



Forest Carbon Management: a Review of Silvicultural Practices and Management Strategies Across Boreal, Temperate and Tropical Forests

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Abstract

Purpose of Review Carbon sequestration and storage in forest ecosystems is often promoted as a solution for reducing CO₂ concentrations in the atmosphere. Yet, our understanding is lacking regarding how forest management strategies affect the net removal of greenhouse gases and contribute to climate change mitigation. Here, we present a review of carbon sequestration and stock dynamics, following three strategies that are widely used in boreal, temperate and tropical forests: extensive forest management, intensive forest management and old-growth forest conservation.

Recent Findings Several studies show that specific forest management strategies can improve carbon sequestration capacity and soil carbon storage. Within these studies, the old-growth forest conservation strategy results in greater carbon storage in soils than do extensive and intensive forest management. Intensive forest management enhances forest carbon sequestration capacity through afforestation using fast-growing species, mechanical soil preparation from low to moderate intensity and N fertilization. Extensive forest management is an intermediate compromise regarding carbon sequestration and soil carbon storage, between conservation and intensive forest management strategies. With respect to silvicultural treatments, partial cutting is a practice that increases forest carbon sequestration rates and maintains higher carbon storage in soils compared to clear-cuts. Each silvicultural practice that is discussed in this review showed a similar effect on forest carbon in all biomes, although the magnitude of these effects differs mainly in terms of heterotrophic respiration.

Summary To achieve sustainable management and fulfill industrial demand and profitability, specific gaps must be dealt with to improve our scientific knowledge regarding forest carbon sequestration in a climate change context, mainly through the integration of the three aforementioned strategies in a functional zoning approach at the landscape scale. We present a review with promising strategies for guiding sustainable forest management in such a global context.

Keywords Carbon sequestration and storage · Sustainable forest management · Silviculture · Climate change · Partial harvest

Abbreviations

C Carbon
CC Clear-cutting
CSS Carbon sequestration and storage

EFM Extensive forest management
FMS Forest management strategies
GPP Gross primary production
HWP Harvested wood products
IFM Intensive forest management
MSP Mechanical soil preparation
NEP Net ecosystem production

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NPP	Net primary production
PC	Partial cuts
PCT	Pre-commercial thinning
R_a	Autotrophic respiration
R_h	Heterotrophic respiration
SOC	Soil organic carbon

Introduction

Forest ecosystems offer crucial and diverse services to societies around the world, by acting as primary habitats for a wide range of species, supplying wood, supporting biodiversity maintenance and conservation and being indispensable to both indigenous societies and the overall maintenance of human health [1]. Second only to the oceans, world forests play a major role in the carbon (C) cycle as they account for a greater part of C exchange between the atmosphere and terrestrial biosphere than do other land biomes, thereby contributing to climate change mitigation [2•, 3]. Forest ecosystems store more than 80% of all terrestrial aboveground C and more than 70% of all soil organic carbon (SOC) [4]. In 2011, world forest C stocks were estimated to be 861 Pg, where soil to a depth of 1 m constituted the main pool (44%), followed by biomass (42%), deadwood (8%) and litter (5%) [2•]. Between 1990 and 2015, this stock declined by 13.6 Pg; most of this decline has occurred in living biomass and soils, and mainly in tropical forests [5]. Recently published work has indicated that world forest ecosystems remove nearly 2 Pg year⁻¹ of C from the atmosphere through net growth, thereby absorbing about 30% of anthropogenic CO₂ emissions [5], [6].

For the purpose of this review, we have divided forest management practices and strategies between intensive and extensive forest management. Intensive forest management (IFM) is a strategy that is widely used to increase productivity and timber quality in the shortest period to meet growing industrial needs and increase profitability [[7]•]. To achieve potential site productivity, IFM is based upon several practices including planting, genomic improvement, site preparation, fertilization, enhanced protection and silvicultural treatments, which depend upon the frequency and intensity of harvesting during the rotation [7•]. In contrast, an extensive forest management (EFM) strategy has been defined as “the practice of forestry on a basis of low operating and investment costs per acre” [8]. EFM involves the use of modified cuts (partial cuts and selective cutting) and other silvicultural treatments to promote natural regeneration [7•]. Furthermore, EFM that is based upon moderate harvesting intensities and long rotations could be used not only to increase C storage, but also to provide other economic and ecosystem

services [9]. However, Irland [7•] noted several broad contrasts between the ends of the spectrum of intensive versus extensive forest management: (a) IFM uses an even-aged structure with single species and is characterized by short rotations, (b) whereas EFM is based upon a multiple-age structure, with or without mixtures, and is characterized by longer rotations. The concept of EFM is also different from that of the ecosystem-based management approach, in that the latter aims to maintain forest composition and structure in an attempt to emulate natural disturbance regimes and natural vegetation patterns [10]. IFM and EFM strategies could be represented in the form of an ecological gradient that ranges from a state that is considered to be natural to a state that is considered to be artificial, which is strictly artificial in the case of IFM and natural or semi-natural in the case of EFM. The two strategies represent a gradient ranging from intensive (plantation) to extensive management and from lower to high harvesting intensity and rotation length.

Earth’s human population has reached 7.7 billion and is expected to reach 9.2 billion by 2050 [11]. Global population increase and land use expansion to supply human demands for wood products and other services are the main challenges of forest management [12] and one of the main causes of deforestation (e.g. forest conversion to agricultural land and urban areas). The three major forest biomes are tropical, temperate and boreal forests. These biomes mostly occur at different latitudes and experience different climatic conditions with a large community of vegetation. Over 25 years (1990 to 2015), global forest area decreased from 4.128 to 3.999 Gha [13]. The vast majority of forest loss has been observed in the tropics, where the rate of loss fell by 39%, from 10.4 Mha year⁻¹ in the 1990s to 6.4 Mha year⁻¹ from 2010 to 2015 [13]. Over the same period, boreal forests showed an increase in area, while temperate forests had a lower deforestation rate (–0.01%), compared to tropical forests [14]. The recent Food and Agriculture Organization (FAO) report showed that between 2015 and 2020, the world rate of deforestation was estimated at 10 Mha year⁻¹, down from 16 Mha year⁻¹ in the 1990s [14]. Yet, maintaining and enhancing forest ecosystem carbon sequestration and storage (CSS) is progressively becoming a fundamental goal for sustainable forest management [15••]. In fact, according to the Kyoto Protocol and United Nations Framework Convention on Climate Change (UNFCCC), the potential mitigation of forest ecosystems (C sequestration) makes C management a promising solution to climate change [15••], [16••].

