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Review and synthesis

Effects of forest management on productivity and carbon sequestration: A review and hypothesis ☆

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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.

Contents

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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 CO_2 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 references therein), particularly in the young stands, and the allocation patterns may be outside the range of data (Malhi et al., 2011). Although the process-level understanding of carbon partitioning has made strides in the past decade (section: soil carbon dynamics), a cohesive modeling framework that would tie them all together is yet to emerge (Franklin et al., 2012). Chen et al. (2014) analyzed a number of global ecosystem models, and traced the allocation submodels back to that used by Friedlingstein et al. (1999), who had acknowledged that the modeled biomass estimates were very sensitive to the allocation algorithms used – with nearly 6-fold range in the root:shoot ratio at low-NPP sites. Thus, it is critical that the dynamic responses in allocation, and disturbance-related changes in different C fluxes be realistically depicted in land-surface models.

Given the regular removal of stemwood during harvests, long-term carbon sequestration at the site can occur only in the soil and detritus (assuming fixed land use type, and stable mean aboveground biomass). A growing number of recent reviews have pointed to declining soil C stocks across the world (Bellamy et al., 2005; Xie et al., 2007), and the phenomenon is mostly attributed to land use change and intensive agriculture (Maia et al., 2010; Don et al., 2011; Yan et al., 2011). As forest management, too, represents intensified land use, its effects on soil C dynamics need to be understood. In an earlier study about the balance between detritus inputs to and heterotrophic respiration losses from soil and detritus pools in a loblolly pine chronosequence (Noormets et al., 2012), we reported that Rh exceeded detritus inputs on year-to-year basis, and that the pulse of harvest residue may have barely offset those losses, if at all. We also showed that the ratio of respiration fluxes to gross primary productivity can serve as an indicator of the carbon sequestration potential, but much remains unknown about the magnitude and temporal dynamics of different components of respiration. Although both heterotrophic respiration (Rh) and the ratio of autotrophic respiration to gross primary productivity (Ra:GPP) are quite conservative across sites (Gifford, 1994, 1995; Tjoelker et al., 1999; Templeton et al., 2015 2015), there is growing evidence of interannual variability in response to climate fluctuations and resource availability. There may also be a latitudinal gradient in Rh, possibly controlled by differences in belowground allocation and priming of soil C mineralization (de Vries, 2014). In fact, it has been hypothesized that the latitudinal gradient of NEP in European forests may be driven by higher Rh at higher latitudes (Valentini et al., 2000). It remains unclear to what extent the patterns in Rh are driven by GPP, but correlative evidence does suggest dependence for both ecosystem respiration (Re) and soil respiration (Rs) (Tang et al., 2005; Vickers et al., 2009 and references therein). It is curious that the continental patterns support this substrate-limitation model as proposed by Dewar et al. (1999), even though the vast majority of upscaled respiration estimates today have been derived through the admittedly imperfect temperature-based models (Vargas et al., 2011). As the effect of the choice of a particular respiration model on Ra and NPP (and likely on carbon sequestration) can be significant (Kruijt et al., 2004; Wythers et al., 2005), it is critical that we refine the functional relationship between productivity and respiration in the ecosystem and land surface models, and properly characterize the key mechanisms affecting forest productivity and carbon sequestration. While well recognized, the GPP–Re relationship has been viewed cautiously among the eddy covariance community, because of the different assumptions involved and the interdependence of respiration and GPP estimates (Kruijt et al., 2004; DeLucia et al., 2007; Vickers et al., 2009; Lasslop et al., 2010). Nevertheless, conceptually these two fluxes are related to one another, defining ecosystem's carbon storage capacity, and it is only a question of how, not whether, to include the link explicitly in models.

The main management practices that have been identified as contributing to improved productivity (Fox et al., 2007a; Goncalves et al., 2013; see above) were reclassified in the current study as disturbance (later divided further into structural and soil disturbance), nutrition, and genetic factors (Fig. 1). Their effect on soil carbon sequestration (or sequestration potential, as we do not consider the soil properties here) is expected to manifest through the following processes: (1) more frequent disturbance through harvesting and site preparation stimulates heterotrophic decomposition; (2) shorter disturbance interval makes the stand spend relatively more time in the post-disturbance recovery phase; (3) the altered allocation patterns by the selected species and genotypes and in response to nutrient availability may alter biomass partitioning, soil C inputs and the balance between auto- and heterotrophic

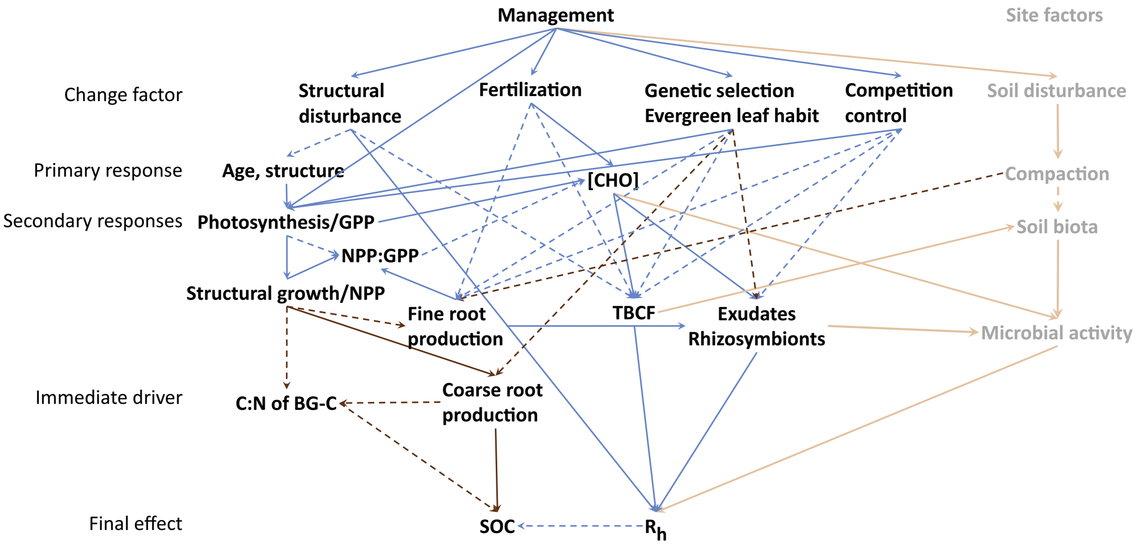

Fig. 1. Flow chart of management effects on forest productivity and carbon sequestration. Solid arrows indicate positive effect, and dashed arrows negative. Brown arrows mark processes affecting the recalcitrance of soil carbon. Orange arrows mark processes operating through soil disturbance that in the current study are discussed only superficially. Abbreviations: GPP – gross primary productivity, NPP – net primary productivity, [CHO] – carbohydrate concentration, TBCF – total belowground carbon flux, C:N – the ratio of carbon to nitrogen, BG-C – belowground carbon, SOC – soil organic carbon, R_h – heterotrophic respiration. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 1
Global datasets relevant for addressing questions of productivity and carbon sequestration in managed forests. Abbreviations: NEE – net ecosystem exchange of CO_2, Re – ecosystem respiration, GEP – gross ecosystem productivity, Rs – soil CO_2 efflux, Rh – heterotrophic component of Rs, Ra – autotrophic component of Rs, [C] – carbon content, TBCF – total belowground carbon flux (estimated as the difference between Rs and aboveground litterfall), NPP – net primary productivity, ANPP – aboveground net primary productivity, *R* – respiration.

Database	Temporal coverage	Key data	Source	Comments
FLUXNET	1990–2007 active	NEE	Baldocchi et al. (2001)	Limited management metadata
		Re		
		GEP		
SRDB (version 20120510a)	1953–2011 active	Rs, Rh, Ra, [C]	Bond-Lamberty and Thomson (2010a)	3 management classes
		Litterfall		
		Root biomass		
		TBCF		
NPP	1960–2006	NPP by component Rs, Rh, Ra	Luyssaert et al. (2007)	6 management classes
TBCF	1969–2006	ANPP (total, wood, foliage)	Litton et al. (2007)	No management metadata
		R (total, wood, foliage)		Age relationships
		TBCF, GEP		
GlobAllomeTree	Active	Allometric partitioning coefficients	http://www.globallometree.org/	No management metadata
FIA database (USA only)	1930-current active	Carbon pools, stand metadata, land use history	http://www.fia.fs.fed.us/	Detailed management and site history data

respiration; and (4) the changes in allocation may affect LAI:sapwood area ratio, and may thus change plant water dynamics and drought sensitivity. Specifically, the goals of this study are to review (i) available information on the controls of photosynthetic carbon gain, allocation, and respiration in forest ecosystems, (ii) the responses of these processes to disturbance and management-related drivers, (iii) evaluate the consistency of observations with broader evidence of physiological responses to management-related changes in site conditions, and (iv) assess opportunities for and obstacles to managing forests for long-term C sequestration.

