Forest Ecology and Management 305 (2013) 177–188

Contents lists available at SciVerse ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Full length article

Wood decay resistance moderates the effects of tree mortality on carbon storage in the indigenous forests of New Zealand

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ARTICLE INFO

Article history:
Received 13 November 2012
Received in revised form 14 May 2013
Accepted 15 May 2013
Available online 25 June 2013

Keywords:
Carbon sequestration
Coarse woody debris
Disturbance
Emissions management
Greenhouse gasses
REDD+

ABSTRACT

The maintenance of carbon (C) storage in indigenous forest is a key component of efforts to manage atmospheric carbon dioxide concentrations. Increased pressures from extreme climatic events and invasive pests and pathogens pose major threats to the future stability of C storage in indigenous forests through elevated canopy-tree mortality. We assessed the potential for interspecific differences in wood decay resistance to moderate decadal-scale net C losses following canopy tree mortality. We recorded tree mortality, growth and recruitment over a period spanning almost 40 years in repeatedly surveyed plots spanning a wide range of mortality rates. We combined these survey data with national data on species-specific wood decay resistance (i.e. retention of wood density) to estimate contemporary C lost through decay of trees that died during our study. We also included C losses from CWD contributed by a major synchronous mortality event before the study period (legacy CWD C loss) for a subset of the plots where CWD C storage measurements were available. C flux from live to dead biomass (1.36 Mg ha^{-1} year^{-1}, s.e. 0.16) was the main factor influencing estimated net contemporary changes in C storage, with the largest net contemporary C losses (−1.5 Mg ha^{-1} year^{-1}) observed in plots experiencing high mortality. Estimated net contemporary C loss from tree mortality was reduced when the dominant species had highly decay-resistant wood. The ability to predict contemporary changes in C was significantly improved when a plot-level indicator of CWD decay resistance was included in multiple regressions. Mean legacy CWD C loss was 0.39 Mg ha^{-1} year^{-1}, s.e. 0.16. When legacy losses were incorporated in net C change estimates, both the size of the legacy CWD pool and its interaction with legacy CWD decay resistance explained a significant amount of variation in net C change in multiple regressions. In plots losing large (around 3 Mg ha^{-1} year^{-1}) amounts of C from live biomass (or with more than 300 Mg ha^{-1} C stored in legacy CWD at the start of the study) wood decay resistance altered the net C balance by as much as 1.11 Mg ha^{-1} year^{-1}, which is a considerable effect given that the mean annual C assimilation rate across plots was 1.38 Mg ha^{-1} year^{-1}. Thus, our study reveals strong potential for interspecific variation in decay resistance to moderate the impact of canopy tree mortality on C storage in forests. We suggest that research effort on wood decay rates should be prioritised toward areas, such as drought-prone regions of Amazonia, where forests are likely to experience synchronous mortality events more frequently in future.

1. Introduction

Carbon (C) storage in indigenous (i.e. non-plantation) forests is a key component of efforts to manage atmospheric carbon dioxide (CO_2) concentrations (e.g. Nabuurs et al., 2003; Pan et al., 2011), and underpins international mechanisms such as the REDD+(Reducing Emissions from Deforestation and forest Degradation) programme, which has a particular focus on the role of conservation, sustainable management of forests and enhancement of forest carbon stocks in developing countries. However, the increasing frequency of extreme climatic events associated with global climate change is likely to increase mortality rates of canopy trees in indigenous forests (Chambers et al., 2007; Phillips et al., 2009; van Mantgem et al., 2009). Evidence suggests that climate change is also likely to increase both the variety and intensity of attacks by pests and pathogens, resulting in elevated canopy tree mortality rates (Logan et al., 2003; Lovett et al., 2006; Kurz et al., 2008). Therefore we need to know the implications of elevated

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http://dx.doi.org/10.1016/j.foreco.2013.05.028

Fig. 1. An example of legacy coarse woody debris (CWD) emergent above forest in the Kokatahi River valley in 1996. The standing dead trees pictured are all *Metrosideros umbellata* that died in the 1950s. Photograph supplied by Peter Bellingham.

mortality rates for C storage in indigenous forests, especially the degree to which C loss due to mortality might be mitigated by tree growth and recruitment as forests regenerate (Coomes et al., 2012) and by the decay resistance of coarse woody debris (CWD) (Rubino and McCarthy, 2003; Grove et al., 2009). Synchronous canopy tree mortality events obviously result in multi-decadal loss of C from live biomass (e.g. Bradford et al., 2008; Coomes et al., 2012), and we know that the decay resistance of wood entering the detritus pool may vary considerably among sites and tree species (Harmon et al., 1995; Yatskov et al., 2003; Cornwell et al., 2009). However, there has been little work quantifying the effect of differences in wood decay resistance on C storage after disturbance. This study assesses the potential for interspecific differences in wood decay resistance to influence the effects of canopy tree mortality on C storage in indigenous forests.

