different methods were used depending on where the forking occurred. If the tree forked above 1.3m, the diameter was measured below the fork at the point where there was no deformation or swelling of the trunk. If the tree forked below 1.3m, each stem was measured as a separate tree. For strangler fig trees, which usually have more than one stem, the diameter at breast height was estimated.

Heights were measured using a Nikon laser range finder. If the top was not easily visible, the height was estimated using the measured trees around it as a reference. For lianas, the height was the estimated length of the stem.

2.2.4 Pioneer Species Survey

In each of the subplots, data was collected on all pioneer plant species (see Appendix A for the list of species surveyed) with diameter <10cm. The reason larger trees were not included was because tree above 10cm diameter are too old for the CWD on the ground to be related to their presence. For each subplot, the presence of any pioneer sapling (≥1cm and <10cm diameter) and seedling (<1cm diameter) was recorded. For non-tree species, such as vines and gingers, they were recorded as saplings even if their diameter was <1cm. This is because these are more mature at smaller sizes. For each species, an abundance score was assigned on a scale of one to five. A score of one meant that the species was present only 1 to 3 times in the subplot, two meant 4 to 6 times, three meant 7 to 10 times, four meant 11 to 15 times, and five meant more than 15 times. A score of zero obviously meant the species was absent from the subplot.

2.3 Data Analyses

2.3.1 Calculations

To calculate CWD volume, a modified formula for the volume of a cylinder was used. The volume (V) of a cylinder is calculated by using this formula:

$$V = L[\pi(D/2)^2]$$

where L is the length and D is the diameter. Because many of the logs tapered at one end, the diameter was not consistent throughout and using this formula would result in an incorrect value. Instead, the calculation inside the brackets was performed for both diameters and then those values were averaged, as displayed by this formula:

$$V = L\left[\frac{\pi(D_1/2)^2 + \pi(D_2/2)^2}{2}\right]$$

To calculate basal area of live trees (BA), this formula was used:

$$BA = \pi(D/2)^2$$

Since the species abundance scores for the pioneer species represented a range, the average of the range was used when calculating abundances for the subplots. A score of one represented an abundance of 2 individuals, two meant 5 individuals, three represented 9 individuals, four equaled 13 individuals, and five meant 25 individuals for saplings and 100 for seedlings.

2.3.2 Statistical Analyses

Statistical analysis was performed using the STATISTICA software, version 8 (StatSoft, Inc. 2004). Results were not considered significant unless the observed trends had less than 5% chance of being random ($P < 0.05$).

3 RESULTS

3.1 CWD Volume

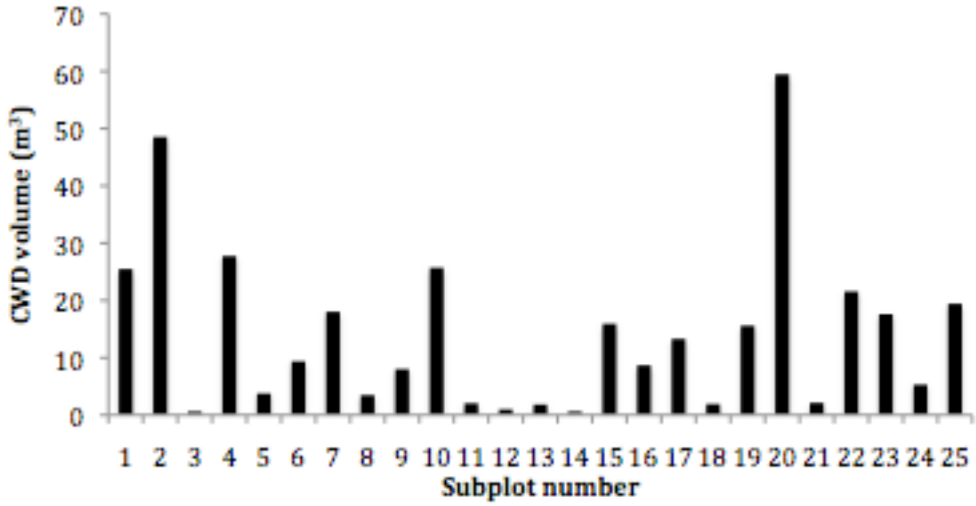


Figure 3. Total CWD volume (m^3) in each of the 25 subplots.