2. Methods

2.1. Defining “managed forests”

Human activities have dramatically altered the environment, including the biogeochemical cycling of major elements (Schlesinger, 1997), which affects the growth and productivity of forests. Factors like temperature, CO_2 concentration and nitrogen deposition undoubtedly have large effects on forests (Caspersen et al., 2000; Magnani et al., 2007). Although these changes affect both natural and managed forests, the productivity of managed forests may already be maximized for a given temperature regime (Litton and Giardina, 2008), possibly leaving less room for further increase (Wynne, Burkard, Evans, personal communication).

Human influences on forests span a continuum, from assisted regeneration to intensive culture with regular irrigation, fertilizer application and competition control (Fox et al., 2007a; FAO, 2009), and the predominance of different practices may vary by region and over time. Therefore, the terminology across and between large datasets may not always be consistent, yet uniformity is essential for attribution of effects to specific management practices. For example, the forest NPP database (Luyssaert et al., 2007) includes more detailed management information than many others (including 6 primary categories: managed, unmanaged, recently disturbed, fertilized and irrigated, polluted, and no information). Of these, the managed, recently disturbed or unmanaged categories can each include plantations and burned stands. Thus, it is possible that despite the best efforts of database builders, the delineation between the categories may not always be clear or consistent, possibly confounding the detection of patterns. For the purposes of the current review, it is practical to define “managed forests” as those with active cultivation practices and preplanned rotation cycles, and fall under “planted forests” and “managed natural forests” in FAO classification (FAO, 2010; Birdsey and Pan, 2015). The discussion is focused on aspects that are modified by management activities and that are expected to affect productivity, heterotrophic respiration and soil C pool (Fig. 1).

2.2. Literature review

Developing a conceptual map of management effects on forest productivity and carbon sequestration as a guide (Fig. 1), we review the current knowledge of the individual driving factors on stand productivity and carbon sequestration.

2.3. Global datasets

The compilation of different global datasets (Table 1) over the past decade has created unprecedented opportunities to ask questions about difficult-to-measure processes at a global scale. While some of the earlier analyses (Litton et al., 2007) have considered some individual management activities as factors when analyzing the variance of pools or fluxes, the definition of “managed forest” varies widely across databases and analyses (see Section 2.1). In fact, only a fraction of the essential metadata about the effect of human activities of ecosystem processes is classified in these datasets.

However, understanding of how land–atmosphere interactions may change with the gradual transition from predominantly natural to intensively managed forests remains unclear. Here we will use two datasets that include explicit categorization of forests to “managed” and “unmanaged” or “natural” ones. We will not assess changes over time, though a land cover change, but simply compare forests based on their management status. Combining stands with different ages and land use histories smoothes over these drivers of variance, and will have to be considered when interpreting the results. The Global Soil Respiration Database (Bond-Lamberty and Thomson, 2010a) and Global Forest Ecosystem Structure and Function Data for Carbon Balance Research (Luyssaert et al., 2009) contain similar data and allow testing of broad hypotheses, and identify other data and knowledge gaps. With improved mechanistic models, more insight may be gained through proxies (such as age and LAI) that covary with management activities and are widely available. Specifically, we evaluate the consistency of explicit management-status based differences in C allocation with the general patterns reported above. Second, we will evaluate the carbon sequestration potential in the soil, and how it differs by management status by using the ratio of Rh:Detritus production, which summarizes carbon balance on annual scale.

Table 2
Global mean (±SE) carbon pools, fluxes and their ratios in managed and unmanaged forests. The significance of the differences is indicated with the superscript letters, and is considered significant at $p < 0.05$ level. The analyses were based on the NPP (Luyssaert et al., 2009) and SRDB (Bond-Lamberty and Thomson, 2010a) databases.

Database	NPP		SRDB	
Metric (C pool, flux or flux ratio)	Managed	Unmanaged	Managed	Unmanaged
Aboveground biomass carbon (g m^{-2})	n/a	n/a	3465 ± 1104^{b}	8870 ± 1042^{a}
Belowground biomass carbon (g m^{-2})	n/a	n/a	821 ± 249^{b}	1463 ± 178^{a}
Coarse root carbon (g m^{-2})	n/a	n/a	515 ± 191^{a}	599 ± 189^{a}
Fine root carbon (g m^{-2})	n/a	n/a	235 ± 197^{b}	439 ± 176^{a}
Litter carbon (g m^{-2})	n/a	n/a	1164 ± 366^{a}	1764 ± 258^{a}
Mineral soil carbon (g m^{-2})	n/a	n/a	6246 ± 1749^{b}	11356 ± 1305^{a}
LAI (m^{2} m^{-2})	n/a	n/a	3.4 ± 0.3^{b}	4.5 ± 0.2^{a}
Mean tree age (yr)	n/a	n/a	21 ± 3^{b}	68 ± 3^{a}
GPP (g C m^{-2} yr^{-1})	1817 ± 32^{a}	1806 ± 41^{a}	1989 ± 169^{a}	1887 ± 159^{a}
TNPP (g C m^{-2} yr^{-1})	668 ± 65^{a}	675 ± 68^{a}	674 ± 75^{a}	595 ± 32^{a}
NPPstem (g C m^{-2} yr^{-1})	196 ± 33^{a}	170 ± 35^{a}	n/a	n/a
NPPfr (g C m^{-2} yr^{-1})	n/a	n/a	181 ± 18^{b}	225 ± 13^{a}
ANPP (g C m^{-2} yr^{-1})	365 ± 51^{a}	357 ± 54^{a}	651 ± 51^{a}	373 ± 41^{b}
BNPP (g C m^{-2} yr^{-1})	n/a	n/a	171 ± 21^{a}	173 ± 17^{a}
NEP (g C m^{-2} yr^{-1})	261 ± 16^{a}	176 ± 22^{b}	444 ± 84^{a}	300 ± 84^{b}
Litter production (g C m^{-2} yr^{-1})	n/a	n/a	210 ± 11^{a}	221 ± 9.6^{a}
Root litter production (g C m^{-2} yr^{-1})	n/a	n/a	178 ± 35^{a}	225 ± 28^{a}
Total detritus production (g C m^{-2} yr^{-1})	n/a	n/a	377 ± 43^{b}	491 ± 35^{a}
Re (g C m^{-2} yr^{-1})	1562 ± 27^{a}	1617 ± 35^{a}	1698 ± 94^{a}	1384 ± 80^{b}
Ra$_{total}$ (g C m^{-2} yr^{-1})	1133 ± 102^{b}	1460 ± 112^{a}	n/a	n/a
Ra$_{soil}$ (g C m^{-2} yr^{-1})	n/a	n/a	457 ± 66^{a}	377 ± 66^{b}
Rh$_{total}$ (g C m^{-2} yr^{-1})	471 ± 29^{b}	558 ± 34^{a}	n/a	n/a
Rh$_{soil}$ (g C m^{-2} yr^{-1})	n/a	n/a	499 ± 40^{a}	458 ± 40^{a}
Rs (g C m^{-2} yr^{-1})	923 ± 46^{a}	1013 ± 61^{a}	1006 ± 39^{a}	834 ± 33^{b}
Rlitter (g C m^{-2} yr^{-1})	n/a	n/a	220 ± 33^{b}	308 ± 32^{a}
TBCF (g C m^{-2} yr^{-1})	n/a	n/a	531 ± 111^{a}	561 ± 97^{a}
BGA (BNPP:TNPP)	0.37 ± 0.04^{a}	0.33 ± 0.04^{a}	n/a	n/a
Rh:Litter_flux (unitless)	4.3 ± 2.4^{a}	2.2 ± 2.4^{a}	n/a	n/a
Rlitter:Litter_flux (unitless)	n/a	n/a	0.83 ± 0.11^{b}	1.20 ± 0.07^{a}
Rh:Detritus1 (unitless)[1]	1.4 ± 0.5^{a}	1.5 ± 0.6^{a}	3.4 ± 2.0^{a}	2.8 ± 1.6^{a}
Detritus = [leaves, fine roots]				
Rh:Detritus2 (unitless)[1]	1.0 ± 0.4^{a}	1.0 ± 0.5^{a}	n/a	n/a
Detritus = [leaves, fine and coarse roots]				
Rh:Total detritus flux (unitless)[1]	n/a	n/a	4.4 ± 2.3^{a}	3.8 ± 1.4^{a}
Soil C balance = Detritus1-Rh (g C m^{-2} yr^{-1})	−221 ± 42^{a}	−311 ± 44^{b}	n/a	n/a
Soil C balance = Detritus2–Rh (g C m^{-2} yr^{-1})	20 ± 43^{a}	−55 ± 53^{b}	n/a	n/a
Soil C balance = Total detritus flux–Rh (g C m^{-2} yr^{-1})	n/a	n/a	−214 ± 48^{b}	−114 ± 30^{a}

[1] Detritus1 and Detritus2 were calculated from leaf and root litter production estimates reported in the databases. Total detritus flux is the value reported as the total in SRDB.

