

TRADE-OFF BETWEEN FOREST PRODUCTIVITY AND CARBON SEQUESTRATION IN SOIL

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With the growing fraction of the world's forests being intensively managed plantations, these ecosystems will increasingly be relied upon to provide other ecosystem services, in addition to merchantable timber. Schemes proposing the use of managed forests to mitigate climate change by sequestering carbon, however, are yet to be tested for feasibility and cost. In the current study we will review literature on forest responses to key climate and management factors on the inputs and outputs to the soil C pool in the context of expected changes under management. Recent global reviews indicate that there are distinct tradeoffs in allocation of assimilated carbon to different plant parts with productivity, and that the greater aboveground productivity comes on the account of belowground allocation, particularly on account of fine roots. Despite the proportional decrease in belowground fluxes in proportion to GPP, the absolute respiration fluxes are higher in managed than unmanaged forests, resulting in greater soil C loss. The balance between annual soil C inputs (leaf and fine root production plus mortality of tissue) and losses (soil heterotrophic respiration) indicates that while the imbalance is global, it is greater in the more productive managed than unmanaged forests. This shift triggered by high productivity exaggerates the elevated respiration losses caused by the greater frequency of harvests and physical disturbance of soil, outlining the greater vulnerability of soil C in managed forests.

Increasing global population and expanding land use mean that an ever greater percentage of human needs for wood products is being met by managed forests (Birdsey and Pan 2015, Foley and others 2005, Hansen and others 2013). Currently, about 7 percent of world's forests are plantations and 57 percent 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 percent yr⁻¹ and is accelerating (FAO 2009), whereas total forest area decreased at a rate of about 2 percent per decade. The intensive management practices developed over the past 5 decades have increased productivity of some plantation species by nearly 5-fold (Fox and others 2007), whereas the background increase globally is estimated 15-20

percent over the past century, attributable to forest regrowth, increased atmospheric CO₂ and N deposition (Friedlingstein and others 2006, Piao and others 2011). Whether these changes translate long-term carbon sequestration depends on the allocation and chemical composition of the material, as well as the activity of heterotrophs that decompose the plant-derived detritus. Recent analyses highlight global patterns in allometry, whereby larger and faster growing trees shift their allocation patterns over different phases of canopy development (Chen and others 2013), which differ between natural and managed forests (Noormets and others 2015). Furthermore, there is growing evidence suggesting a decline in soil C pool in the world's forests, particularly in intensively managed plantations (Noormets and others 2015, Noormets and Nouvellon 2015). However, quantitative information about the role of forest management in this remains limited, and further explicit tests and improved understanding of belowground carbon dynamics are required. Although managed have both smaller soil C pool and higher Rh (Noormets and others 2015), the functional relationship to plant allocation and specific management practices is unclear and needs to be elucidated. In the current study, we will explore the relationship between soil C loss as quantified with heterotrophic respiration and belowground productivity.

This study is based on the literature review and the analysis of two global databases published earlier (Noormets and others 2015). The databases include the soil respiration database (SRDB) (Bond-Lamberty and Thomson 2010) and NPP database (Luyssaert and others 2009).

Soil C losses through heterotrophic respiration (Rh) increased in proportion with productivity, whether expressed on total or belowground basis (fig. 1). Although proportional allocation shifts with increasing plant size and NPP in favor of woody tissues and foliage, and away from fine roots (Chen and others 2013), BNPP may increase in absolute terms due to isometric effects. The increase in BNPP brings with it an increase in Rh (fig. 1, top), as a fraction of belowground allocation supports root exudation and the activity of

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Citation for proceedings: Schweitzer, Callie J.; Clatterbuck, Wayne K.; Oswalt, Christopher M., eds. 2016. Proceedings of the 18th biennial southern silvicultural research conference. e-Gen. Tech. Rep. SRS-212. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station. 614 p.