Afforestation and old-growth forest conservation are natural means of countering deforestation. Indeed, some authors have proposed that old-growth forests should be left intact and conserved, given that they continue to conserve considerable

quantities of C, which is stored in aboveground biomass and the soil [17••]. In contrast, others have asserted that in younger managed forests, the C sequestration rate is much higher than in old-growth forests; by increasing harvesting, all at once, C storage in harvested wood products (HWP) would increase [18], [19]. Recent work also has demonstrated that adaptive silviculture practices (e.g. less intensive harvesting) could be among those strategies that would increase long-term CSS, in both ecosystems and HWP [19], [20••], [21]. Thus, it seems that forests can be managed to mitigate global change through three major, non-mutually exclusive strategies: (1) preserving existing forest C stocks through conservation, mainly of the old-growth forest, (2) using EFM that is based upon partial cuts (PC) and selective cutting to increase natural forest productivity and preserve parts of the existing forest C stocks [22], [23], [24•] and (3) achieving high productivity through IFM practices (e.g. afforestation, fertilization, genomics) [25], [26]. These forest management strategies (FMS) must take into consideration all possible ecosystem services, from environmental, economic and social perspectives.

Climate change over the coming decades is expected to exert substantial effects on forest ecosystems worldwide [26]–[28]. Consequently, the development of FMS that would increase forest C sequestration capacity is becoming a priority for forest management around the globe. Yet, integrating CSS into FMS is a challenging prospect for forest managers who have not traditionally included environmental issues among their objectives. The main goal of this review is to synthesize the most relevant information about three globally used FMS (EFM, IFM and old-growth forest conservation) that can be used (separately or combined) to enhance C sequestration in living biomass and SOC storage at the landscape scale, which would subsequently provide instructions and recommendations for managers. First, we briefly recall the general principles of the forest C cycle, and the resulting patterns of C allocation in boreal, temperate and tropical forest ecosystems. Second, we review the effects of different IFM practices on CSS, mainly fertilization, mechanical site preparation, genetic improvement and afforestation. Third, we assess the contrasting effects of IFM and EFM practices on CSS, including silvicultural treatments (e.g. thinning, clear-cuts, partial cuts) and system structures (even-aged/uneven-aged, monoculture/mixtures). Particular emphasis has been placed on old-growth forest conservation to build up SOC stocks. World forest ecosystems are considered as nature-based climate solutions and present exciting opportunities for the private and public sectors to meet their climate goals. This review gathers and provides relevant information to guide sustainable management and implement participatory decision-making in forest planning under global changes.

Boreal, Tropical and Temperate Forest Carbon Cycles: Mechanisms and Allocations

General Forest Carbon Cycle

The forest C cycle is characterized by a biological component (forest ecosystem) and an industrial component (forest products) (Fig. 1) [19], [29]. The forest C cycle is generally assessed and monitored by estimating the following: gross primary production (GPP), autotrophic respiration (R_a) (comprised of maintenance and growth respiration), net primary production (NPP) (Eq. 1), heterotrophic respiration (R_h) and net ecosystem production (NEP) (Eq. 2) [18], [30]. At the same time, HWP could be integrated into this assessment through lifecycle analyses to evaluate the forest sector's net C balance [19], [29]. The biological C cycle is driven by several climatic parameters (e.g. temperature, precipitation) [31] and is influenced by land use and management through natural disturbances and a variety of anthropogenic actions such as afforestation, deforestation, fertilization, irrigation and harvesting [20••], [21], [32]. In the industrial cycle, HWP is considered by the Intergovernmental Panel on Climate Change (IPCC) to be a significant loss of C from forest ecosystems and may remain outside the ecosystem boundaries for a variable period of time. The C that is stored in timber or furniture can remain sequestered for a very long time, while the C in fuelwood results in an immediate emission [19], [29]. HWP contributions to C storage and emissions depend upon their life cycles [20••]. Worldwide, the annual HWP potential for C sequestration is about 2.8 Pg year⁻¹, with contributions of 1.8 Pg year⁻¹ (64%), 0.7 Pg year⁻¹ (25%) and 0.3 Pg year⁻¹ (11%) from tropical, temperate and boreal forests, respectively (Fig. 1) [33].

$$\text{NPP} = \text{GPP} - R_a \quad (1)$$

$$\text{NEP} = \text{NPP} - R_h \quad (2)$$

Forest Carbon Cycle Under Different Climates

There are three major forest types: boreal, temperate and tropical. According to the recent assessment report of FAO [14] and Keenan et al. [13], (i) boreal forests occupy much of the circumpolar region between 50° and 70° N and are considered as the world's second-largest forest biome with an area of 12.2 million km² (27% of world forest in 2020); 43% of this area is in Siberia, 36% is in North America and 21% is in Europe. This forest provides 37% of global wood consumption [34•], [35••], [36]. The dominant genera in the boreal biome are *Picea*, *Pinus*, *Abies*, *Populus* and *Betula*.

