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Forest succession where trees become smaller and wood carbon stocks reduce

M.T. Moroni [a,c,*], R. Musk [b,c], T.J. Wardlaw [b,c]

[a] Private Forests Tasmania, 30 Patrick Street, Hobart 7000, Australia
[b] Forestry Tasmania, 79 Melville Street, Hobart 7000, Australia
[c] ARC Centre for Forest Value, University of Tasmania, Sandy Bay, Tasmania 7005, Australia

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ABSTRACT

As Tasmania's wet forests transition from mixed forest (eucalypt overstory with a rainforest understory) to rainforest they can be expected to lose more than half their total (live + dead, standing + downed) bole wood volume and biomass. On average rainforest sites contained 205 Mg C ha^{-1}, or 708 m^3 ha^{-1} less wood (live + dead, standing + downed) than mixed forests. This occurs as smaller dimension rainforest trees replace the larger eucalypts. On the fertile study sites, the largest rainforest trees were 20 m shorter and 113 cm smaller in breast height diameter than the mature eucalypts in mixed forests. Tasmanian wet forests do not attain the highest site level C-stocks possible in late succession, as is expected for many other forests. Rather, the maxima is attained for a short period several centuries after disturbance and regeneration of a eucalypt cohort. Hence, the maintenance of the highest C-density stands in the landscape, and potentially that largest landscape level C-stocks among Tasmania's wet forests ironically requires the periodic killing of all, or part, of the large C-dense eucalypt overstory by intense wildfire to allow these large eucalypts to regenerate and persist on these sites. This creates challenges when modeling forest carbon in Tasmanian wet forests, as not only is the area of forest that has progressed sufficiently toward rainforest to be emitting C is unknown, but the rate of C emission and the amount that will be lost over time across the various site fertility types is also unknown. Certainly, setting aside Tasmanian wet eucalypt forest to store C will not deliver the usual long term C accumulation benefits common to forests elsewhere. Maximizing landscape level C-stocks is likely to require periodic disturbance to maintain the C-dense eucalypts in the landscape.

1. Introduction

Tasmania's wet forests are among the world's tallest (Sillett et al., 2015), they include the world's tallest flowering plant, *Eucalyptus regnans*, that can achieve heights of up to 100 m tall. Consequently, these forests store large amounts of C when compared against other forest types (Moroni et al., 2010; Sillett et al., 2015). However, during succession, these disturbance driven open canopied tall eucalypt forests are gradually replaced by gap driven, closed canopied shorter rainforest species (Gilbert, 1959; Stone, 1998; Wood et al., 2010). In high rainfall areas, eucalypt and rainforest are interchangeable on sites, depending on disturbance history, due to their contrasting regeneration requirements. The difference in overstory tree dimensions between these two interchangeable forests types is very large (Moroni et al., 2010), and the differences in C-stocks is thus expected to be very large. However, the difference in live and dead tree biomass between eucalypt and rainforest are poorly documented: there is a dearth of information describing the volume and biomass of wood in rainforests and there is a lack of such data from eucalypt forest and rainforest on comparable sites.

The rate of biomass and carbon accumulation in forests with time since disturbance has long been held to increase to a maximum and then decline toward a steady state where stand level gross primary productivity is eventually entirely offset by autotrophic and heterotrophic respiration (Kira and Shidei, 1967; Odum, 1969; Ryan et al., 1997). However, recent evidence from a range of ecosystems suggests that old growth forests continue to accumulate carbon (Desai et al., 2005; Kashian et al., 2013; Luyssaert et al., 2008; Tan et al., 2011). Although in some ecosystems, recent studies have provided evidence for a steady state (Seedre et al., 2015) and a decline (Taylor et al., 2014) in net

* Corresponding author at: Private Forests Tasmania, 30 Patrick Street, Hobart 7000, Australia.
E-mail address: martin.moroni@pft.tas.gov.au (M.T. Moroni).

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ecosystem productivity. It has also been noted that changes in community structure during succession can influence forest ecosystem carbon stock changes with forest age (Drury and Nisbet, 1973; Paré and Bergeron, 1995; Drake et al., 2011).

Eucalypts have open canopies that allow enough light through them to support a shorter forest understory that does not need to outcompete or outgrow the eucalypt overstory to survive. In Tasmanian wet forests, the shorter forest understory that develops is temperate rainforest (Gilbert, 1959; Stone, 1998; Wood et al., 2010). Where a eucalypt overstory and rainforest understory exist, they are known as mixed forests.

Eucalypts in wet forests regenerate following infrequent but usually intense wildfires that kill most or a large proportion of trees, creating canopy openings, consume the abundant leaf litter and much of the understory and expose mineral soil. Eucalypt seedlings are shade intolerant and require bare soil for a receptive seedbed and high light conditions for early rapid growth (Gilbert, 1959; Cunningham, 1960; Ashton, 1981). To maintain eucalypt cover, fire must return before the eucalypt overstory, and seed source, dies (Gilbert, 1959; Jackson, 1968). Eucalypt seedling development in the undisturbed forest understory is rare. In contrast, rainforest species are shade tolerant, fire intolerant and constantly germinate under forest canopies without needing bare soil for germination (McKenney and Kirkpatrick, 1999; Read, 1999; Simkin and Baker, 2008). Consequently, in mixed forests, while the rainforest is continuously regenerating through gap dynamics, the eucalypt overstory cannot regenerate, and in the absence of fire the eucalypts gradually die and are replaced by the shorter rainforest. Conversely, when rainforest is burned, adjacent eucalypts will seed into burned areas and the eucalypts can return (Cunningham and Cremer, 1965; Hickey, 1994). Thus the extent and frequency of wildfire determines both the spatial and temporal distribution of wet eucalypt forest, mixed forest and rainforest.