2.4. Data coverage and analyses

Of the 4707 data points in the SRDB, 2986 were forests, and 877 of them were managed. In the NPP database, 568 forests were managed (i.e., description contained mention of planting, thinning or harvesting), 142 recently disturbed (i.e., harvested or burned in the past 25 years), and 301 unmanaged (i.e., no management during past 50 years). Stands characterized as 'no information' (191), 'fertilized or irrigated' (37) and 'high deposition' (7) were excluded from the analysis due to the ambiguity about their management status. Although there is overlap between the "managed" and "recently disturbed" sites, and they could be grouped together, in the current study we reported the statistics for each category. In the SRDB database, the 'unmanaged' and 'natural' forests were grouped together, and contrasted to the 'managed' ones. Given that not all studies in the databases report all pools and fluxes, the means reported in Table 2 represent different subsets of sites. This, and differences in methodology may explain some internal inconsistencies between different estimates, like NPPfr exceeding BNPP. However, this should not affect the comparison of managed and unmanaged forests. On the other hand, as the NPP database does not include age information, management effects may be obscured by stands of different ages being lumped together. The SRDB indicates that the managed stands were significantly younger (21 years) than unmanaged and natural stands (68 years; Table 2), a contrast slightly exaggerated by a few old-growth forests (200–450 years) in the temperate and tropical biomes. To account for these differences, the analysis of variance was conducted both with and without age as a covariate. However, as the age-normalized differences confirmed the patterns in unadjusted means, they are not reported in the current study. The management effects were estimated with the mixed procedure in SAS (v9.4), using either biome or biome and age as covariates. However, the contrasts are dominated by the temperate forests, as the boreal and tropical zones had limited number of "managed" forests available. Tukey's honestly significant difference test was used for post-hoc tests. All differences were considered significant at $p = 0.05$ level, unless explicitly stated otherwise. Finally, the literature review part of this study focuses solely on factors affected by management activities, and will not cover other major drivers of plant growth and productivity like light and water availability.

3. Results and discussions

3.1. Key differences between managed and unmanaged forests' carbon cycles

The differences between managed and natural forests were to a great extent structural – the unmanaged or natural stands were nearly 50 years older than managed ones (68 vs 21 years), and had roughly twofold greater live carbon as well as soil carbon stocks (Table 2). The proportion of coniferous stands was greater among managed than unmanaged forests (70% vs 53%). The gross

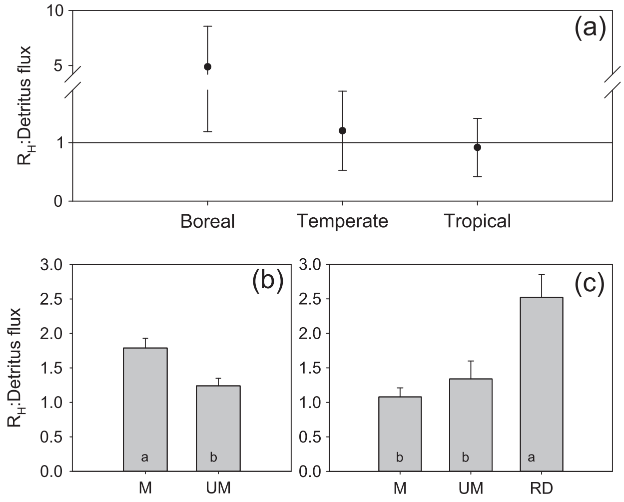

Fig. 2. The ratio of heterotrophic respiration (Rh) to total detritus production (detritus flux) as an estimate of soil carbon balance on an annual basis. (a) the global means of forests by biome, (b and c) means by management type – managed (M), unmanaged (UM) or recently disturbed (RD) – in the temperate biome (the only biome where data from managed forests was available). Panels (a) and (b) are based on SRDB database (Bond-Lamberty and Thomson, 2010a), and panel (c) is based on the NPP database (Luyssaert et al., 2009). Pairwise differences were considered significant at $p < 0.05$ level.

productivity (GPP) was similar, whereas aboveground net primary productivity (ANPP) and net ecosystem productivity (NEP) were higher in managed forests (+48%). In contrast, belowground net primary productivity (BNPP) did not differ, which may explain the similarity in total net primary productivity (TNPP). Total detritus production per year was greater in unmanaged forests, particularly due to greater fine root production. The apparent contradiction in the differences in respiratory fluxes based on different databases (with NPP database suggesting unmanaged stands having higher respiration rates, whereas the SRDB database indicated the opposite) could be due to the NPP database reporting ecosystem-scale fluxes, whereas the SRDB reports partitioning of the soil fluxes alone (see Ra in Table 2). Similarly, the greater Rh_{total} in unmanaged forests is likely due to the contribution from coarse woody debris, as the Rh_{soil} did not differ by management status. Greater NEP in managed than unmanaged forests while TNPP was unaffected by management status is consistent with a lower total Rh in managed than unmanaged forests. However, due to each flux being estimated from a different subset of studies, there remain several inconsistencies both between and within databases that require further evaluation and accounting for potential covariates, particularly for the belowground C dynamics. As actual belowground carbon flux is exceedingly challenging to measure accurately, and total belowground C flux (TBCF, estimated as the difference between soil CO_2 efflux and litterfall, and accounting for changes in forest floor, soil and root C pool sizes) cannot distinguish changes in allocation from those in belowground pools, the variability and control of BGA, and the role of rhizosphere interactions in belowground pools warrant further research.

The respiratory costs in relation to GPP did exhibit some variability in relation to management, but the two databases gave opposite results as to the predominant pattern. Although the Rh_{soil} may be marginally greater in managed forests, we did not detect a broad trend with age (time since disturbance) as hypothesized (data not shown). Instead, Rh_{soil} scaled with belowground C pool size, peaking at around 1500–2000 g m^{-2}, and declining thereafter. It is also likely that given the lags in dead organic matter inputs to soil and subsequent lags in availability to the decomposer community following a disturbance event (Noormets et al., 2012), and the likelihood of multimodal Rh dynamics in a stand's development (Harmon et al., 2011), a monotonic Rh dynamic that characterizes the decay of a single sample, may not be applicable in a disturbed ecosystem. Yet, understanding the properties of disturbance-related Rh pulses like the magnitude, lags following a disturbance, and proportionality of the increase above baseline are all essential for simulating and projecting the implications of disturbances on carbon sequestration potential at a landscape scale. The consistency of the global Rh:Rs ratio is notable, but when normalized for age, it appears that heterotrophic activity may be higher in managed than unmanaged forests.

The balance between annual soil carbon inputs and losses, as assessed by the ratio of Rh to total detritus production, exceeded unity in the majority of forests regardless of their management status (Table 2; Fig. 2b and c). Although only the temperate zone had a sufficient number of "managed" stands to allow a comparison with "unmanaged" ones (Fig. 2b and c), and the classification scheme differed between the two databases, a few consistent trends emerge. First, the difference between the "managed" and "recently disturbed" categories in the NPP database suggests that the management effect apparent in the SRDB (Fig. 2b) is primarily age-related, and that combining these categories may be appropriate for some analyses. Second, the latitudinal differences in the Rh:Detritus ratio (Fig. 2a) were consistent with broad patterns of the frequency of disturbance, soil carbon pool size, mean stand age and rate of warming. While "unmanaged" and "recently disturbed" forests exhibited a roughly 0.3 unit increase in the Rh:Detritus flux ratio for every 100 g increase in Rh, the change was about 10-fold smaller in "managed" stands due to some stands exhibiting higher Rh:Detritus ratios at low Rh values (data not shown). Broadly, the patterns in Rh:Detritus flux ratio were consistent with accumulating evidence of declines in soil C across the globe (Bellamy et al., 2005; Xie et al., 2007), and increase in soil CO_2 efflux (Bond-Lamberty and Thomson, 2010b) that are typically attributed to land use change and intensifying agriculture (Maia et al., 2010; Don et al., 2011; Yan et al., 2011). Despite lower frequency and magnitude, there is the potential for forest management practices to contribute to global soil C loss, yet the C dynamics in forest soils has not received similar attention. However, the attribution of the 2-fold lower soil C stock in managed than unmanaged stands (Table 2) to repeat disturbance events cannot be made without knowing individual site histories. As there remain significant uncertainties about belowground carbon allocation, from the magnitude of interannual variability to its fate, they may translate to poorly defined errors in the Rh:Detritus flux ratio. Nevertheless, given our current understanding that leaf, fruit and fine root litter make 80–90% of soil C inputs on annual basis, and the estimated mean Rh:Detritus flux ratios frequently exceed 1.25 (1/0.8; Rh:Detritus1 in Table 2), it seems likely that forest soils may run a C deficit on annual basis. Even when including annual coarse root production with detritus, which is an exceedingly conservative assessment (but could be viewed as accounting for root exudation), the global mean suggests a balanced budget based one dataset (NPP database), and soil C deficit based on another (SRDB; Rh:Total detritus flux, Table 2).