Forest Carbon cycle

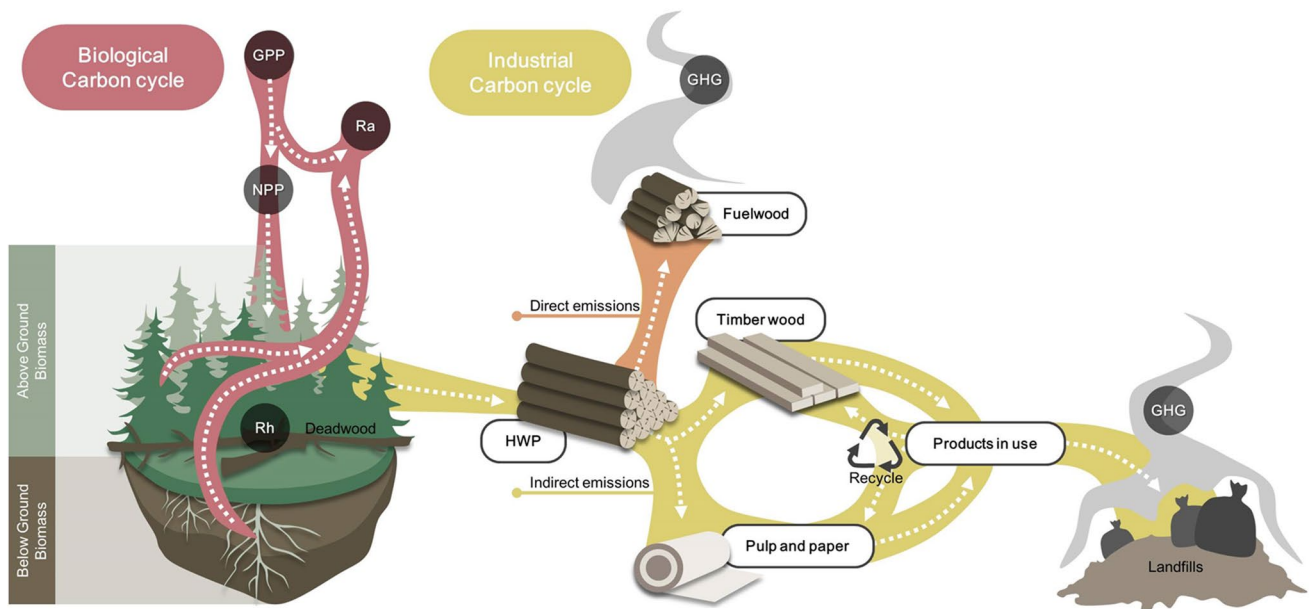


Fig. 1 Forest carbon cycle and biological and industrial components, including gross primary production (GPP), net primary production (NPP), autotrophic respiration (R_a), heterotrophic respiration (R_h)

and harvested wood products (HWP). HWP greenhouse gases (GHG) emissions depend upon their life cycles and uses, [29][19] adapted from Gower and Smyth et al.

(ii) Of the 25 to 33 million km² of forests covering the globe, about 6.9 million km² (16% of world forests in 2020) is temperate forests, which are found between the tropical and boreal regions. These forests cover both hemispheres at latitudes ranging from 25 to 50°. In this biome, the dominant tree genera include broadleaved deciduous (e.g. *Fagus*, *Acer*, *Fraxinus* and *Quercus*) and needle-leaved evergreen (e.g. *Picea*, *Abies*, *Pinus*) [37]. (iii) In contrast, almost half of the world's forested areas consist of tropical forests (47%) [14]. The tropical rainforests, which globally constitute one of Earth's largest biomes (major life zones), are dominated by broad-leaved trees that form a dense upper canopy (layer of foliage) and contain a diverse array of tree species (more than 20,000 species have been observed) (e.g. *Ceiba*, *Cecropia*, *Agathis*) [38]. Those forests grow mainly in three regions: the Malesian botanical subkingdom, tropical South and Central America (especially the Amazon Basin) and West and Central Africa [38].

Biomass Carbon Pool

GPP, NPP, R_a and R_h of boreal evergreen forests are 873 g m² year⁻¹, 334 g m² year⁻¹, 539 g m² year⁻¹ and 314 g m² year⁻¹, respectively. For the same parameters, values of 1201 g m² year⁻¹, 446 g m² year⁻¹, 755 g m² year⁻¹ and 275 g m² year⁻¹ were estimated respectively in boreal

deciduous forests (Fig. 2) [35••]. With an average GPP exceeding 3000 g m⁻² year⁻¹ in tropical evergreen and deciduous stands, those forest ecosystems have greater C sequestration capacity, despite also having higher average values of R_a and R_h (> 2000 g m⁻² year⁻¹) (Fig. 2). These respiratory demands can reduce the tropical forest NEP substantially [35••]. In contrast, temperate evergreen and deciduous forests respectively sequester 811 g m² year⁻¹ and 702 g m² year⁻¹ [35••], [39]. Temperate evergreen forest R_a and R_h values are 951 g m⁻² year⁻¹ and 420 g m⁻² year⁻¹, correspondingly, while deciduous forest R_a and R_h estimates are 673 g m² year⁻¹ and 387 g m² year⁻¹, respectively (Fig. 2). However, the total C sink of boreal forests is about 0.50 Pg year⁻¹, lower than that observed in temperate (0.72 Pg year⁻¹) and tropical (1.2 Pg year⁻¹) biomes [34•]. Boreal forest ecosystems store 88 Pg of C in living biomass (aboveground and belowground), which is higher than that observed in temperate forests (59 Pg) and lower than that estimated for tropical forests (212 Pg) [34•]. The tropical forests, on average, can store 50% more C in the trees than any other type of forest [2•]. These forests hold more C in their biomass than do temperate and boreal forests combined, but the high rates of deforestation that they are currently experiencing will likely cause more C to be released into the atmosphere (1–2 Pg year⁻¹) [40].

Soil Carbon Pool

Despite the lower observed C storage in living biomass in boreal forests, they store 471 Pg in soil, which is a very high value compared to tropical (216 Pg) and temperate (100 Pg) ecosystems [34•]. Boreal forest soils store 60% of the world's SOC [2•]. The C distribution in common boreal forest soils has been described by Deluca and Boisvenue [36]; Cambisols and Podzols house 5–40 Mg ha⁻¹ of C in the O horizon, and about 10–90 Mg ha⁻¹ in surface mineral soils (0–15 cm). An additional 10–150 Mg ha⁻¹ is stored at 15–45 cm depths in upland forest soils, while there is generally little C below 1 m in upland soils [36], [42•]. Yet, boreal forest stores more C in organic soil (84%) than in living biomass (16%), while 55% of C in temperate and tropical forests is stored in living biomass [34•]. During a 17-year period (1990–2007), SOC stocks in boreal and temperate forests increased by 4.5% and 7.6%, respectively, as forest area expanded following agricultural abandonment and immature forests grew with reduced harvesting. Meanwhile, SOC in tropical forests declined by 7.7%, which was caused by deforestation within intact tropical forests [43].