Succession of wet forests from mixed forests to rainforest results in a large reduction in forest tree dimensions, from 34–100 m tall eucalypts to 8–40 m tall rainforest (Gilbert, 1959; Hickey and Felton, 1991; Jackson, 1968; Stone, 1998). This is expected to reduce standing tree biomass, and subsequently the biomass of downed dead wood, thus releasing C to the atmosphere with succession (Moroni et al., 2010). While eucalypt forests have been extensively inventoried (Stone, 1998; Whiteley, 1999; Moroni et al., 2010), little information is available describing the volume and biomass of live or dead wood in Australia's and particularly Tasmania's temperate rainforest. Such data is required to enable biomass and thus C-mass of this biome to be estimated and modelled, including the consequences of potential changes in the distribution of these forest types with management or climate change. The objective of this study is to quantify the reductions in live and dead bole-mass and tree height and diameter, with the progression from mixed forest to rainforest in Tasmania.

2. Method

2.1. Site selection and sampling design

Selected sites are natural forest with no evidence of harvesting or other direct human impacts. Paired sample sites were selected (14 pairs) comprising a rainforest site and a mixed forest site where each pair of sites were <2000 m apart and growing on a similar soil types. This maximized confidence that, within site pairs, the mixed forests would, over time, transition to rainforests similar to those measured. Mixed forests were characterized as having a low density of large eucalypts over a rainforest understory. Rainforest contained no large living eucalypts.

A list of potential sites was generated from GIS analysis of Forestry Tasmania's Forest Class 2005 layer as a classifier (Stone, 1998). Priority was given to polygons of the target forest types that were larger in area, lowest in slope and had the least distance between potential site pairs. Sites were visited in order of desktop prioritization and selected for measurement if they agreed with mapped attributes during site visits, until 8 pairs of sites were located for southern Tasmania and 3 pairs located in each of Tasmania's northeast and northwest (Table 1, Fig. 1). Sites were measured between September 2012 and July 2013. Mean annual temperatures (MAT) and precipitation (MAP) at weather stations located near selected sites were, 16.1 °C (MAT) and 1166.9 mm (MAP) at Maydena in southern Tasmania, 17.3 °C (MAT, Scottsdale) and 1208.4 mm (MAP) at Ringarooma in the Northeast, and 15.5 °C (MAT) and 1520.1 mm (MAP) at Luncheon Hill in Northwest Tasmania.

In each site three plots were established, avoiding areas not consistent with the targeted forest types, ensuring plots were at least 25 m from the forest type boundary and plot centers were at least 50 m apart. Each plot consisted of two concentric circular subplots (radius 12 m and 20 m, respectively) and two 50 m (horizontal length) line transects, perpendicular to each other, their midpoint crossing at the plot center.

Diameter at breast height (1.3 m; DBH), distance and bearing from plot center and species identity were recorded for each living trees $\geq$ 10 cm DBH within the 12 m radius circular subplot. Height, DBH, distance and bearing from plot center of all canopy trees were measured within the 20 m radius circular subplot. Tree heights were determined for a minimum of five trees or 10% of the trees $\geq$ 10 cm DBH within the 20 m circular plot using a Vertex Forester hypsometer, consistent with Forestry Tasmania's LiDAR plot measurement protocol (Hodge, 2011). Heights of all other trees $\geq$ 10 cm DBH were estimated from unpublished Forestry Tasmania equations that use as inputs tree diameter and cohort (eucalypt or rainforest) mean dominant stand height calculated from the measured tree heights on each plot. Standing tree bole volume (>10 cm diameter) was estimated by integrating unpublished Forestry Tasmania species-specific stem taper equations. Standing tree bole biomass was estimated by multiplying wood volumes by species specific wood densities (Ilic et al., 2000), and woody biomass was assumed to be 0.5 C.

Coarse woody debris (CWD; $\geq$10 cm) diameters and decay classes were estimated at their point of intersection along the 50-m transects. CWD volumes were calculated using the Line Intersect Method (Marshall et al., 2000). Grove et al. (2009) describe 5 decay classes with wood densities decreasing with state of decay and having densities of 488, 362, 284, 180, and 86 kg m^{-3}. Dead wood biomass was estimated by multiplying dead wood volumes in each decay class by a wood density for each decay class (Grove et al., 2009). Dry wood density varied inversely with decay class.

2.2. Statistical analysis

A Bayesian data analysis (Gelman et al., 1997) was used to describe the magnitude of the differences in tree volume and biomass between rainforest and mixed forest sites. We take this approach over the *t*-test as it provides credible intervals on the domain of the predicted distribution of the differences in means. Credible intervals are analogous to confidence intervals in frequentist statistics and constitute a much richer information source about the samples than that provided by a simple p-value. Following Kruschke (2012) the data from the two groups were modelled using *t* distributions with separate mean ($\mu_{1\ and\ 2}$) and standard deviation ($\sigma_{1\ and\ 2}$) parameters for each group and a shared normality (ν) parameter that governed the heaviness of the distribution