There was a total 476 pieces of CWD (≥10cm diameter) present in the 1-ha plot, 50 of which were snags. The total volume of CWD in the 1-ha plot was 357.51m^3 and the mean CWD volume per 20-by-20m subplot was 14.30m^3 (SD 14.89). CWD made up 23.99% of the total volume of live and dead wood (≥10cm diameter). Figure 3 displays the total CWD volume found in each of the 25 subplots. The subplot CWD volumes varied greatly, ranging from 0.63m^3 (subplot 3) to 59.49m^3 (subplot 20).

3.2 CWD and Stand Structure

A total of 948 trees (≥10cm diameter) were measured in the 1-ha plot, with a mean of 72.92 (SD 7.38) trees per subplot. The total basal area of all trees in the plot was 45.22m^2. There were 165 large trees (≥30cm diameter) in the plot, which averages to 6.6 (SD 2.18) large trees per subplot. Large trees contributed 27.44m^2 (60.7%) of the total basal area.

There was a trend for CWD volume to decrease as subplot basal area increased, but the relationship was not significant (R^2 = 0.113, P = 0.100, figure 4a). There was also no significant relationship between CWD volume and large trees (≥30cm diameter) in each subplot (R^2 = 0.095, P = 0. 133, figure 4b).

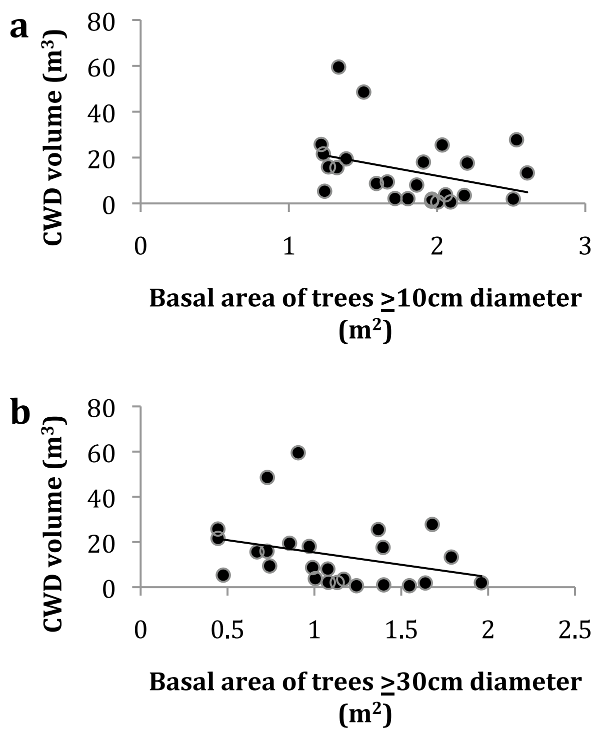


Figure 4. a) Total CWD volume (m^3) versus total basal area (m^2) for all measured trees (≥10cm diameter) in each subplot. The solid line represents the linear regression, y = -11.761x + 35.573 (R^2 = 0.113, P = 0.100). **b)** Total CWD volume (m^3) versus total basal area (m^2) for all large trees (≥30cm diameter) in each subplot. The solid line represents the linear regression, y = -10.886x + 26.249 (R^2 = 0.095, P = 0.133).

There was no significant relationship between the CWD volume and the number of stems in each subplot (R^2 = 0.021, P = 0.486, figure 5a). A trend was more evident but still not statistically significant for CWD volume and the number of large stems (≥30cm diameter) in each subplot, with CWD volume decreasing as the number of large stems increased (R^2 = 0. 102, P = 0. 120, figure 5b).