4. Literature review

4.1. Climate effects on productivity, belowground flux and soil carbon

The climate change factors (CO_2 and temperature), while secondary in effect size to stand age, disturbance and management history (Luyssaert et al., 2007), influence plant physiology by modifying the availability of vital resources. These factors determine the shifting baseline against which the management effects will be evaluated. Elevated CO_2 is known to stimulate productivity (typically 20–30%; Norby et al., 1999; King et al., 2005; Norby et al., 2005; Kubiske et al., 2006; Liberloo et al., 2006; Noormets et al., 2010), increase allocation to woody tissues (including coarse roots; Palmroth et al., 2006), primarily on the account of fine roots (Schäfer et al., 2003; but see Norby et al., 2004; Bader et al., 2009; Wolf et al., 2011b), whereas the increase in leaf area (Ward et al., 2013) is isometric with changes in GPP, and the allocation coefficients for foliage remain unchanged (Wolf et al., 2011b; Chen et al., 2014). The net effect of elevated CO_2 on soil C stocks documented so far has been limited (+5.6%), although consistent across studies (Jastrow et al., 2005). This could vary, of course, based on the symbionts and decomposer community (Gilbertson, 1980 as cited by Harmon et al., 2011), as well as by plant water and nutrient status (Lukac et al., 2009; Wolf et al., 2011b).

Temperature effects on productivity are generally more limited (broad temperature optimum of photosynthesis) than on respiration (but see Niu et al., 2012). The response of respiration, however, is mediated by carbohydrate availability in plants. The dependence on substrate availability is thought to be the cause behind dynamic temperature sensitivity (Chen et al., 2014), or ‘acclimation’, observed in short to medium term (Dewar et al., 1999; Atkin et al., 2000; Crous et al., 2011), and is consistent with the lack of it in the long term and in regional analyses (Chen et al., 2014). In fact, Chen et al. (2014) concluded that the temperature effect on C fluxes on global scale manifests primarily through day-length, which increased GPP and total belowground carbon input, whereas the kinetic properties of temperature-driven decomposition of SOM changed little. The effect of temperature on Rh in the long term likely depends on the factors that affect productivity and allocation (Caprez et al., 2012; Giardina et al., 2014), as they determine the input of organic matter that fuels Rh and support the putative priming of the mineralization of the more recalcitrant soil C (Fontaine et al., 2007; Crow et al., 2009a). Although elevated temperature can decrease root lignin concentration, few effects have been detected on root turnover (but see King et al., 1999b; Chen et al., 2008 as cited in Crow et al., 2009b).

4.2. Factors altered by management and their effect on carbon cycling

4.2.1. Nutrient availability/fertilization

The growth of most ecosystems is limited by soil nutrient availability (LeBauer and Treseder, 2008), and forests are no exception. While many factors contribute to productivity enhancements in modern plantation forestry, in loblolly pine in SE-US about 17% has been attributed to fertilizer amendments (Fox et al., 2007a,b). After age, disturbance and climate, nutrient availability is a major controller of forest productivity globally (Magnani et al., 2007). However, nutrient amendments do not translate solely to bigger trees, nutrient availability also alters proportional allocation to different organs, the temporal dynamics of growth, the chemical composition of the synthesized biomass, and through various feedback loops can alter the functioning of a large part of the entire ecosystem (Giardina and Ryan, 2002; Janssens and Luyssaert, 2009; Hasselquist et al., 2012; Vicca et al., 2012). The effects of nitrogen addition include stimulation of photosynthesis and net primary productivity, increase of either total leaf area or the areal concentration of photosynthetic enzymes, and decreased allocation to fine roots and exudates to root symbionts (Albaugh et al., 1998; Maier et al., 2004; Janssens and Luyssaert, 2009). The allocation to coarse roots increase similarly to that to stemwood (King et al., 1999a; Maier and Kress, 2000; Litton et al., 2007; Vicca et al., 2012; Chen et al., 2013). In weathered tropical soils, potassium fertilization also strongly influences productivity and allocation, increasing GPP and its partitioning to wood production at the expense of belowground sinks (Laclau et al., 2009; Epron et al., 2012). The proportional increase in coarse root production can thus be viewed as a potential mechanism for increased long-term carbon sequestration (Cseq) in the soil at improved N availability (Crow et al., 2009b). The potential for greater Cseq is also favored by reduced microbial activity, which may be suppressed either by direct effect on microbial physiology and enzyme activity (Fog, 1988), or through the lower level of root exudates as well as by lower fine root area (and turnover) (Giardina et al., 2003; Högberg et al., 2003; Pregitzer et al., 2008; Janssens et al., 2010). In fact, Högberg et al. (2003) reported that allocation to fungal symbionts was the process most reduced by N addition. The declines in immediate root symbionts translate throughout the rest of soil fauna, typically resulting in lower microbial biomass and lower heterotrophic respiration (Janssens et al., 2010). It has been argued that the differences in plant-available nutrients and the C:N ratio of organic matter inputs are sufficient to trigger a shift in the saprotrophic community (Högberg et al., 2003; DeForest et al., 2004), which in the long term could alter the competitive status of different species (Fog, 1988; Wallenstein et al., 2006). Furthermore, elevated N may have direct effects on microbial physiology and enzyme activity (Fog, 1988) that could potentially account for the observed decline in mineralization without invoking changes in exudation. Nevertheless, as a whole, both autotrophic and heterotrophic components of soil respiration decrease in response to relieving nitrogen limitation, with root respiration being more responsive (Sun et al., 2014). As the result of these shifts in production, allocation, C:N ratio of the litter, and microbial activity, increased nitrogen availability is likely to lead to increased accumulation of C in the soil (Li et al., 2006; Magnani et al., 2007 and references therein; Janssens et al., 2010; Chen et al., 2013), although the uncertainty of this increase is greater than for the aboveground stimulation (Li et al., 2006; de Vries et al., 2009) and the accumulation may be limited to surface soils (Li et al., 2006; Hyvonen et al., 2008; Pregitzer et al., 2008). Furthermore, the increase in soil C has been observed only in mineral and not in organic soils (McNulty et al., 2005; Nave et al., 2009). 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 et al., 2012). Nitrogen may also be an important factor modulating priming (Fontaine et al., 2004) thus decreasing SOM decomposition. Finally, it is important to note that all these effects manifest not only in fertilized plantations, but also when nitrogen fixing species are introduced in forest plantations (Epron et al., 2013; Forrester et al., 2013; Koutika et al., 2014), when large amounts of harvest residues are left on site providing substrate to the decomposer community (Mendham et al., 2003; Walmsley et al., 2009; Kumaraswamy et al., 2014), and in any nitrogen-limited ecosystem exposed to anthropogenic atmospheric nitrogen deposition (Ndep), which now rivals that fixed by natural processes (Galloway, 1998). In fact, it has been postulated that anthropogenic Ndep may be responsible for much of the observed terrestrial C sink in recent decades (Magnani et al., 2007), and the reduction in nitrogen deposition is viewed as one of the potential causes of the slowdown in stem volume increment in European forests (Nabuurs et al., 2013). However, the effect of Ndep on Rh and Ra may be non-linear and exhibit a threshold response (Hasselquist et al., 2012).