Boreal Peatland Carbon

Peatlands occupy about 4% of the global land surface and are located mainly in the boreal biome; they store about 30% of global SOC [42•]. In addition to boreal C storage in biomass and soil pools, boreal peatlands contain an additional soil C stock of 260–600 Pg [[44]]. Yet, forested peatlands have a lower C sequestration potential (15.9 g m⁻² year⁻¹, averaged over six peatland study sites) compared to natural forests and afforestation efforts [45••]. Magnan et al. [45••] noted that the quantity of C stored in the peat at 50–350 cm depths (62–172 kg m⁻²) greatly exceeds aboveground tree biomass C (1.5–5.3 kg m⁻²), while the organic layer (≤ 30 cm) in adjacent paludified stands holds around twice as much C as does the live biomass. Under climate change, Lavoie et al. [42•] have suggested that most northern forested peatlands (located in eastern Canada, Alaska, Russia and Fennoscandia) will continue acting as C sinks for the foreseeable future, given that precipitation is expected to increase in these areas. In contrast, C sequestration rates in forested peatlands of Western and Central Canada will decline, thereby becoming potential C sources, since precipitation is predicted to decrease [42•].

The dynamics of C budgets differ considerably among biomes (Fig. 2). Tropical forests sequester more C (high GPP, 3351 g m² year⁻¹) than temperate forests, but their estimates of R_h and R_a are very high, given the long growing season and hot climate [34•], [41••]. In contrast, the boreal forest is characterized by a cold climate and a short growing season, which results in a lower C sequestration

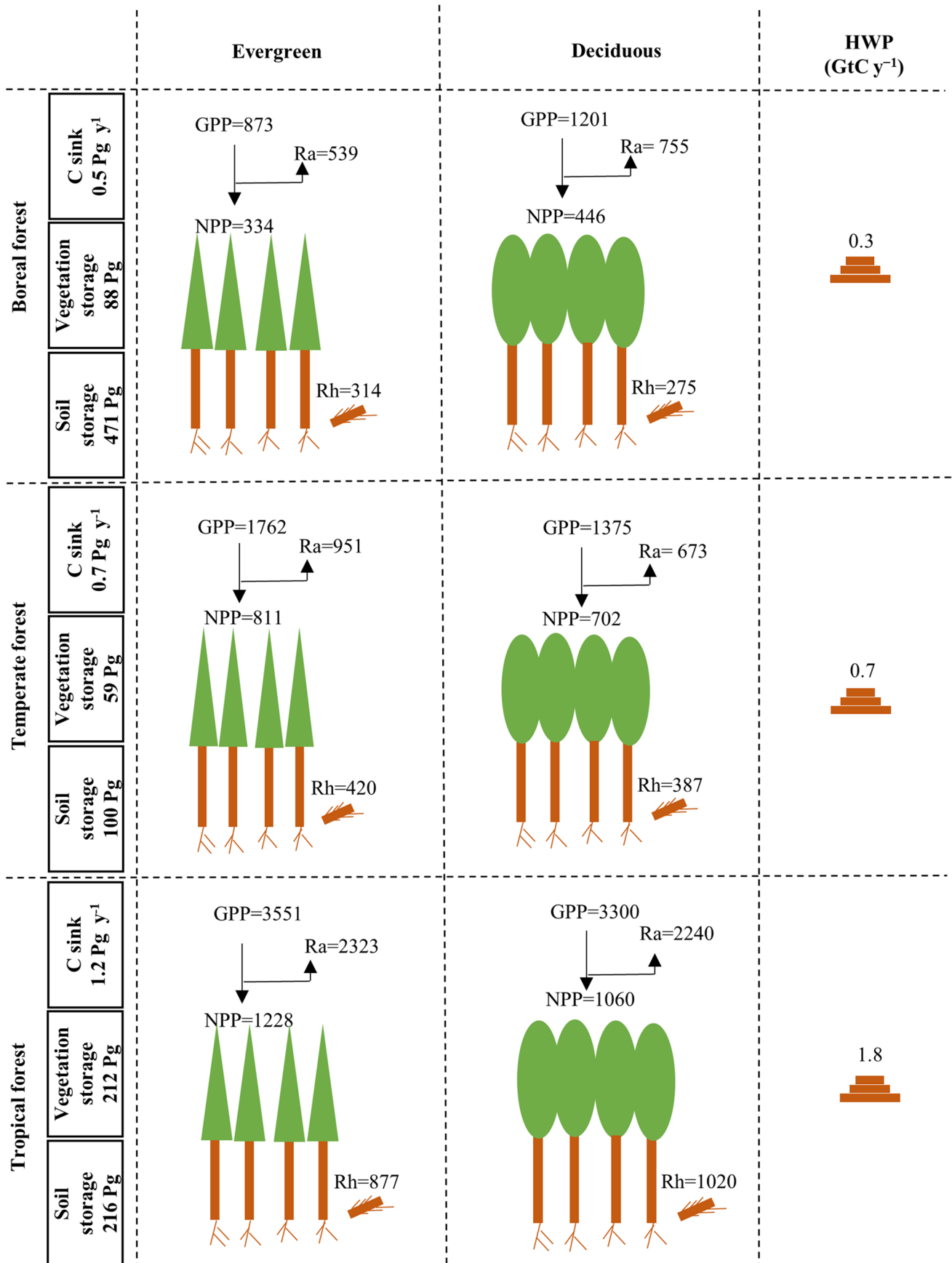
capacity, together with slow decomposition and growth rates [41••]. The highest NEP values are observed in temperate forests (> 200 g m² year⁻¹ for both coniferous and broadleaf forests); this may be related to forest management, which is more intensive in this biome and aims to increase the production of woody biomass [35••]. Yet, there are small differences among these biomes in terms of C sequestration efficiency. For instance, if we calculate production efficiency (NPP/GPP) for the evergreen forests, as defined by Goulden et al. [18], we find efficiency values of 34%, 38% and 46% for tropical, boreal and temperate forests (Fig. 2), respectively. Nevertheless, these differences in C dynamics may affect the ability of FMS to increase C sequestration and storage for each biome.