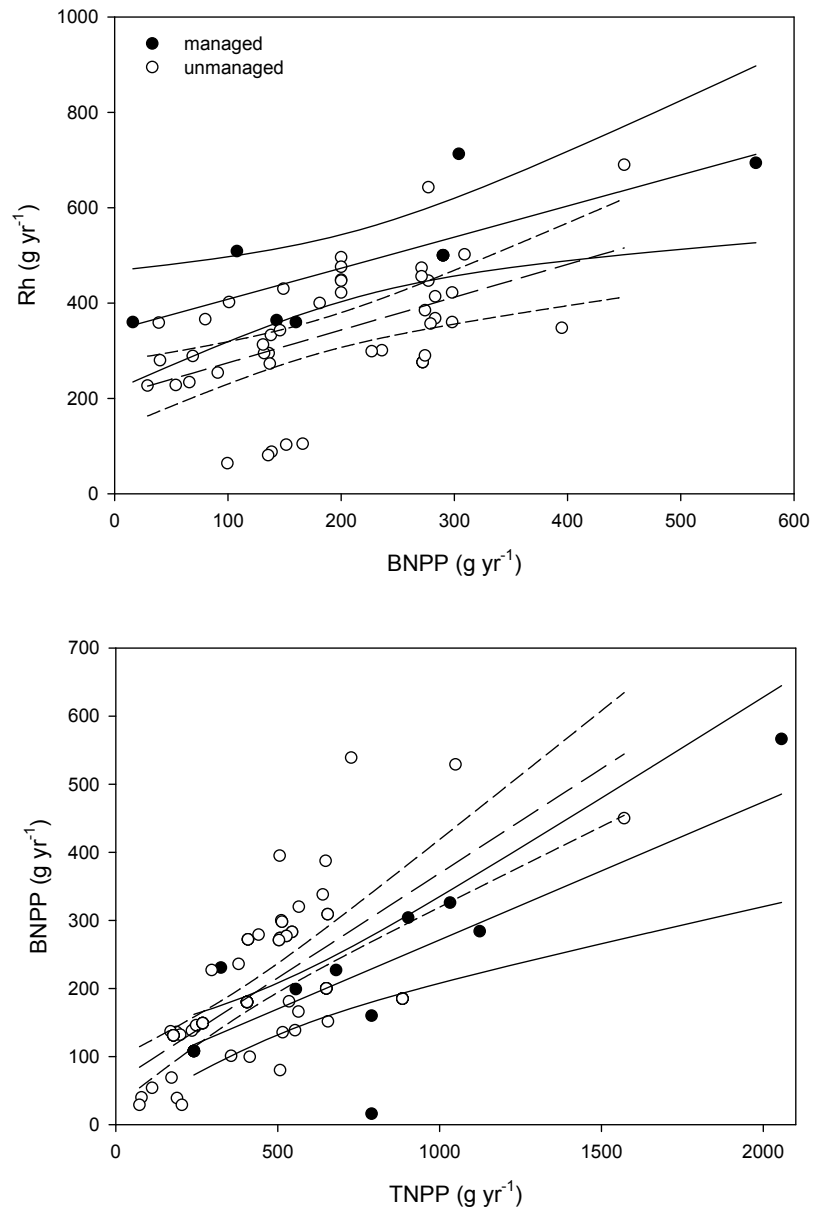


Figure 1—Top: The relationship between heterotrophic respiration (Rh) and belowground net primary production (BNPP) in managed (filled symbols and solid lines) and unmanaged (open symbols and dashed lines) temperate forests. Bottom: Relationship between BNPP and total net primary production (TNPP) in managed and unmanaged temperate forests. The linear regression fits include 95% confidence.