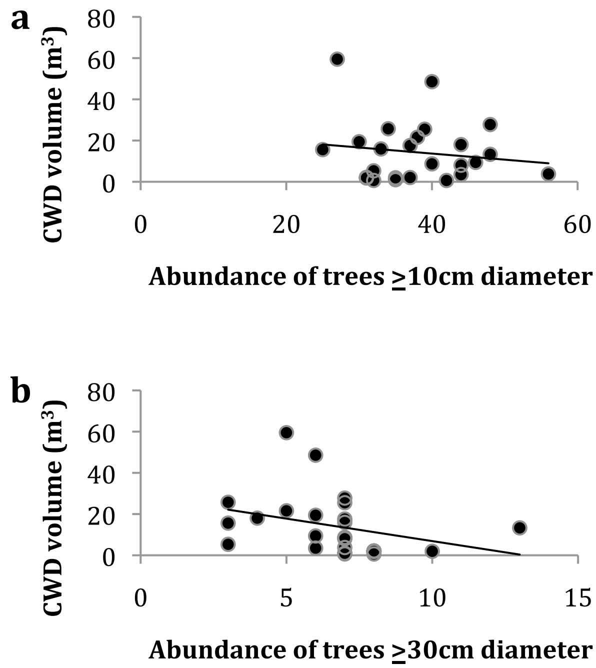
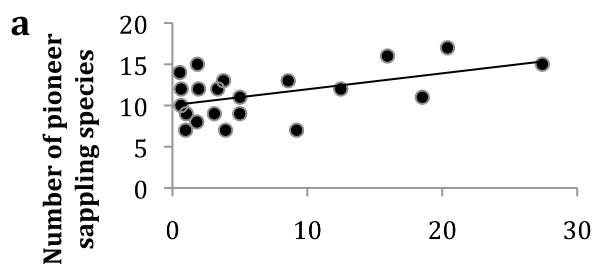


Figure 5. a) Total CWD volume (m³) versus total number of stems for all measured trees (≥10cm diameter) in each subplot. The solid line represents the linear regression, y = -0.295x + 25.484 (R^2 = 0.021, P = 0.486). **b)** Total CWD volume (m³) versus total number of stems for all large trees (≥30cm diameter) in each subplot. The solid line represents the linear regression, y = -2.179x + 28.681 (R^2 = 0.102, P = 0.120).

3.3 CWD and Disturbance

Of the 28 surveyed pioneer plant species, there was an average of 11.38 (SD 3.01) sapling (≥1cm and <10cm diameter) species and 8.10 (SD 2.17) seedling (<1cm diameter) species in each of the 25 subplots. There was a significant linear relationship between the number of pioneer sapling species and CWD volume in each subplot (R^2 = 0.243, P = 0.023, figure 6a). The number of pioneer sapling species increased as CWD volume increased. There was a similar linear trend for pioneer seedling species, but the relationship was not significant (R^2 = 0.131, P = 0.107, figure 6b).

In total, there were 1327 pioneer sapling individuals and 917 pioneer seedling individuals. The average number of individuals per subplot was 63.19 (SD 19.24) for saplings and 43.67 (SD 36.55) for seedlings. There was no significant relationship between the number of pioneer saplings or seedlings and CWD volume (P = 0.964; P = 0.724).



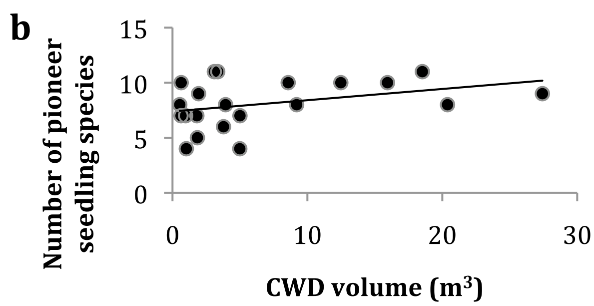


Figure 6. a) Number of all pioneer sapling species (≥1cm and <10cm diameter) versus total CWD volume (m^3) for each subplot. The solid line represents the linear regression, y = 0.193x + 10.036 (R^2 = 0.243, P = 0.023). **b)** Number of all pioneer seedlings species (<1cm diameter) versus total CWD volume (m^3) for each subplot. The solid line represents the linear regression, y = 0.102x + 7.385 (R^2 = 0.131, P = 0.107).

4 DISCUSSION

4.1 CWD Volume

The total volume of CWD in the 1-ha plot in North Queensland was greater than reported from other forests around the world. Undisturbed and logged forests in the eastern Amazon, Brazil, contained 103 to 205m^3 per hectare respectively (Keller *et al.* 2004). Other Australian forest types, such as eucalypt woodlands, had CWD volumes ranging from 34 to 247.2m^3 per hectare (Manning *et al.* 2007).