Impacts of Forest Management Strategies on Carbon Dynamics

Intensive Forest Management

Genetic Improvement

Given that the primary metric of a forest's value has been its merchantable volume, plantation forestry that is based upon successful breeding of superior tree genotypes (fast-growth species) is becoming used more widely to maximize productivity [16••], [26], [41••]. Selection for fast-growing genotypes may generally increase C sequestration rates by approximately 10 to 20%, depending upon what species is being grown [46]. Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) is grown as a plantation species in Europe, South America, New Zealand and Australia, and throughout its extensive natural range in western North America. Chappell et al. [47] reported that Douglas-fir growing on a good site (site index = 32 m) would be expected to yield 174 m³ ha⁻¹ at the end of a 50-year rotation if they were naturally regenerated. Through a similar site regeneration process using genetically improved stock, which was subsequently thinned and fertilized, Douglas-fir can produce 643 m³ ha⁻¹ in 50 years [47]. In Canada, boreal forest hybrid poplar clones (e.g. *Populus balsamifera* L. × *P. simonii* Carrière, *P. deltoides* × *P. × petrowskyana*) are generally selected for C uptake because of their rapid rates of growth [48]. In addition, there is a difference between monoclonal and polyclonal cultures, in terms of growth and tree size, thereby affecting the C stock in the aboveground biomass [48], [49]. Elferjani et al. [49] showed that the stem volume of hybrid poplar in a monoclonal culture is 6.1 m³ ha⁻¹, while it is 21% higher in a polyclonal culture (7.4 m³ ha⁻¹). Fast-growing tree species typically sequester more C at a young age, whereas C sequestration rates for slow-growing trees may



◀**Fig. 2** Carbon sequestration and storage in the boreal, temperate and tropical forests, together with estimates of important carbon cycle components: gross primary production (GPP), net primary production (NPP), autotrophic respiration (R_a) and heterotrophic respiration (R_h), estimated in $\text{g m}^{-2} \text{ year}^{-1}$. Estimated values are [32], [33], [34•], [35••], [36] adapted from literature reports on the carbon cycle. They require careful scaling up over very heterogeneous forest landscapes. In fact, there is a substantial variation among the geographic regions within each biome

reach a peak after many years have elapsed, depending on growth rate patterns and rotation length [25].

Today, the main issues of concern around the application of genetic engineering in forestry are about native biodiversity and the provision of ecosystem services. Using such techniques may reveal several drawbacks, such as less genetic diversity, invasive behaviour and less favourable habitat than natural forests [50]. Maintaining natural patterns of heterogeneity, including species diversity, across spatial and temporal scales is consistent with current principles of ecosystem management. The risk assessment of using such techniques is considered important and should include aspects such as the evaluation of the probability of establishment, spread and related undesirable consequences of establishing species that have been improved genetically [51]. Given the complex nature of the risks, Mathews and Campbell [51] state that an interdisciplinary approach including ecologists and molecular biologists is required.

Fertilization

The most critical elements for forest NPP are macro-nutrients (N, P, K, Mg and Ca). Both N and P are particularly important nutrients for ecosystem structure, processes and function, since their absence limits the production of plant biomass and growth. From previous work, N has been found to limit forest NPP on relatively young soils, whereas P is limiting on old soils [[52]]. Economically optimal intensive fertilization increased timber supply by 20% [47], [53], [54]. Fertilization is usually associated with forest plantations, especially those composed of conifer species, such as Douglas-fir, spruce (*Picea* spp.) or maritime pine (*Pinus pinaster* Aiton); supplemental nutrient applications can dramatically increase forest C sequestration capacity [54]–[56]. For instance, Jassal et al. [56] found that fertilization of 58-year-old Douglas-fir stands with 200 kg ha^{-1} of urea–N elevated NEP by 64%, i.e. NEP increased from 326 to 535 g m^{-2} of C. Generally, nutrient limitation can reduce leaf area index (LAI), photosynthetic capacity or both [[52]]. Higher soil nutrient contents could increase soil decomposition and microbial activity, thereby decreasing SOC in the short term [57]; SOC could increase in the long term, since fertilization increases vegetation growth. Yet, N fertilization has been demonstrated to be the only forest management practice

that has had a positive effect on the soil C pool, mainly in the mineral soil (A horizon) [58]. Many recent studies also have demonstrated that fertilization of temperate and boreal forests has a high potential for reducing ecosystem respiration (R_h and R_a) [54]. Nevertheless, in boreal forests as the growing season is likely to be prolonged by ongoing climate change, this would lead to higher N demand. N can be supplied by atmospheric deposition, but deposition is unlikely to cover the N demand at the appropriate rate, particularly in boreal forests where the inputs are lower [59] and tend to be intercepted by the thick bryophyte groundcover [60], [61]. Beyond macro-nutrients, forest C sequestration capacity may be limited by deficiencies of some trace elements, such as Fe, Cu and Zn [55].

The fertilization timing and frequency generally depend upon the site nutrient content and the planted species (broad-leaves vs. coniferous) [53]. In contrast, the application of fertilizers releases nutrients (including phosphate P) to the freshwater bodies that contribute to their eutrophication (accumulation of minerals and nutrients), particularly nearby rivers or lakes [62]. However, in order to both improve forest C sequestration capacity and reduce environmental pollution, appropriately balanced fertilization is required.

Mechanical Soil Preparation

Forest C sequestration capacity can be significantly enhanced by careful mechanical soil preparation (MSP) prior to afforestation or following forest harvesting. Scarification, mounding, sub-soiling/ripping and deep soil cultivation (ploughing to 50 cm depth) are common MSP treatments that are used in forestry. Superficial cultivation of soil layers could be included among those treatments, since this process aims to remove competing vegetation and logging slash, to facilitate planting or direct seeding [63], [64•]. MSP is carried out for many reasons: to promote natural regeneration, to reduce competition between tree seedlings and understory vegetation, to create micro-sites that favour seedling survival and to enhance forest growth by increasing nutrient content, and element mobilization in soils [55], [61], [64•].