4.2.2. Soil disturbance

The physical disturbance of soil, and mixing of the litter layer with surface soil during harvesting and site preparation activities results in significant redistribution of C between different pools, and triggering accelerated carbon losses (Mallik and Hu, 1997). Mixing of litter layer with topsoil effectively removes this structural element and exposes it to diverse microbial communities (Yanai et al., 2003; Nave et al., 2010; Noormets et al., 2012), whereas the breaking of the physical structure of soil aggregates exposes carbon that may previously have been protected (Six et al., 2002b; Diochon and Kellman, 2009; Schmidt et al., 2011). While the change in the relatively large soil C pool may not be detectable immediately following a single harvest (Nave et al., 2010), land use conversion almost invariably results in soil C loss upon conversion from forest to agriculture (Guo and Gifford, 2002) and in an increase in soil C upon reforestation of previously cultivated land (Paul et al., 2002; Six et al., 2002a,b; Li et al., 2012; Nave et al., 2013; Chang et al., 2014). Whether the roughly 2-fold difference in soil organic carbon stock between managed and unmanaged forests (Table 2) is the result of increased mobilization triggered by compounded disturbance requires the assessment of site history data in each case, but it is consistent with the narrative of disturbance-driven change in SOC stock. Also consistent with the intensity of disturbance is the observation that changes in SOC content are typically greater in the surface than deep soils (Nave et al., 2013), but in some boreal stands destabilization of deep (>20 cm) soil C has also been documented (Diochon and Kellman, 2008). This latter came primarily from the destabilization of carbon in the organo-mineral fraction (Diochon and Kellman, 2009), which at the site represented the greatest soil C pool (70%), and is often assumed to be the best protected from mineralization (Conen et al., 2008). These findings are corroborated by increased N mineralization in the deep (>20 cm) soil (Kellman et al., 2014), and are consistent with the current understanding of soil C dynamics, which recognizes the spatial heterogeneity in physical accessibility, sorbtion–desorbtion, and solubility (Sollins et al., 1996; Trumbore and Czimczik, 2008; Schmidt et al., 2011), whereas the role of chemical recalcitrance seems much more limited (Sollins et al., 1996; Rasse et al., 2005). This new framework explicitly allows for interactions between surface and deep soil, including substitution of older carbon with newer in the organic-mineral fraction (Baisden and Parfitt, 2007). As recent evidence illustrates the dynamic nature of soil C stocks, our understanding is also improving about the mechanisms that lead to soil C stabilization (Strukelj et al., 2012, 2013). While data on the origins of soil C is exceedingly scarce, the presence of biochemical markers specific to roots and ectomycorrhizal extramatrical mycelium suggests that root-derived organic matter is stabilized to a greater extent than shoot-derived, and makes the majority of soil carbon (Rasse et al., 2005; Godbold et al., 2006; Dijkstra and Cheng, 2007; Adair et al., 2008; Mendez-Millan et al., 2010; Zhu and Cheng, 2011; Ekblad et al., 2013). These findings are consistent with the recognition of the role of surface- and litter-dwelling mesofauna in decomposition dynamics (Prescott, 2005; Wall et al., 2008; Cotrufo et al., 2010), as well as the chemical protections achieved through chemical interactions with mineral surfaces (Rasse et al., 2005). It is not clear which properties contribute to carbon stabilization in soil, but the latest studies suggest that it is much more dynamic than previously recognized (Schmidt et al., 2011).

4.2.3. Stand structural disturbance and age

Harvesting-related disturbances are the most visible, and also among the most functionally significant effects in managed forests, and on a landscape scale can account for over 90% of the variability in observed carbon exchange (Magnani et al., 2007; Noormets et al., 2007; Amiro et al., 2010; Dangal et al., 2014). The removal of stemwood, along with the conversion of foliage and branch biomass to detritus represents a greater redistribution of pools than any natural disturbance, even fire (Harmon et al., 2011). The forest floor C pool decreases by about 30 ± 6% following a harvest, with slightly greater effect in angiosperms than in gymnosperms (but see Epron et al., 2006; Nave et al., 2010; Nouvellon et al., 2012). Even in natural forests that experience disturbances at a much lower frequency, the associated increases in heterotrophic respiration (Rh) constitute up to a half of total carbon losses over time (Harmon et al., 1986, 2011). In managed forests, where stand-replacing disturbance in the form of a harvest is not a rare event, but an integral part of the life cycle of the ecosystem, the effect is likely to be even greater. For example, in loblolly pine plantations in the Southeast of USA, with a 25-year rotation cycle, the recovery of leaf area index and carbon fluxes from the harvest to the preharvest level may take 10–15 years (compared to about 20 years in unmanaged forests, Amiro et al., 2010), or 50% of the total stand rotation length (Noormets et al., 2012). The recovery of pools and structural complexity, obviously, takes even longer. The canopies of fast-growing species cultivated on short rotation (e.g. eucalypts, poplars, willows) may never regain the structural complexity of a native pre-disturbance forest. Furthermore, often there is no native pre-disturbance reference, as anthropogenic land use change has shaped the landscape longer than we have monitored its carbon exchange. As one possibility, the fluxes in managed forests could be considered in reference to the potential equilibrium state that the ecosystem may reach in the absence of future management-driven disturbances. For example, in tropical eucalypt plantations canopy closure occurs rapidly, whereas litterfall reaches about 90% and the mass of forest floor about 60% of documented maxima by the end of a regular rotation cycle (Nouvellon et al., 2012).

As the result of major structural changes, the balance between fluxes also changes. The increase in Rh, associated with the inputs of dead organic matter into the soil and litter layer, may increase by up to 2-fold (e.g. Noormets et al., 2012). While the pulse of harvest residue represents a major input to the litter layer, with potentially large effects on ecosystem C cycling, the cessation of fine root production and exudation may be equally important from a soil perspective, and could potentially compensate changes in Rh. Furthermore, the intricate feedbacks between nutrient status, rhizosphere activity, amounts and nature of detritus input, and soil mineralogy can trigger different responses of Rh in different forests (Crow et al., 2009b). Nevertheless, in proportion to total soil CO_2 efflux (Rs), Rh increases from the typical 20–40% in mature forests to about 70–95% in young regenerating ones following the harvest (Wang et al., 2002; Bond-Lamberty et al., 2004b; Epron et al., 2006; Noormets et al., 2012). In addition to the decomposition of harvest residues, the increase results from a combination of physical disturbances affecting substrate availability to microbes, the microclimate at the soil surface, and the high C:N ratio of the woody litter, which has been shown to be a key factor affecting microbial activity (Fontaine et al., 2004). It is notable that the suppression of Rh by nutrient addition that has been observed in mature stands is smaller or even non-existent in young ones (Janssens et al., 2010), possibly due to high nutrient demand and ample substrate availability for microbes. Similarly, Cheng (2009) reported evidence of decoupling of C and N dynamics in high-demand situations, where nearly 4-fold stimulation of soil C mineralization did not lead to a similar increase in N mineralization. The net effect of priming on soil C pools in the longer term is not clear, however, as in a litter manipulation experiment the increase in Rh has been documented simultaneously with an increase in soil C (Crow et al., 2009b), and offsetting C:N ratio does not always lead to priming (Epron et al., 2015).

It has been argued that understanding time trends of net ecosystem productivity (NEP) requires understanding of processes controlling Rh (Pregitzer and Euskirchen, 2004). The balance between NEP and Rh may vary in different systems, but is determined by mutual constraints of substrate and nutrient availability for both plants and microbes. While some understanding of chemical characteristics of organic compounds that confer recalcitrance to microbial decomposition has emerged from recent studies (Crow et al., 2009a; Strukelj et al., 2012, 2013), quantitative characterization of the effect of substrate availability on Ra and Rh remains a challenge (Wutzler and Reichstein, 2008; Crow et al., 2009b; Wutzler and Reichstein, 2013). The dynamics are further complicated by the time lags between the harvest/disturbance, the death of different plant parts, and their becoming available for Rh (Goulden et al., 2011; Lambert, 1980 as cited by Harmon et al., 2011). These lags should be strongly climate dependent with faster decomposition in wet tropics where harvest residue decomposition may support initial tree growth (Versini et al., 2013), whereas immobilization of nutrients may limit tree growth under colder or drier conditions (Palviainen et al., 2010). The multiplicity of pools, the differences in their chemical composition, and delayed mortality and delayed decomposition (Harmon et al., 2011) lead to a complex temporal dynamics of the compound heterotrophic CO_2 production on an interannual scale. Although few studies have quantified Rh explicitly through stand harvest and early regrowth (Law et al., 2003; Epron et al., 2006; Goulden et al., 2011; Noormets et al., 2012), the available data on total ecosystem respiration is consistent with the proposition that Rh continues to increase for a few years following the disturbance (as opposed to peaking immediately after) as more dead biomass becomes available for decomposers (Litvak et al., 2003; Amiro et al., 2010). As the available substrate is consumed, Rh then declines, until it begins increasing in later stages of stand development when the aboveground biomass and annual litter production increase (although the ratio of Rh:Rs is more stable since Rh is functionally dependent on root activity and Ra). However, modeling the bulk flux is associated with large uncertainties, as the factors controlling the delayed mortality and delayed decomposition of different pools are poorly characterized and understood. On short time-scales, the variability of Rh also appears to be tied to Ra and the availability of substrate, whereas its intrinsic temperature sensitivity seems to be low (Davidson et al., 2006; Sampson et al., 2007; Vargas et al., 2010; Templeton et al., 2015). Although the disturbance caused by the harvest and site preparation practices can move surface litter either to a more or less favorable environment for decomposition, the homogenization of surface horizons typically leads to a net increase in Rh. Large uncertainty surrounds the fate of coarse roots, with limited information about their turnover time (Harmon et al., 2011; Wolf et al., 2011b). Anecdotal evidence exists about very slow coarse root turnover (Yanai et al., 2003 and citations therein), whereas most decomposition studies report similar decay constants to aboveground CWD (Harmon et al., 2011). However, the chemical signature of soil C suggests that root- and mycorrhiza-derived C is retained preferentially to aboveground inputs, and constitutes the majority of long-lived soil C (Godbold et al., 2006; Dijkstra and Cheng, 2007; but see Crow et al., 2009b; Mendez-Millan et al., 2010; Zhu and Cheng, 2011; Ekblad et al., 2013).

