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Carbon and water exchange of the world's tallest angiosperm forest

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ABSTRACT

Old growth forests have traditionally been viewed as an insignificant sink or source in the global carbon cycle and therefore, flux tower studies of net ecosystem exchange (NEE) and evapotranspiration (LE) using flux measurements in these ecosystems are limited. Here we report eddy covariance (EC) fluxes of carbon dioxide and water above and below the canopy of an old growth Mountain Ash (*Eucalyptus regnans*) forest over an 18 month period. Mountain Ash species are the world's tallest angiosperm and recognized as the most carbon-dense forests, which potentially makes them an important component of the terrestrial carbon and water budgets in Australia. Results showed that for 2006, the ecosystem was a large net sink of carbon of $377 \pm 49\,g\,C\,m^{-2}\,year^{-1}$. Throughout the study period, daytime Gross Primary Productivity (GPP) was limited mainly by radiation, but there were important secondary drivers regulating carbon uptake, especially in summer, when atmospheric and soil water deficits were high. The highest rates of NEE occurred during spring, when the ecosystem was not limited by radiation or moisture, and the lowest rates were observed during autumn and winter. In 2006, GPP for the ecosystem was $2615\,g\,C\,m^{-2}\,year^{-1}$, and ecosystem respiration (Re) was $2238\,g\,C\,m^{-2}\,year^{-1}$. During the summer and autumn of 2006, the understorey fluxes accounted for 29% of ecosystem GPP, 33% of evapotranspiration, and 53% of night time Re, a significant proportion of carbon dioxide and water exchange given that the understorey biomass is only one tenth of the ecosystem biomass. Results from this study highlighted the importance of the understorey vegetation in regulating old growth forest carbon and water balances, which has important implications for forest management practices.

1. Introduction

One of the crucial issues in climate change is predicting potential shifts in the global carbon budget. Terrestrial ecosystems mediate a large part of the carbon flux between the Earth's surface and the atmosphere by sequestering $\sim$120 Pg C year^{-1} via photosynthesis and releasing most of the carbon back to the atmosphere via respiration (Chapin et al., 2002). Therefore, a detailed understanding of the relationships of carbon exchange between the atmosphere and biosphere is required to improve our knowledge of the global carbon cycle (Baldocchi, 2008). Significant progress has been made over the last three decades in understanding and quantifying land atmosphere-exchange across a wide range of ecosystems. However, old growth forests have been traditionally ignored in carbon and water balance studies since they are believed to be insignificant net carbon sinks (Kira and Shidei, 1967; Odum, 1969; Dixon, 1994).

During first stages of succession post-disturbance, forests are typically net carbon sources (Harmon et al., 1990), but can become large carbon sinks as they mature due to a rapid increase in stems and Leaf Area Index during peak growth (Kira and Shidei, 1967; Gower et al., 1996). As forests move through successional stages from pole stands to old growth, carbon sink strength is thought to decline in magnitude to ultimately reach neutrality (or is a carbon source) as growth slows and respiration increases. The increase in respiration is attributed to the increasing volume of woody biomass accumulated within the stand. This includes maintenance and growth respiration of sapwood and decomposition of heartwood and coarse woody debris (CWD). Gross Primary Production (GPP) typically peaks in developing stands and declines as stands age due to decreases in stomatal conductance; hydraulic conductivity from increased tree height, nutrient availability, and increased tree and branch mortality, which acts to reduce ecosystem Leaf Area Index (LAI) (Gower et al., 1996). Some forest productivity models assume that the net flux of carbon from the atmosphere into vegetation declines steadily after stem development, and approaches zero for old growth stands (Hunt et al., 1999; Makela and Valentine, 2001).

Recent results directly challenge this prevailing paradigm of old growth ecosystem carbon dynamics. A number of investigators,

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using eddy covariance and biomass sampling techniques have indicated that old growth forest ecosystems do not reach a steady state, but continue to act as a net sink of atmospheric CO_2 (Fan et al., 1990; Hollinger et al., 1994; Grace et al., 1995; Law et al., 2001; Knohl et al., 2003; Loescher et al., 2003; Chen et al., 2004; Paw et al., 2004; Harmon et al., 2004; Desai et al., 2005; Zhou et al., 2006; Hirata et al., 2008; Yu et al., 2008). However, these studies have been inconclusive in explaining the driving mechanisms for the maintenance of carbon sinks, and have suggested that forests may be responding to changes in climate. A recent statistical analysis by Luyssaert et al. (2008) indicated that boreal and temperate old growth forests may be the 'missing carbon sink'; they estimated that northern hemisphere ecosystems are currently sequestering 1.3 ± 0.5 Pg C year^{-1}. Furthermore, it has been shown that accumulated carbon is stored in the roots and soil organic matter by modelling studies (Luyssaert et al., 2008) and observations by Zhou et al. (2006), who described a net accumulation of carbon in the soils over decadal periods in old growth forests of China.

It is essential to understand the exchange of carbon and therefore the sink/source status of various aged stands to develop more informed climate change mitigation strategies and frameworks for international agreements. For example, in many parts of the world, intensive human-induced land use changes have led to the conversion of undisturbed old growth forests into younger stands, which have consequences for carbon exchange and storage (Harmon et al., 1990). However, the paradigm of age related decline in productivity is still central to forest ecology, and has been used by forest management as an argument for replacing old forests with younger even aged stands to increase forest productivity (Smith et al., 1997).