MSP techniques could also temporarily reduce soil C stocks for the short or medium term, since they can increase decomposition rates [65••]. Nevertheless, the real effect of MSP on forest soil C depends upon the methods that are used and their intensities [63], [64•]. For instance, Jiménez Esquilín et al. [66] noted that soil C (O horizon and uppermost mineral soil) had decreased by 50%, as measured 24 years after scarification. Nordborg et al. [63] asserted that no differences emerged among MSP treatments when the whole soil profile was considered; however, losses were higher in the O horizon after patch scarification (5 cm deep) compared to deep-soil cultivation. Also, Mjöfors et al. [[67]••] demonstrated that site preparation increases forest ecosystem

C stocks over the long term. They further recommended mounding or disc trenching to promote C sequestration, since these treatments did not affect soil C stocks down to a depth of 30 cm. Consequently, low- or moderate-intensity MSP techniques had no appreciable effect on soil C, but increased the volume of soil that roots can readily exploit by decreasing bulk density. Therefore, these treatments enhanced forest productivity, leading to greater litter production, thereby increasing soil C content over the long term [63], [64•], [68], [69]. In previous studies, roots have been shown to concentrate in micro-sites with mixed soil organic matter and mineral soil in a deep cultivated soil profile [69]. If the organic material is ploughed into the mineral soil, water relations are often improved by higher infiltration capacity so that moisture is preserved, thereby enhancing forest NPP [68].

By contrast, intensive MSP treatments are recommended in wetland soils, since these enhance tree establishment, lower the water table and increase oxygenation of the soils [20••], [42•]. All MSP techniques definitely reduce soil C sequestration and turn peatlands into significant C sources, because of the high rates of decomposition. Moreover, MSP reduces the water content while improving soil and root aeration, thereby enhancing tree productivity and increasing ecosystem R_h [42•], [70]. Yet, Lavoie et al. [42•] have stressed that in peatlands where wildfires are severe and frequent, MSP could become problematic for future C emissions. Nevertheless, peatlands hold vast stocks of C in their soils; their conservation is potentially a natural solution for mitigating climate change.

Afforestation and Reforestation

Planted forest areas have increased from 168 to 278 Mha since 1990 [14]. These plantations account for 7% of the world's forest area due to massive afforestation programs to achieve CO₂ emissions reduction targets (Kyoto Protocol, REDD+) [13]. The Kyoto Protocol allows countries to claim as credit any C that is sequestered as a result of reforestation and afforestation. C sequestration in both soil and above-ground biomass is one of the essential benefits of afforestation and reforestation, as is increasing HWP C stocks [25], [71]. However, fast-growing species are the most frequently used species in afforestation, given that they have a high potential for C sequestration [25], [46], [47]. Species composition, genetics (fast-growth species), spacing and initial land use are the main factors affecting CSS in forested land [46], [72•]. Also, the C sink capacity of forest plantations can be maximized by prolonging the rotation length and adopting suitable practices for each species (e.g. spacing, fertilization, MSP and composition) [50], [54], [55].

Some frequently planted species are more vulnerable than others to disturbances. For example, *Eucalyptus* is a

major component of fire-prone or fire-driven ecosystems of its native Australia. Yet, species in this genus are vulnerable to wildfires in the Mediterranean basin and other regions of the world. Moreover, regions where it has been introduced have undergone massive land use change, especially when they are planted as industrial monoculture forest stands [73]. Likewise, balsam fir (*Abies balsamea* [L.] Miller), white spruce (*Picea glauca* [Moench] Voss) and black spruce (*Picea mariana* [Miller] BSP) are vulnerable to a co-evolved insect defoliator, i.e. the spruce budworm (*Choristoneura fumiferana* [Clemens]) in the boreal forest of eastern North America [74], [75]. For these tree species, their C sequestration potential and stability of C stocks during a disturbance event is still a matter for research and debate. In the interim, tree species that are less vulnerable to catastrophic fire, wind damage, insects and drought can be planted or maintained on the landscape [76]. Yet, with genetic control, planted species vulnerability could be reduced. For instance, Dale et al. [76] have noted that tree invasion by phloem-feeding insects, such as bark beetles (e.g. *Dendroctonus* spp., *Scolytus* spp.), is controlled in part by the ability of trees to produce oleoresins; indeed, the primary defence of pine trees (*Pinus* spp.) is oleoresin, which is a mixture of monoterpenes and resin acids that provides a chemical and physical barrier against biotic intrusions [77], [78]. Wildfires are not only followed by bark beetle outbreaks in coniferous forests (e.g. *Pinus radiata* D. Don, *P. pinaster*), but insect irruptions can result in their genesis by weakening and killing susceptible individuals, thereby creating a ready source of fuel [79]. Therefore, planting selected tree species and genotypes with relatively high oleoresin contents could limit insect outbreaks. Furthermore, the use of mixed stands may reduce the risk of pest and pathogen outbreaks, compared to monocultures, since there is a negative correlation between tree species diversity and the level of damage [80].

The effects of afforestation and reforestation on SOC are not fully understood. Some researchers have pointed out that afforestation could decrease SOC, whereas others have reported positive effects. For instance, afforestation of pastures with pine plantations leads to decreased SOC [81], but other studies have presented contradictory results [82]. For broadleaf plantations, the results are quite variable [81], [83]. A review of the literature suggests that the effect of afforestation on SOC is generally related to initial land use (e.g. forest land, grassland, cropland) [20••], [84]. From a meta-analysis on data that were obtained from 74 publications, Guo and Gifford [81] determined that soil C declines after land use conversions from pasture to plantation (−10%) and native forest to plantation (−13%), but it increases after land use changes from cropland to plantation (+18%) and cropland to secondary forest (+53%).