In the process of recovery, young trees allocate new biomass differently than mature ones. Proportional to the existing live biomass, the role of maintenance respiration is lower in younger trees, whereas production of fine roots as a proportion of GPP or NPP is greater than in mature trees (Litton et al., 2007). While the overall flux of carbon to root production and maintenance (total belowground carbon flux, TBCF) continues to increase with increasing GPP, the proportional allocation belowground (TBCF:GPP) typically decreases with increasing GPP (Chen et al., 2013). As the proportional cost of maintenance increases with tree size, carbon production and carbon storage efficiencies (calculated as the ratios of NPP:GPP and NEP:NPP, respectively) decrease with increasing biomass and age (Goulden et al., 2011).

While stand thinning imposes similar effects on stand structure as harvesting, they are much more limited in scope, and most studies report that the effects on fluxes are indistinguishable from natural interannual variability (Vesala et al., 2005; Granier et al., 2008) or are very short-lived (Epron et al., 2004; Magnani et al., 2007; Lindroth et al., 2009). Using Forest Inventory and Analysis (FIA) data for Eastern USA, Zhou et al. (2013) reported that in from 1973 to 2011, thinning more than doubled diameter growth, increased understory biomass 4-fold, and did not have a discernible effect on forest floor and mineral soil C pools.

4.2.4. Genetic and species selection

Plantation forestry targets a subset of species and genotypes with the greatest merchantable biomass production in the shortest time possible (Fox et al., 2007b). The major pulp species are *Eucalyptus* sp., *Populus* sp., *Pinus taeda*, *Pinus radiata* and *Liquidambar styraciflua* (Palo et al., 2001), and the main timber species are *P. taeda*, *Pseudotsuga menziesii*, *Eucalyptus* sp., *P. radiata*, *Pinus patula* and *Picea abies* (Palo et al., 2001; Cubbage et al., 2007). The factors contributing to the selection are many, including high photosynthetic capacity, preferential allocation to stemwood, crown form, disease resistance and ease of cultivation (Tyree et al., 2009). For loblolly pine, in the SE US, about 23% of overall productivity is attributed to genetic improvement over the past 50 years, and particularly in the past 20, as the seed from second-generation seed orchards and controlled pollination of elite parents became widely available (Fox et al., 2007a,b). It is expected that another 50% growth enhancement may be possible with clonal material, and genetic engineering of disease resistance (Fox et al., 2007b).

Although one might expect that the year-round active foliage may give evergreen species the advantage and exhibit a higher GPP compared to deciduous forests, other than a few exceptions, this does not seem to be the case (Luyssaert et al., 2007). However, stem growth scales with overall productivity better in gymnosperms than in angiosperms (Wolf et al., 2011b). The same study finds that gymnosperms allocate a greater fraction of photosynthate to coarse roots than do angiosperm species, whereas Chen et al. (2011) noted greater root contribution to soil CO_2 efflux in deciduous broadleaved than coniferous forests. Although the data are very sparse, some studies suggest that gymnosperm wood decomposes more slowly and forms more complex chemical structures than that of angiosperm species, potentially leading to greater accumulation of carbon in soils (Rock et al., 2008; Strukelj et al., 2013). On the other hand, the construction and maintenance costs, as expressed by the Ra:GPP ratio, are reportedly higher in gymnosperms than in angiosperms, although the absolute respiration rates are often higher in the latter (Tjoelker et al., 1999). It may be that these higher construction costs and chemical composition of gymnosperms contribute to the lower loss of forest floor C following a harvest compared to angiosperms (−20% vs −36%; Nave et al., 2010). Recent findings also point to the importance of the type of mycorrhizal symbionts in plant nutrient uptake and decomposer activity (Averill et al., 2014).

4.3. Mechanisms

The broad patterns described above suggest that soil carbon balance in managed forests depends on both altered inputs and the loss dynamics compared to natural forests, and that the decomposition dynamics are partly predictable from the chemical composition of the litter. With increases in productivity (both GPP and NPP), increased allocation to foliage and stemwood due to climate forcing, fertilization, N fixation or Ndep, and lower decomposition due to fertilization and Ndep, managed forests could potentially sequester greater amounts of carbon belowground than their unmanaged counterparts. However, the temporal dynamics and variability of belowground carbon flux, and disturbance-related losses of old C remain largely unknown, and could offset the tendencies established during the active growth phase.

4.3.1. Allocation, heterotrophic respiration and soil carbon

As we discussed in preceding sections, many of the management effects (e.g. fertilization, disturbance, and species selection) affect allocation patterns. Long-term Cseq in the soil could respond to (i) the belowground carbon flux, (ii) its specific breakdown between coarse and fine roots, symbionts, and exudates, (iii) allocation shifts among aboveground C pools, (iv) changes in detritus chemistry, and (v) changes in the soil environment. The latter could, in turn, be influenced directly by management-related disturbance, or by plant-mediated changes, and manifest in altered temperature, moisture, affecting microbial and microinvertebrate activity. In this section we will discuss what is known of the regulation of allocation patterns in the context of factors expected to change in managed forests.

4.3.1.1. Measuring belowground flux. Direct measurement of belowground flux is difficult, and over time different proxies have been used instead. A powerful and commonly used approach is the total belowground carbon flux (TBCF), originally proposed by Raich and Nadelhoffer (1989) and Giardina and Ryan (2002):

$$\mathrm{TBCF} = \mathrm{Fs} - \mathrm{Fa} + \mathrm{Fe} + \mathrm{dCs} + \mathrm{dCr} + \mathrm{dCl} + \mathrm{dS}$$

where Fs is soil surface CO_2 efflux, Fa is aboveground litterfall, Fe is loss through leaching and erosion, dCs is change in soil C, dCr is change in root C, dCl is change in litter layer C, and dS is change in plant C storage. Often, in actual applications, terms Fe, dCs, dCr, dCl and dS are considered negligible, which may not always be justified. The error is likely to decrease as the integration period increases, but the TBCF estimates may not be reliable on short timescales (i.e. annual and shorter) over which the assumption of invariable C pools may not hold, and may be difficult to validate. To capture the short-term variability, quantification of several difficult-to-measure processes would be required. The belowground carbon flux, as controlled by the plants' physiological state at any given point, would help to understand the belowground allocation (BGA) in functional terms and to better predict its response to environmental drivers. BGA is the ratio of belowground carbon flux to GPP, that is often approximated as BNPP:TNPP, which is true if the carbon use efficiency (CUE) is the same for roots and the whole plant. Although TBCF and BGA are strongly correlated (Raich and Nadelhoffer, 1989), the significant variance in the relationship could be seen as an indicator of violation of the assumption of invariance of the belowground pools on a year-to-year basis. Understanding of how belowground carbon flux translates to changes in different belowground pools remains unclear. Some studies have found that new C inputs accumulate in the litter layer or surface soil, whereas other times they do not (Giardina et al., 2014), and were instead respired, fueled priming of old soil C mineralization or were transferred to deeper horizons as they get progressively processed (Baisden and Parfitt, 2007; Kalbitz et al., 2007; as cited by Crow et al., 2009b), possibly facilitated by fungi (Frey et al., 2003; Williams et al., 2006).

4.3.1.2. Biomass vs flux partitioning. The relative mass relationships between different tissue C pools have been the subject of extensive allometric research. To date, detailed species- and location-specific (sometimes management-specific) relationships between tree diameter at breast height and the mass and volume of different pools have been assembled (e.g. Perala and Alban, 1994; Ter-Mikaelian and Korzukhin, 1997; King et al., 1999a, 2007; Peichl and Arain, 2007; Feldpausch et al., 2011). While the mass relationships are remarkably conserved (Ise et al., 2010) and the component fluxes correlate with GPP and NPP (Litton et al., 2007), the actual allocation of resources on an annual basis can vary significantly (Wolf et al., 2011b). Although biomass ratios are often used as proxies for C allocation, they generally do not correlate with the latter (Litton et al., 2007; Wolf et al., 2011b), likely due to the longevity of the woody tissues, fluxes to the symbionts, and excretions to the rhizosphere. An exception to this rule is the tight relationship between fine root biomass and fine root productivity (Finer et al., 2011), as the short life cycle of fine roots removes the main confounding factor.