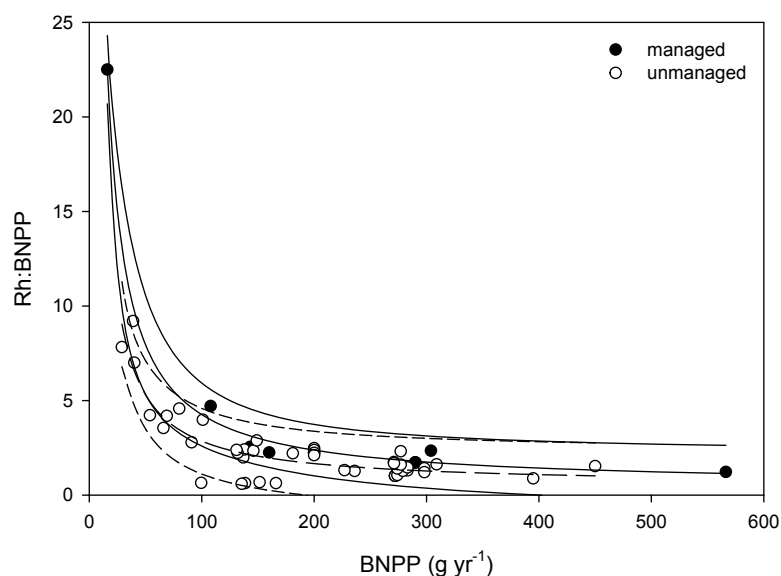


Figure 2—The relationship between the ratio of heterotrophic respiration to belowground net primary production (Rh:BNPP) to BNPP in managed (filled symbols and solid lines) and unmanaged (open symbols and dashed lines) temperate forests. The inverse second order polynomial models are plotted with 95% confidence intervals.

both root-associated and free-living microbes. This observation is consistent with the report by Chen and others (2014). Furthermore, Chen and others (2014) also showed that as the ratio of Rh:GPP (gross primary production) decreased with increasing productivity, that of root respiration increased.

Given the dependence of both belowground allocation and root exudation, as well as of microbial activity and Rh on GPP-derived carbohydrate substrates, respiration and GPP interact through both positive and negative feedback loops (Chen and others 2014, Noormets and others 2015). Despite lower proportional allocation to BNPP (fig. 1, bottom) the overall Rh was about 150 g m⁻² yr⁻¹ greater in managed than unmanaged forests (fig. 1, top). The ratio of Rh:BNPP decreased with BNPP, particularly at low productivity levels (young, recently disturbed stands), but still exceeded unity in most stands, even at high BNPP (fig. 2). Notably, even though Rh overall was higher in managed than unmanaged forests (fig. 1, top), the ratio of Rh:BNPP did not clearly differ by management status in any but the youngest stands (fig. 2).

These findings indicate that factors that contribute to increased Rh can lead to a decline in soil C, and that unadjusted Rh was greater in managed than unmanaged forests. On the other hand, managed forests that receive fertilizer inputs, have also been reported to have lower fine root production and exudation to the rhizosphere (Janssens and

Luysaert 2009, Maier and others 2004), which in turn suppresses microbial activity and reduces Rh (Fog 1988, Högberg and others 2003, Janssens and others 2010). As the result of the combined effect of increased photosynthesis, decreased belowground allocation and decreased root respiration, higher nutrient availability results in higher biomass production efficiency (defined as the ratio of NPP to GPP) (Vicca and others 2012). Consequently, managed forests may potentially sequester greater amounts of carbon belowground than their unmanaged counterparts (Noormets and others 2015), provided that the ongoing losses through Rh are offset by the harvest residue input at the end of the rotation cycle.

Factors contributing to increased productivity also increase belowground carbon flux and Rh. The observed net change reflects the counteracting effects of shifts in allocation patterns and isometric increases in absolute fluxes. Altered allocation patterns in managed forests decrease detritus production, as the improved nutrient availability and genetic selection favor preferential allocation to woody tissues and foliage over fine roots and root exudation. The isometric increase in total belowground C flux, on the other hand, may promote Rh through priming. The greatest contributor to Rh, however, is the harvest-related disturbance. The realized carbon sequestration in managed forests depends on the extent to which the effect of management activities on Rh can be minimized.

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