The reason for these discrepancies can be attributed to differences in CWD recruitment and decay rates. The eucalyptus woodlands in Australia have a lower tree density and biomass than tropical rainforests, and therefore have a lower potential for trees to become CWD. The differences in CWD volume between this Australian rainforest and Amazonian rainforests can be the result of decomposition rates, which vary depending on the climate. The rate of decomposition processes is enhanced by increases in temperature and moisture (Bridges 1970). The Amazonian sites may receive more annual precipitation than the Australian study site. Thus, the rates of decomposition in the Amazonian rainforests would be higher than those in the study site. This means CWD volumes would decrease at a faster rate in the Amazon rainforest sites.

While this study is only one hectare of rainforest, similar trends should be seen in other tropical rainforests in Australia. Furthermore, this region experiences frequent and often intense cyclones, which significantly contribute to the amount of CWD on the forest floor. These events promote biodiversity in two ways. First, the increased amount of CWD following cyclones provides many new habitats for forest organisms. Secondly, the new canopy gaps allow light-demanding species to establish in the understory. The ultimate consequence of this is a heterogeneous forest that is better prepared to endure more severe disturbances, both natural and human-made.

4.2 CWD and Stand Structure

The subplot variation in CWD volume (figure 3) cannot be explained by stand characteristics examined in this study. It was expected that CWD volume would increase as subplot live basal area and number of stems decreased. While these relationships were not statistically significant, general trends were still observed (figure 4 and 5). These results suggest that if more wood exists as live trees, then there is less on the ground as CWD. The relationship between CWD volume and number of stems was more apparent for large trees than all trees possibly due to the larger volume contributions of bigger trees.

Perhaps the results would have been more conclusive if all trees within the subplots were measured, not just those with diameter $\geq$10cm. In the study site, the majority of the trees had diameters <10cm. When conducting future research on this topic, it would be important to determine if the smaller trees did in fact influence the variations observed in the volumes of CWD across the rainforest plot.

4.3 CWD and Disturbance

The differences found in the number of pioneer plant species can be attributed to CWD volume for saplings but not seedlings. It was expected that the number of both sapling and seeding species would be greater in subplots with more CWD volume. While the relationship between CWD volume and the number of pioneer species was significant only for saplings, the trend was still observed for seedlings. The number of pioneer plant individuals did not, however, show a relationship with CWD volume for either saplings or seedlings. This could be attributed to the fact that the disturbance resulting from the input of CWD allows for the invasion of many pioneer species, but only a limited number of stems can establish and grow in the available space.

It would be more definitive to survey all seedling and sapling species in the plots, and determine if CWD volumes relates to total diversity. These results could provide insight into the intermediate disturbance hypothesis, which suggests that intermediate levels of disturbance maintain high diversity (Connell 1978). Following a disturbance, pioneer species thrive and therefore species diversity is low. If disturbance occurs too frequently, only these few pioneer species will grow to maturity. As time following a disturbance increases, more species are able to invade. This increases the diversity of the system. However, if too much time passes between disturbances, the best competitor will exclude other species and diversity will decrease. Forests containing high levels of CWD recently experienced disturbance, and are expected to contain high levels of pioneer species diversity but not necessarily overall biodiversity.

5 CONCLUSION

Since CWD is essential for forest biodiversity and productivity, understanding the factors that influence its quantities and qualities is highly important. This information can help forestry operations properly manage forests. This study collected CWD measurements to determine its relationships with stand structure and disturbance. The trends observed supported the hypotheses, but most were not statistically significant and therefore not conclusive. CWD was found to generally decrease as number of live stems and live basal area increased in the subplots. The number of pioneer seedling species generally was found to increase as CWD volume increased. The only significance found in this study was that the number of pioneer sapling species increased as CWD volume increased. While the results of this study did not entirely contradict the hypotheses, most were not significant enough to be definitive. Future studies similar to this should be conducted to further explore the different factors that contribute to the differences observed in CWD volume across the rainforest landscape.