4.3.1.3. Allocation and GPP. Although allocation cannot be reliably estimated from biomass pools, strong relationships have been identified between relative partitioning and stand-level GPP and NPP (Litton et al., 2007; Malhi et al., 2011; Wolf et al., 2011b; Chen et al., 2013). Furthermore, clear prioritization and trade-offs between different plant parts have been identified (Chen et al., 2013, 2014). For example, as GPP increases, there is a strong prioritization of resources to woody support structures at the expense of fine roots, rhizosymbionts and exudates (Litton et al., 2007; Vogel et al., 2008; Wolf et al., 2011b; Chen et al., 2013, 2014). However, total net production of biomass and foliage, and autotrophic respiration, remained a constant fraction of GPP across its range. Allocation to woody tissues increases along with GPP, and C allocation to foliage and autotrophic respiration are isometric with GPP (that is, the proportional allocation does not change) (Chen et al., 2013, 2014), likely due to the inverse relationship between average tree size and productivity, and the increasing competition for light as the canopy closes. To the extent that GPP varies latitudinally with mean annual temperature (MAT), the described allocation patterns correlate with MAT and MAP (Litton and Giardina, 2008).

At a single tree level, all components of productivity (total NPP, foliage NPP, wood NPP, stem NPP) scale proportionally with GPP, with the exception of fine root NPP (Chen et al., 2013). There appears to be a threshold above which fine root biomass and productivity no longer increase, and remain invariant of productivity (although there remain hydraulic constraints, Magnani et al., 2000). As GPP continues to increase, the fraction allocated to fine roots, as well as root exudates and support for symbionts must decrease (Chen et al., 2013). In a follow-up study, Chen et al. (2014) identified three major trade-offs that in addition to allometric constraint explained the allocation of resources to different plant parts – (i) fine root vs woody biomass production trade-off, (ii) respiration vs biomass production trade-off, and (iii) photosynthetic vs nonphotosynthetic biomass production trade-off. These conclusions confirm earlier work emphasizing the functional distinction between fine and coarse roots (Dybzinski et al., 2011; Malhi et al., 2011; Wolf et al., 2011b), which had been combined in previous analyses (e.g. Litton et al., 2007) and perhaps confounded the interpretation. A significant implication of this distinction pertains to the respiratory maintenance costs of fine roots (trade-off #2 above and Malhi et al., 2011), such that BGA would not depend solely on resource limitation (as in most current ecosystem models, Friedlingstein et al., 1999) but there would be a respiration cost, and new root production would be secondary to the maintenance of standing root stock and rhizosymbionts, which can consume a significant fraction of TBCF (Kuzyakov and Cheng, 2001; Högberg and Högberg, 2002; Robinson, 2004; Fahey et al., 2005; Chen et al., 2014 and references therein).

4.3.1.4. Carbon use efficiency and component respiration. As GPP-derived carbohydrates support both plant and microbial productivity and respiration, and microbial activity translates to decomposition of existing soil carbon (Migliavacca et al., 2011), it should not be surprising that respiration may depend on GPP through both positive and negative feedbacks (Chen et al., 2014).

The balance between the belowground carbon inputs (through both belowground productivity, and exudation as well as aboveground litter inputs) and losses (primarily mineralization) is often expressed via biomass production and carbon storage efficiencies (NPP:GPP (also called carbon use efficiency, CUE) and NEP:NPP ratios, respectively). Both of these decrease with increasing biomass and stand age as the respiratory costs for maintaining existing biomass increase (Litton et al., 2007; Goulden et al., 2011). The extent to which carbon in dead biomass is stabilized varies greatly by ecosystem, and has been proposed as an intrinsic ecosystem property related to is species composition (Metcalfe et al., 2011; Schmidt et al., 2011). Typically, autotrophic respiration consumes 30–80% of GPP (Litton et al., 2007; Chen et al., 2013), and heterotrophic respiration and exudation to rhizosphere may consume another 10–40% (Bond-Lamberty et al., 2004b; Noormets et al., 2012). Given the rapid turnover of fine roots and the high metabolic cost of rhizosymbionts (belowground CUE = 0.2–0.5, Litton and Giardina, 2008), much of the C allocated below ground returns to the atmosphere as respiration (Trumbore, 2006; Giardina et al., 2014). However, there may be a significant temporal decoupling between transfer of carbon belowground, and its processing by heterotrophs. It has also been found that nutrient availability can significantly decrease plant respiratory costs and allow for higher carbon storage efficiency (Fernandez-Martinez et al., 2014).

While the Ra:GPP ratio is generally conservative across plant functional types, there is also significant unexplained variability, and no universal dependence of Ra on GPP has been found (Chen et al., 2013). This appears to be due, at least in part, to greater temperature- and precipitation-sensitivity of GPP at mid- and lower ranges of these variable (MAP < 1500 mm and MAT < 10 °C), whereas above these thresholds Ra increases more than GPP, leading to a divergence in the global patterns of GPP and NPP (Luyssaert et al., 2007). Curiously, changes in plant allocation patterns appear to be possible while maintaining constant CUE (Maier et al., 2004). However, there are negative relationships (i) between the fine root NPP vs Rr trade-off and Rs, and (ii) between the ratio of root respiration to total soil respiration (Rr:Rs) and the ratio of total autotrophic respiration to soil respiration (Ra:Rs) (Chen et al., 2014) suggesting that although the relative respiratory cost may increase with increasing BGA, there may also be a growing fraction of GPP sequestered as soil organic matter. Nevertheless, it is not clear if there are parallel changes in root exudation and Rh. Typically, variations in Rs have been associated with those in Rr rather than Rh (Bond-Lamberty et al., 2004a; Subke et al., 2006), and the primary source of variation in the latter may be disturbance (Noormets et al., 2012). If the rate of Rh and the extent of priming of soil carbon decomposition is determined by the equilibrium between plant carbohydrate status and the level of exudation, then the additional litterfall associated with greater biomass could contribute to greater long-term C sequestration, even though a part of it is lost through enhanced respiration (Crow et al., 2009a). Although our understanding of key mechanisms is still evolving, it is clear that plant carbohydrate status represents an important feedback loop that must be considered when attempting to manage forests (or other ecosystems) for long-term carbon sequestration in soil. Carbon can only accumulate in soil if progressively more C is deposited than decomposes, and until it reaches saturation (Six et al., 2002b). Better understanding of the contribution of different litter fluxes to C accumulation and priming effects by variable TBCF is required, as these counteracting processes affect the long-term stability of soil C stocks.

4.3.2. Net ecosystem productivity and long-term carbon sequestration in soil

Understanding of the dynamic nature of plant allocation has evolved with the refinement of methods and growing body of data. For example, earlier conclusions based on C allocation estimates using the TBCF framework and other indirect methods that allocation was relatively conserved regardless of stand age, resource availability, aboveground biomass and competition, have since been revised (Wolf et al., 2011b). Pregitzer and Euskirchen (2004) and Magnani et al. (2007) showed that variability in NEP was primarily associated with age, disturbance, and management, clearly trumping differences attributable to climate. Furthermore, they also pointed to the relationship between NEP and NPP that holds very well in all except the young stands, a difference attributable to deviations in the allocation patterns and disturbance-driven shift in the Rh:NPP relationship. Some studies have for this reason excluded young stands from global analyses (Luyssaert et al., 2007). However, as new models are developed, capable of accounting for the feedbacks discussed above, it may be time to take another look at the disturbance-mediated variability in C dynamics, and the controls of long-term carbon sequestration.

4.4. Soil carbon dynamics

According to the current paradigm of soil C dynamics (Sollins et al., 1996; von Lutzow et al., 2006), the longevity and stability of organic matter in soil is determined by physical accessibility, stabilizing interactions with minerals, and chemical recalcitrance. This represents a shift away from earlier recalcitrance-centered perspective, which based on recent estimates may only contribute about 25% of total regulation (Rasse et al., 2005). The chemical and physical interactions contributing to stability are reversible and co-occurring simultaneously (Sierra et al., 2011), and both physical accessibility and stabilizing interactions could be sensitive to water movement in soil (Cardon et al., 2013) which by solubilizing compounds could bring to contact previously nonadjacent microbes and substrates.