Applied Silvicultural Treatments in Extensive and Intensive Forest Management

This section presents common silvicultural treatments and practices that are applied in EFM and IFM (or both), and which are used to improve forest growth and stand harvested volume after stand establishment. Generally, practices with high operating and investment costs such as pre-commercial thinning (PCT) and pruning (including coniferous brushing and formative shaping of broadleaves) are used in IFM (afforestation) [85]–[88]. PCT also could be used in EFM to improve the uneven-aged stand volume over a long rotation period. Clear-cutting (CC) is globally the most widely used silvicultural treatment that is applied in IFM [89]–[91]. About 50% and 93% of all timberlands in temperate and boreal forests respectively involve CC methods [90], [93•], while both CC (mainly in the tropical rainforest) and selective logging have been widely employed to harvest tropical forests [91]. In EFM, PC and selective cutting treatments are frequently used to promote natural regeneration [93•]. PC ranges from retention silviculture to more selection-oriented treatments that have been adapted to the boreal forest. It generally has been more recently applied to this biome (<20 years) [89], despite being used in other biomes for at least a century [91].

Pruning

Pruning is applied to specific high-value tree species to improve stem quality (reduce knots size and presence) and vigour, together with overall tree growth [85], [86]. Pruning can also increase forest C sequestration rates. For example, a study by Medhurst et al. [85] on native Australian blackwood (*Acacia melanoxylon* R. Brown) demonstrated increased photosynthetic capacity between 2 and 6 weeks after pruning, to levels that were as much as 50% higher than the no-pruning controls, depending upon pruning location (i.e. upper-, middle- or lower-crown). C sequestration was found to be 33% and 62% higher in the upper- and middle-crown treatments, respectively, compared to the unpruned treatment [85]. Yet, Pinkard and Beadle [86] have claimed that lower pruning of 50% of the crown depth had no effect on height or diameter increment, while removal of 70% of the lower crown depth resulted in severe reductions in both parameters, thereby reducing forest C sequestration rates. Regarding SOC, pruning has an effect similar to stem-only harvesting [94]. Indeed, when the branches are removed and left in situ, their C and nutrient contents are transferred to the deadwood pool, increasing SOC in the long term as a direct result of the decomposition process.

Pre-commercial Thinning

PCT is conducted in the interval between canopy closure and final harvest, removing the smaller-, weaker- and poorer-quality stems, and could be applied several times during the rotation period [95], [96]. It is largely applied in even-aged, post-fire stands of black spruce and jack pine (*Pinus banksiana* Lambert), and to second-growth stands of balsam fir. PCT generally precedes the final cut by 15–20 years [89], [97]. PCT from below initially redistributes C among pools, i.e. from the biomass to deadwood, and increases forest C sequestration capacity as a long-term effect, which mainly is expressed in the biomass [87], [88]. In fact, the application of this method reduces competition for light, water and nutrients, thereby improving tree growth; this positive effect depends upon the intensity and frequency of thinning [95], [98]. Moreover, in a 25-year study by Hoover and Stout [96], thinned-from-below plots (about 35% basal area removal) had greater volume production and C sequestration rates than plots where thinning from the middle or above was applied (Supplementary Information). Thinning-from-below as a pre-commercial treatment could increase CSS, because all harvested trees remain on the ground (increasing soil C stocks), while residual trees accumulated C at a faster rate, depending upon the species [87], [94], [99••], [100]. For instance, Ruano et al. [100] report that 5 years after thinning, the height and the basal area of Aleppo pine (*Pinus halepensis* Miller) had increased by 20% compared to control stands. PCT treatments from above or middle have been shown to display negative C sequestration rates, storing significantly less C than thinning-from-below or control treatments (no thinning) [96]. Thinning-from-above could increase the decomposition process and ecosystem respiration (C loss), since this treatment exposes deadwood and litter to light and stimulates microbial activity [101]. For instance, Concilio et al. [102] and Campbell et al. [101] report a 43% increase in soil respiration 2 years following thinning-from-above of a mixed-conifer forest. On the other hand, thinning could stimulate the shrub layer, which can also result in net C loss and a lower C sequestration rate of the stand [101]. In some circumstances in boreal forests, root grafting could affect the growth response to thinning. For instance, in jack pine boreal forest, root grafting could considerably increase the radial growth of trees after thinning [103].

Harvesting Treatments: Clear-Cuts Versus Partial Cuts

Like severe wildfires, CC may switch forests from being a sink to a source of C by increasing respiration and reducing leaf biomass and, therefore, photosynthesis in the period following disturbance (Fig. 3) [30]. Using more than 180 site-years of eddy covariance measurements of C fluxes that were made on forest chronosequences in North America,