5.1 Management Implications

The results of this study reveal that CWD volume is dependent on the death of trees, especially large trees. To promote biodiversity and healthy ecosystem function, forest managers need to consider the ramifications of removing large quantities of trees, particularly larger trees, from forests. To retain high levels of species richness, at least 50%, but preferably more, of the natural levels of CWD should remain in the landscape (Bunnell and Houde 2010). Additionally, CWD pieces left on the forest floor should vary in size and decay stage so that a wider range of species can utilize the various habitats that different types of CWD can offer. It is particularly important to allow large pieces to remain, as they provide ecosystem services for much longer, since they take longer to decompose than smaller pieces (Bunnell and Houde 2010).

Forest managers should aim for the CWD in their forests to resemble natural stocks of CWD. For example, some CWD should be dispersed and others placed in piles, to represent different types of tree mortality and disturbances. Piled CWD is particularly beneficial for some vertebrates (Bunnell and Houde 2010). Logging operations should consider harvesting patches of forest at different times to provide a variety of decay stages. It is also important for them to allow some trees to remain in the forest, because these will inevitably become CWD. The most important concept to keep in mind is to differ in the methods of forest management regarding CWD, as naturally occurring CWD is the results of many different factors and therefore is very heterogeneous across the landscape.

REFERENCES

Abott DT, Crossley DA Jr. 1982. Woody litter decomposition following clear-cutting. *Ecology* 63: 35-42.

Andersson LI, Hytteborn H. 1991. Bryophytes and decaying wood – a comparison between managed and natural forest. *Holarctic Ecology* 14: 121-130.

Baker TR, Honorio Coronado EN, Phillips OL, Martin J, van der Heijden GMF, Garcia M, Espejo JS. 2007. Low stocks of coarse woody debris in a southwest Amazonian forest. *Oecologia* 152: 495-504.

Brattstrom BH. 1979. Amphibian temperature regulation studies in the field and laboratory. *American Society of Zoologists* 19: 345-356.

Bridges, E.M. 1970. *World Soils*. New York, NY: Cambridge University Press, 89 p.

Brown JK, Reinhardt ED, Kramer KA. 2003. Coarse woody debris: managing benefits and fire hazard in the recovering forest. General Technical Report RMRS-GTR-105. *USDA Forestry Service.*

Brown S, Lugo AE, Iverson LR. 1992. Processes and lands for sequestering carbon in the tropical forest landscape. *Water, Air, and Soil Pollution* 64: 139-155.

Bunnell FL, Houde I. 2010. Down wood and biodiversity – implications to forest practices. *Environmental Reviews* 18: 397-420.

Christy EJ, Mack RN. 1984. Variation in demography of juvenile *Tsuga heterophylla* across substratum mosaic. *Journal of Ecology* 79: 519-530.

Connell JH. 1978. Diversity in Tropical Rain Forests and Coral Reefs. *Science* 199: 1302-1310.

Crome FHJ, Moore LA, Richards GC. 1992. A study of logging damage in upland rainforest in north Queensland. *Forest Ecology and Management* 49: 1-29.

DeLong HB, Lieffers VJ, Blenis PV. 1997. Microsite effects on first-year establishment and overwinter survival of white spruce in aspen-dominated boreal mixedwoods. *Canadian Journal of Forest Research* 27: 1452-1457.

Graham SA. 1925. The felled tree trunk as an ecological unit. *Ecology* 6: 397-411.

Hale CM, Pastor J. 1998. Nitrogen content, decay rates, and decompositional dynamics of hollow versus solid hardwood logs in hardwood forests of Minnesota, USA. *Canadian Journal of Forest Research* 28: 1276-1285.

Harmon ME, Anderson NH, Franklin JF, Cline SP, Swanson FJ, Aumen NG, Sollins P, Sedell JR, Gregory SV, Lienkaemper GW, Lattin JD, Cromack K Jr., Cummins KW. 1986. Ecology of coarse woody debris in temperate ecosystems. *Advances in Ecological Research* 15: 133-302.

Harmon ME, Hua C. 1991. Coarse woody debris dynamics in two old-growth ecosystems. *BioScience* 41: 604-610.

Harvey AE, Jurgensen MF, Larsen MJ, Graham RT. 1987. Relationships among soil microsite, ectomycorrhizae, and natural conifer regeneration of old-growth forests in western Montana. *Canadian Journal of Forest Research* 17: 58-62.