1.1. Mortality, growth, decomposition and stability of C storage

The vast majority of C in the live biomass pool of forests is usually contributed by canopy trees (e.g. Mason et al., 2012), and this C is typically accumulated over several centuries. Forest C fluxes have long been characterised as "slow in, rapid out" (Körner, 2003), with centuries' worth of C sequestration fluxing from live to dead biomass during major canopy disturbance, and with live biomass being replaced only gradually through growth of surviving individuals and recruitment after disturbance. Carbon entering the dead pool is often accounted for as committed C loss from the ecosystem (e.g. Chambers et al., 2007). However, tree species differ markedly in the rate at which their wood decays once it enters the dead biomass pool (Chave et al., 2006; Weedon et al., 2009), and this interspecific variation in decay rates could have significant implications for the impact of canopy tree mortality on C storage. Where the flux of C from live to dead biomass pools is dominated by species with rapidly decaying wood, rates of C loss due to mortality should be high. On the other hand, mortality of trees with highly decay resistant wood may cause a large proportion of the C transitioning from live to dead biomass pools to be stored for many decades (Rubino and McCarthy, 2003; Grove et al., 2009). However, while it has often been asserted that variation in wood decay resistance could have a large effect on C storage stability after widespread canopy tree mortality, there is a lack of work quantifying this effect (Peltzer et al., 2010).

Tree mortality rates, and hence the flux of C into the dead biomass pool caused by abiotic (e.g. storms, earthquakes and droughts) and biotic (e.g. pests and pathogens) factors, can vary widely for a number of reasons. Mortality caused by a storm event depends on disturbance severity, topographic exposure and stand structure (Boose et al., 1994; Bellingham and Tanner, 2000; Chambers et al., 2007). Pests alone may often merely cause chronic morbidity in trees, only inducing mortality in individuals occurring on vulnerable sites during extreme climatic events, such as drought (Cowan et al., 1997; Lovett et al., 2006). Mortality rates due to pathogens are highly dependent on resistance levels in tree populations (Lovett et al., 2006). This stochasticity makes it extremely difficult to explicitly include canopy tree mortality in forest dynamics models. However, examination of various rates of mortality and C flux from live to dead biomass allows us to at least discern the degree to which the severity of a mortality event influences changes in C storage. Repeatedly surveyed forest plots with varying tree mortality rates provide an excellent opportunity to do this (Coomes et al., 2012).

1.2. Aims and objectives

Our study focuses on montane rain forests in New Zealand that contain mixtures of two dominant canopy trees with vastly different wood decay resistance (Coomes et al., 2002) – the rapidly decaying *Weinmannia racemosa* L.f. (Cunoniaceae) and the highly decay resistant *Metrosideros umbellata* Cav. (Myrtaceae). These forests experienced synchronous canopy tree mortality during the 1950s (partly due to browsing by the invasive brushtail possum, *Trichosurus vulpecula*; Allen and Rose, 1983; Rose et al., 1992) with isolated canopy dieback occurring since this main mortality event. The relative abundance of these dominant species varies considerably within our study area (Reif and Allen, 1988). This provides an excellent opportunity to assess the potential for variation in wood decay resistance and C-sequestration rates to influence C storage stability during a major mortality event. We use repeated surveys of permanent forest plots to estimate the total flux of C from live trees to dead biomass (dead flux C) and coarse woody debris (i.e. standing dead or fallen trunks >10 cm in diameter and of any length, CWD flux C), and C gain through tree growth and recruitment. We estimate species-specific decay resistance using data on wood density in live trees and CWD logs of known ages collected from forests throughout New Zealand (aged using plot survey data from the National Vegetation Survey Databank, NVS, http://nvs.landcareresearch.co.nz/). We combine these national estimates of species-specific decay resistance with our repeated forest plot measurements to estimate C losses though decay of trees dying during our study. We also use measurements of CWD on our plots to estimate the impact of C losses from CWD contributed by trees that died before the start of the study period (legacy CWD C loss). In doing this, we aim to determine the relative influence of C fluxes from live to dead biomass, CWD decay resistance, and C gain through tree growth and recruitment on estimated changes in C storage (in both live biomass and CWD) over a period of nearly 40 years. Ultimately, we aim to assess the resilience of C storage in response to widespread canopy tree mortality, and the effect of growth and CWD decay resistance on C storage stability.

2. Materials and methods

2.1. Study area

The study site comprises two approximately 10-km^2 areas within the Hokitika River catchment (the Whitcombe and Kokatahi River valleys), western South Island, New Zealand. The area has a high rate of geological uplift (>10 mm year^{-1}; Whitehouse, 1988), with high rates of erosion and periodic (i.e. once every