A second factor that is likely to play a major role in the dynamics and processing of soil C in managed forests is *priming*, which refers to the accelerated mineralization of more recalcitrant material by the infusion of small quantities of easily decomposable material from aboveground and root litter, and exudates (Kuzyakov et al., 2000; Fontaine et al., 2004). While priming is now understood to be a universal mechanism, affecting organic matter turnover in all ecosystems (Hamer and Marschner, 2005; Kuzyakov, 2010; but see Epron et al., 2015), it is likely more variable in time and space in actively managed forests that experience dramatic changes of C allocation and detritus input associated with harvesting and subsequent regrowth. However, the effect of priming on soil C balance in the longer term remains uncertain because the presumably increasing recalcitrance of the remaining C could effect a different stoichiometric balance at a given rate of new C inputs. Whether the lack of detectable change in soil C content in harvest management studies (Olsson et al., 1996; Huang et al., 2013; Epron et al., 2015) can be viewed as evidence in support of this hypothesis is too early to say, as quantifying the total soil C pool is complicated by the continual transformation and translocation by both physical and biological processes, and high inherent variability in SOC content and biochemistry. Yet, the role of live roots and rhizosymbionts in the process is implied, as some studies have reported greater priming effects in the presence of active roots than in their absence (Crow et al., 2009a).

Most ecosystem and land surface models remain simplistic in their treatment of soil C dynamics, using lumped pools, single rate constants, and ignoring feedbacks, particularly at broader spatial scale (Manzoni and Porporato, 2009). However, Sulman et al. (2014) recently developed a priming module for global C cycle models, which they then used to estimate the effect of elevated CO_2 on the balance between SOC stabilization and priming globally. Separating rhizosphere and bulk soil processes, they allowed the same substrate to have different turnover rates depending on the availability of root exudates, and the presence of different microbial taxa. This effort may be the first of its kind to incorporate SOC stabilization and priming interactions in an integrated carbon cycle model. With its novel capabilities, it would be interesting to review the simulations by Piao et al. (2009) in terms of the attribution of their detected SOC change in some systems over recent decades, which most models fail to capture. The implications for broader ecosystem C cycling might be rather different depending on whether the increased soil CO_2 efflux is the result of warming (Piao et al., 2009; Bond-Lamberty and Thomson, 2010b) or priming (Sulman et al., 2014).

5. Summary

The effect of management on forest C exchange manifests largely through age-related structural effects (e.g. LAI, allocation, live-dead balance), and secondarily through responses to altered environmental conditions (e.g. temperature, nutrient and water availability, atmospheric CO_2). Despite over a 3-fold age difference between the managed and unmanaged forests, their mean GPP is similar. The differences that emerge in NPP and particularly in NEP, are attributable to lower BGA, and lower expenses on rhizosymbionts, that result in greater aboveground growth efficiency and production efficiency in managed than unmanaged forests. However, while the ratio of both auto- and heterotrophic respiration in proportion to GPP was not found to differ significantly, the respiration fluxes in absolute terms were higher in managed forests. That is, the isometric increase in belowground carbon flux exceeds the proportional decrease in BGA. The suggestion from the literature review of potential increase in sequestration of C in soils with good nutrient availability is supported by the results of the NPP database, showing lower Rh in managed than unmanaged forests, whereas the SRDB indicates greater soil C losses in managed than unmanaged forests. Our reviewed literature suggests that this may, in part, be due to priming of soil C mineralization, thus undermining additional C sequestration potential by managed forests. The C losses are compounded by disturbances associated with management activities and shorter rotation lengths. As a result, the soils in managed forests could be in greater C deficit than those in unmanaged forests, even though over the past 2–3 decades the losses appear to exceed gains globally, regardless of the management status. Whether and how the annual imbalance correlates with the observed long-term changes in soil C stock is yet to be elucidated. It is important to acknowledge that the notion of C loss in forest soils has not been detected in earlier studies, and is typically associated with intensive and regular disturbances, like agriculture (see Section 1). Yet, the current assessment of annual inputs and outputs may be more sensitive to detecting a change, as the metric is designed for this purpose.

Owing to the trade-offs in the C allocation to different plant parts (Wolf et al., 2011b; Chen et al., 2013, 2014), the effects of the main climate change and management factors (temperature, CO_2 concentration, water availability, nutrient availability, age, soil disturbance, species) on productivity are generally positive, and on belowground allocation negative. The decline in relative BGA is partially offset by allometrically based increase in root growth, confounding the overall change in belowground carbon. As the decline comes from reduced allocation to fine roots, rhizosymbionts and exudation, priming is likely to decline, slowing soil C mineralization. The greater allocation to woody tissues (including coarse roots), and the greater chemical recalcitrance of litter in gymnosperms would be expected to potentially contribute to greater soil C accumulation potential. However, the meta-analysis by Guo and Gifford (2002) found that the conversion of native forests to gymnosperm plantation resulted in greater soil C loss than when converted to angiosperm plantation. Increased inputs of aboveground litter, on the other hand, may be promptly consumed and either result in limited net change in soil C (Pregitzer et al., 2008; Crow et al., 2009b) or even prime the accelerated decomposition of old soil C (Hamer and Marschner, 2005; Crow et al., 2009b). However, it remains unclear, how much this contributes to the observed recent increase in Rs (Bond-Lamberty and Thomson, 2010b), and how fast the plant carbohydrate pool reaches a different equilibrium, which can be expected to stabilize respiration. The net long-term effect on soil C pool would be very different depending on whether the observed increase in Rs derived from an increased disturbance regime and consumed old soil C, or if it was supported by greater inputs due to increased productivity, in which case it would represent intensification of C cycling in soil with little net change in the pool size.

While some likely interactions of climate change and management forcing have been explored (e.g. CO_2 and nitrogen, Oren et al., 2001), several surprises may await as management affects ever broader reaches of the world, or if climate variability increases. Modeling studies suggest that the efficiency of management may have taken trees to their physiological limits even without removing all climatic constraints (Wynne, Burkard, Evans, personal communication). Conversely, the relative efficacy of management activities may be reduced in future climate.

Finally, although the recent global analyses of allocation patterns and trade-offs have provided invaluable and novel insight, the methods have often been explicitly tailored for resolving spatial patterns (Wolf et al., 2011b; Chen et al., 2013, 2014), suppressing site-level interannual variation (e.g. averaging different years from a given site). However, it is the latter that is of interest when projecting future changes in response to climate change, or shifts in management practices and increasingly popular cultivation of species in novel locations.

6. Final remarks. Balancing forest productivity with carbon sequestration in the soil

As anthropogenic pressure on the natural environment increases, the area under plantation forestry and the fraction of wood products, as well as environmental services appropriated from them is expected to grow. With the expansion of the suite of services expected from managed forests, i.e. moving beyond maximizing the merchantable biomass, several optimization questions arise. The questions addressed in the current study have focused on on-site carbon sequestration rather than the life-cycle analysis of forest products more commonly used to quantify the carbon benefits of forestry. However, tracing the fate of newly assimilated carbon from forest overlooks the fact that it can come at the expense of releasing carbon that had been previously sequestered in the soil.

The managed forests of tomorrow should strive to strike a balance that maximizes as many benefits as possible, but without an explicit valuation scheme of all components the optimum may be difficult to define. Regardless of whether the value of non-woody products is based on the extent of reduced productivity under the compromise scenario or some other metric, there remain several ecological questions to be answered. For example, (i) the interannual variation and functional regulation of belowground allocation, (ii) the extent and mechanism of priming of the decomposition of old soil C by new inputs, and (iii) the stabilization mechanisms of above- and belowground plant litter, and incorporation to long-lived soil C pools all remain significant unknowns. Furthermore, to what extent can interannual differences in allocation and fluxes be inferred from the spatial differences between sites described here? These questions address fundamental ecosystem properties that affect their stress tolerance (including drought), as well as the potential of managed forests to mitigate the increase in atmospheric CO_2 concentrations. The consideration of managed forests for bioenergy production also needs answers to the effect of different management activities on the plant and soil C pools, and which rotation length and harvest residue management practices would allow maintaining long-term sustainability of a particular operation, without compromising the nutrient and water holding capacities of the soil. As both plant productivity and microbial respiration depend on nutrients released from decomposing harvest residue, it is important to understand how these processes relate to one another. In addition to the aspects already mentioned, the search for optimal management decisions will need to consider forests as complete ecosystems with multiple feedbacks. For example, while increasing nutrient availability may promote productivity along with C accumulation in soil (at least in the short term), it also has implications for plant drought sensitivity and fertilizer run-off. In all, the data clearly point to a trade-off between plant productivity and carbon sequestration in the soil, and future forest management needs to understand this relationship in quantitative terms to help forests provide a full range of the potential benefits. While Allen et al.'s (2005) conclusion that "long-term productivity of intensive silviculture is sustainable only if soil is cared for" is still true, there are aspects of soil condition that once compromised are nearly impossible to restore within the timeframe of modern forest management planning.

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