Hely C, Bergeron Y, Flannigan MD. 2000. Coarse woody debris in the southeastern Canadian boreal forest: composition and load variations in relation to stand replacement. *Canadian Journal of Forest Research* 30: 674-687.

Hodge SJ, Peterken GF. 1998. Deadwood in British forests: priorities and a strategy. *Forestry* 71: 99-112.

Jurgensen MF, Harvey AE, Graham T, Page-Dumroese DS, Tonn JR, Larsen MJ, Jain TB. 1997. Impacts of timber harvesting on soil organic matter, nitrogen, productivity, and health of inland Northwest forests. *Forest Science* 43: 234-251.

Keller M, Palace M, Asner GP, Pereita R Jr., Silva JNM. 2004. Coarse woody debris in undisturbed and logged forests in the eastern Brazilian Amazon. *Global Change Biology* 10: 784-795.

Manning AD, Lindenmayer DB, Cunningham RB. 2007. A study of coarse woody debris volumes in two box-gum grassy woodland reserves in the Australian Capital Territory. *Ecological Management and Restoration* 8: 221-224.

Morrison GJ, Raphael MG. 1993. Modeling the dynamics of snags. *Ecological Applications* 3: 322-330.

Savely HE Jr. 1939. Ecological relations of certain animals in dead pine and oak logs. *Ecological Monographs* 9: 321-385.

Sharmila P, Pardha Saradhi P. 2002. Evaluating Performance of Plants Infected with Vesicular Arbuscular Mycorrhizal Fungi for Alleviating Abiotic Stresses. In: *Techniques in Mycorrhizal Studies* (Mukerji, K.G., *et al*., eds.). Boston: Kluwer Academic Publishers, 469-492.

Shiels AB, Zimmerman JK, Garcia-Montiel DC, Jonckheere I, Holm J, Horton D, Brokaw N. 2010. Plant responses to simulated hurricane impacts in a subtropical wet forest, Puerto Rico. *Journal of Ecology* 98: 659-673.

Spetich MA, Shifley SR, Parker GR. 1999. Regional distribution and dynamics of coarse woody debris in Midwestern old-growth forests. *Forest Science* 45: 302-313.

Spies TA, Franklin JF, Thomas TB. 1988. Coarse woody debris in Douglas-fir forests of western Oregon and Washington. *Ecology* 69: 1689-1702.

Stamets, P. 2000. *Growing Gourmet and Medicinal Mushrooms*, 3rd Edition. Berkeley, CA: Ten Speed Press, 614 p.

Stamets, P. 2005. *Mycelium Running: How Mushrooms Can Help Save The World*. Berkeley, CA: Ten Speed Press, 339 p.

StatSoft, Inc. 2004. *STATISTICA (version 8)*. StatSoft, Inc. Tulsa, OK, USA.

Stone EL. 1975. Windthrow influences on spatial heterogeneity in a forest soil. Eidgenoessiche Anstalt feur das forstliche Versuchswesen Mitteilungen 51: 77-87.

Woldendorp G, Keenan R, Ryan M. 2002. Coarse woody debris in Australian forest ecosystems. Report for the National Greenhouse Strategy, Module 6.6. *Bureau of Rural Sciences, Australia.*

APPENDIX A

List of light-demanding pioneer plant species that were included in the survey:

Acronychia acidula
Acronychia vestita
Alphitonia petriei
Alphitonia whitei
Alpinia caerula
Alpinia modesta
Alstonia muelleriana
Calamus australis
Calamus moti
Caldcluvia australiensis
Cardwellia sublimis
Daphnandra repandula
Darlingia darlingiana
Elaeocarpus grandis
Elaeocarpus largiflorens subsp. largiflorens
Elaeocarpus ruminatus
Eleangus triflora
Flindersia bourjotiana
Flindersia brayleyana
Flindersia laevicarpa
Flindersia pimenteliana
Franciscodendron laurifolium
Glochidion hylandii
Litsea leefeana
Macaranga inamoena
Melicope elleryana
Melicope vitiflora
Melicope xanthoxyloides
Neolitsea dealbata
Placospermum coriaceum
Pleuranthodium racemigerum
Polyscias australiana
Polyscias elegans
Polyscias murrayi
Rubus molucannus
Sloanea langii
Solanum mauritanium