



Review and synthesis

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ABSTRACT

With an increasing fraction of the world's forests being intensively managed for meeting humanity's need for wood, fiber and ecosystem services, quantitative understanding of the functional changes in these ecosystems in comparison with natural forests is needed. In particular, the role of managed forests as long-term carbon (C) sinks and for mitigating climate change require a detailed assessment of their carbon cycle on different temporal scales. In the current review we assess available data on the structure and function of the world's forests, explore the main differences in the C exchange between managed and unmanaged stands, and explore potential physiological mechanisms behind both observed and expected changes. Two global databases that include classification for management indicate that managed forests are about 50 years younger, include 25% more coniferous stands, and have about 50% lower C stocks than unmanaged forests. The gross primary productivity (GPP) and total net primary productivity (NPP) are the similar, but relatively more of the assimilated carbon is allocated to aboveground pools in managed than in unmanaged forests, whereas allocation to fine roots and rhizosymbionts is lower. This shift in allocation patterns is promoted by increasing plant size, and by increased nutrient availability. Long-term carbon sequestration potential in soils is assessed through the ratio of heterotrophic respiration to total detritus production, which indicates that (i) the forest soils may be losing more carbon on an annual basis than they regain in detritus, and (ii) the deficit appears to be greater in managed forests. While climate change and management factors (esp. fertilization) both contribute to greater carbon accumulation potential in the soil, the harvest-related increase in decomposition affects the C budget over the entire harvest cycle. Although the findings do not preclude the use of forests for climate mitigation, maximizing merchantable productivity may have significant carbon costs for the soil pool. We conclude that optimal management strategies for maximizing multiple benefits from ecosystem services require better understanding of the dynamics of belowground allocation, carbohydrate availability, heterotrophic respiration, and carbon stabilization in the soil.

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1. Background: the role of managed forests in land surface carbon exchange

Increasing global population and expanding land use mean that an ever greater percentage of human need for wood products is being met by managed forests (Foley et al., 2005; see Section 2.1 for definitions). Currently, about 7% of world's forests are plantations and 57% are secondary forests recovering from anthropogenic disturbance (FAO, 2010). From 2000 to 2005 the rate of increase in the area of planted forests was 2% yr⁻¹ and is accelerating (FAO, 2009), whereas total forest area decreased at a rate of about 2% per decade. A recent analysis of Landsat TM data series concluded that forest use is intensifying in time (Hansen et al., 2013). For example, 30% of the forestland in the southeastern US was harvested and re-grown between 2000 and 2012. While the exact interplay between factors effecting forest cover change vary by region, and can respond to both local development and global economic forces (Drummond and Loveland, 2010), the trends described above are likely to continue unless the valuation of forest products and services changes dramatically.

As the primary metric of a forest's value has been its merchantable volume, plantation forestry has long selected species and genotypes to maximize productivity. For the most intensively studied species, such as loblolly pine (*Pinus taeda*), it has been estimated that a typical plantation is about 3–5 times more productive than a natural stand, and that growth gains of up to 20-fold can be achieved in intensive culture and outside the species' natural range (Cubbage et al., 2007; Ryan et al., 2010). Fox et al. (2007a) estimated that, on average, the productivity of commercial *P. taeda* plantations is more than 4-fold higher than of natural *P. taeda* stands, with planting, site preparation, competition control, fertilization and genetic improvement contributing 13%, 10%, 13%, 17% and 23% of the total productivity, respectively. The productivity of eucalypts in Brazil has nearly doubled over the past 20 years, owing to intensive management techniques (Goncalves et al., 2013). However, in global databases the management effects are confounded with temperature (Litton et al., 2007), and it remains unclear, whether or how the contribution of forests to global C cycling may change with their transition from natural to managed state (Piao et al., 2009; Stinson et al., 2011). It is the goal of the current study to review the evidence of the effects of management-induced changes on the shifting background driven by climate change factors, so as to allow for an improved mechanistic understanding of the causes of differences between the forests of the pasts and those of the future.

Of the explicit management-related effects, the increased frequency of disturbance makes for a very dynamic and rapidly changing biogeochemical exchange, such that where age-related variability may be the predominant source of spatial variation (Desai et al., 2008), which on the global scale explains more than 90% of the variability in net ecosystem productivity (NEP; Pregitzer and Euskirchen, 2004). Furthermore, much of the high productivity of the forests in eastern USA over the past half a century is attributed to the wide-spread conversion of forests to and later abandonment from agricultural use (Birdsey et al., 2006). The aggradation effect has been amplified by global change factors like increasing CO₂ concentration, temperature and nitrogen deposition, but harvesting and age-related recovery dominate as drivers of C fluxes in comparison with resource availability and genetic factors.

There are significant changes in forest structural and functional traits as related to age (Law et al., 2001a,b; Noormets et al., 2006, 2007), which have been recognized as having far greater influence on forest productivity and C exchange than climate (King et al., 1999a; Pregitzer and Euskirchen, 2004; Magnani et al., 2007). However, it is not only productivity that is altered during the harvesting and management cycle. Long-term accumulation/sequestration of carbon in the ecosystem is determined by the magnitude and types of input (which is part of the management strategy), and the magnitude and pathway of losses, which in turn depend on various C stabilization mechanisms. The allocation of carbon to the production of different organs changes dramatically during stand development, with greater allocation belowground early in the development (King et al., 1999a, 2007; Genet et al., 2010). Second, the stimulation of ecosystem respiratory losses following a harvest is well documented, and results from a number of causes, including (i) disturbance of soil (Diochon and Kellman, 2008; Diochon et al., 2009; Diochon and Kellman, 2009), (ii) production of large amount of dead biomass (Harmon et al., 1986), (iii) change in the stoichiometry of carbon pools (Harmon et al., 2011), (iv) changes in the C:N stoichiometry of the detritus, and (v) changes in the microclimate (Chen et al., 1993; Noormets et al., 2007). These changes have both short- and long-term consequences, as they affect both the pool sizes, and fluxes of carbon between these pools. However, the decomposition of harvest residues sustains both tree growth and soil properties (Laclau et al., 2010; Versini et al., 2013) and thus contributes to maintaining ecosystem C stocks (Huang et al., 2013). As none of these effects are included in the global land surface models, their estimates of allometric proportions between different C pools are often inconsistent with observations (Wolf et al., 2011a and

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