Given that the current terrestrial carbon sink is at risk due to enhanced global warming (Canadell et al., 2007), the carbon sequestration potential of many ecosystems in southern Australia may be limited due to prolonged and more frequent droughts (Murphy and Timbal, 2007) and increased fire risk (Pitman et al., 2007). In Victoria and Tasmania, *Eucalyptus regnans* (F. Muell.) or Mountain Ash forests are an important forest type, as they account for 50% of the canopy cover in water supply catchments for Melbourne, of which 15% is estimated to be old growth (Vertessy et al., 1996; Mackey et al., 2002; Keenan and Ryan, 2004). Flanagan (2007) estimated that nearly 85% of Australian old growth forests have been lost since European settlement in the 1800s, but substantial portions still remain in Victoria and Tasmania (Keenan and Ryan, 2004). However, due to their high rates of production and enormous biomass, these forests are still subject to logging in designated areas (Ashton, 2000). Growth estimates by Ashton (1976) suggest that Mountain Ash is the tallest angiosperm and one of the fastest growing trees in the world, attaining annual growth rates of more than 1 metre in height in the early stages of growth (<30 years of age). Ashton (1976) documented the growth rates of Mountain Ash stands over different ages and found that these species exhibit a decline in productivity with age. This decline is due to high levels of self-thinning in this species coupled with a 50% decline in specific leaf area between the juvenile and old growth stage (England and Attiwill, 2006). However, Ashton (1976) demonstrated that individual Mountain Ash trees continued to grow in size (height and DBH) even at 220 years of age, which may explain the status of these forests as the most carbon dense in the world (up to 2844 t C ha^{-1}; Keith et al., 2009). Although the major overstorey trees (*E. regnans*) were shown to accumulate aboveground biomass, Ashton's results do not give an indication of the whole ecosystem carbon balance. Carbon exchange from woody debris on the surface floor, below ground processes (root and microbial respiration) and fluxes associated with the understorey strata of temperate rainforest species also become increasingly significant as the Mountain Ash forests age.

The ecology and succession of Mountain Ash are reviewed by Ashton (2000). At the old growth stage, these forests are complex ecosystems characterized by variability in structure and composition, and consist of two distinctive layers, a tall (up to 100 m height) emergent overstorey of *E. regnans* trees and an understorey consisting of temperate rainforest species (Ashton, 2000). Although canopy photosynthesis mostly occurs in the overstorey and is typically a function of Leaf Area Index, photosynthetic capacity, light, temperature and moisture, very little is known about the traits and contribution of the understorey in these forests (Misson et al., 2007). Vertessy et al. (1998) elucidated critical information on the partitioning of transpiration dynamics between the overstorey and understorey strata and found that the understorey vegetation contributed roughly 45% of total ecosystem evapotranspiration (LE). This suggests the understorey component may also contribute a significant fraction of total ecosystem productivity. Jarosz et al. (2008) examined the partitioning of overstorey and understorey elements in a pine forest in France and found that understorey fluxes accounted for 38% and 25% of the annual LE and GPP respectively, which closely reflected the LAI partitioning for each strata. Subke and Tenhunen (2004) also determined similar partitioning of overstorey and understorey fluxes to LAI, where the understorey GPP accounted for 12% of the annual ecosystem GPP. These studies suggest that understorey succession may play a significant role in water and carbon exchange and budgets.

Understanding the processes that control the potential of terrestrial ecosystems to sequester carbon has been of wide interest since the implementation of biological carbon sinks in the Kyoto protocol and in future international agreements. However, old growth forests were omitted in the Bonn agreement (part 2 of the sixth Conference of the parties to the Climate Convention – COP6-2 in Bonn, July 2001) because they were assumed to be insignificant carbon sinks (Vrolijk, 2002). We therefore framed our research in terms of the following questions: (1) what are seasonal and annual patterns of carbon and water fluxes from an old growth Mountain Ash forest, and (2) how much of the total ecosystem carbon and water flux is accounted for by the understorey. This work will provide improved quantification of forest carbon sequestration and an understanding of the key processes driving carbon and water exchange in old growth forests, which will allow for better climate change mitigation strategies and frameworks to be developed and adopted.

2. Materials and methods

2.1. Site description

The study site was an old growth Mountain Ash (*E. regnans*) site located in the Wallaby Creek water catchment, Kinglake National Park, Victoria, Australia (37°25′44″ S, 145°11′14″ E). The site is situated on the southern edge of the Hume plateau (∼690 m) with a slope of ∼3°. Long term mean annual rainfall (1885–2006) is 1207 ± 21 mm year^{-1} (±SE), but for the period 1996–2006 the site has received below average rainfall with a mean of 1082 mm year^{-1} (Bureau of Meteorology, 2009). Mean monthly maximum and minimum air temperature in winter is 8 °C and 2 °C and for summer is 28 °C and 6 °C, respectively (Bureau of Meteorology, 2009). The catchment area is dominated by old growth Mountain Ash, which are the world's tallest angiosperm, and may have been the tallest tree ever recorded – measured at 133 m in 1872 (Carder, 1995). At the site, there are 37 ± 2 stems ha^{-1} of Mountain Ash, with a mean diameter at breast height (DBH) of 199 ± 8 cm and canopy height of 80 ± 5 m, though some individual trees are taller than 90 m (van Pelt et al., 2004). Below the Mountain Ash open canopy, there is a dense temperate rainforest understorey (298 ± 14 stems ha^{-1})