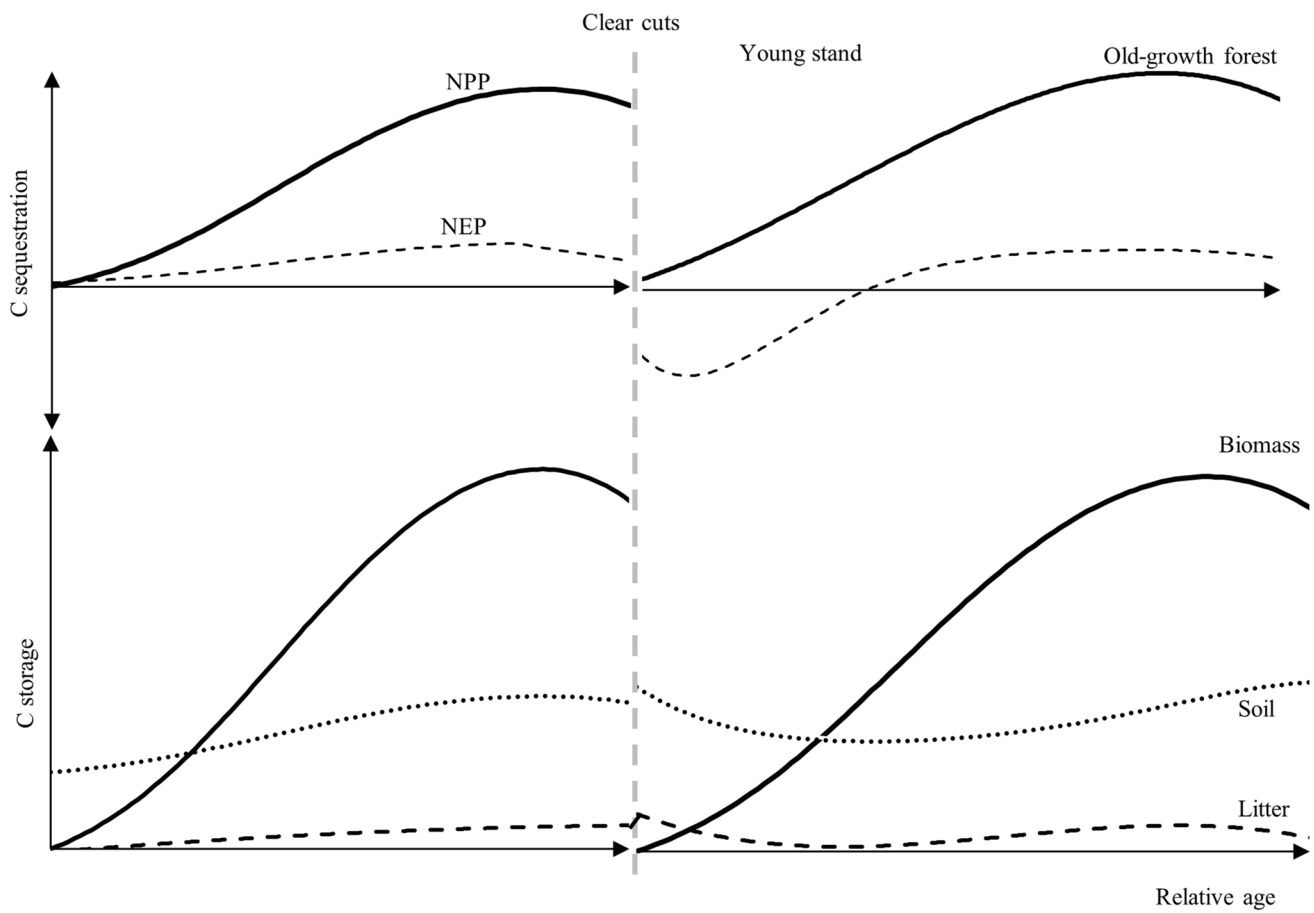


Fig. 3 Theoretical C stock and flux changes of a forest ecosystem following a stand-replacing disturbance event (clear-cut), [18][30] adapted from Goulden et al. and Liu et al. with the changes in net primary productivity (NPP) and net ecosystem productivity (NEP)

Amiro et al. [104] found that NEP exhibited C losses from all ecosystems following a stand-replacing disturbance. Post-disturbance C balances after CC depend upon many ecosystem processes, including regeneration and vegetation succession, photosynthesis and respiration [18]. Canopy removal that is associated with CC can increase the amounts of solar radiation and precipitation that reach the soil surface, thereby increasing soil temperature and soil moisture, and consequently increasing R_h and reducing NEP [105], [106]. Over time, NPP and biomass accumulation increase in the youngest stands, and inputs of new litter cause the detrital pools to build up, resulting in an extended period of C accumulation and a positive NEP. In the oldest stands, mortality and decomposition losses accelerate, which causes NEP to approach zero (Fig. 3) [18], [30]. Overall, the ecosystem attains net C gain after about 20 years following CC, due to forest regrowth [107]. CC exports close to 100% of the aboveground biomass pool as HWP and transfers the rest in the deadwood pool as harvest residues, thereby reducing NEP and altering the ecosystem NPP of the replacement stand [18], [30].

PC are thus gaining interest as alternatives to CC in the face of climate change, since they could enhance forest C sequestration, with possibly lower impacts on SOC [23], [58]. Bose et al. [89] defined PC as “a generic term, which refers to a whole range of treatments from clear-cutting with sparse, dispersed retention in which a few merchantable stems are left on site, to single-tree selection systems where the very evidence of a harvesting treatment might be too subtle to be noticed by an untrained eye”. PC includes a broad range of treatments, such as shelterwood cutting, selection (distant or close), retention systems and seed-tree systems [89], [108•]. Based upon a simulation model in the Canadian boreal forest focusing on red spruce stands (*Picea rubens* Sargent), Taylor et al. [109] found that total ecosystem C increased in PC stands throughout the 240-year simulation from 308.9 to 327.3 Mg ha⁻¹, while it decreased in CC stands to 305.8 Mg ha⁻¹. Based upon an ecosystem process model (CENTURY) that ran for 5000 years, Peng et al. [110] determined that PC could increase C sequestration, by about 36–40% in the boreal forest region.

The positive effect of PC on forest C sequestration depends upon harvesting intensity. In fact, Lee et al. [92] affirm that annual C assimilation rates in the post-harvest period (after 5 years) in boreal mixedwood stand were substantially higher in control (uncut forest: 3.1 Mg ha⁻¹ year⁻¹) than PC with two-thirds of the volume being removed (1.8 Mg ha⁻¹ year⁻¹), or when clear-cut (0.3 Mg ha⁻¹ year⁻¹). Most empirical studies, however, have been conducted at the plot scale (e.g. [23], [92], [111], [112]). Furthermore, experimental results from individual studies are highly variable, mainly due to differences in harvest intensity (removed volume) and the number of recovery years after cutting. For example, some studies have documented substantial increases in forest NPP and soil C storage following PC [92], [111], whereas others have shown non-significant effects or decreases in forest CSS [101], [113]. Consequently, the intensity at which PC is conducted is a very important consideration, to maintain this positive effect on residual trees. We must be able to predict long-term changes in forest C dynamics at regional and global scales under different intensities. For instance, Øyen and Nilsen [114] reported that PC intensity should not exceed 65% in southeast Norway to maintain forest biomass sustainability and preserve its contributions to C sequestration.

The success of the PC approach requires consideration of not only its intensity, but also its form. In fact, some forms of PC could increase post-cutting mortality that is incurred by disturbance, particularly windthrow [108•], thereby reducing NEP. It was determined from several studies that post-cutting mortality following PC ranges from 15 to 74%, which is attributable to windthrow [108•], [115]. Previous research has shown that mortality is proportional to harvest intensity ($r^2 = 0.3988$ [109]); it was highest for the treatment that had the highest intensity compared to the control and other treatments [108•], [116•]. Mortality rates that are associated with PC depend upon a range of factors: spatial patterns (edge, residual strips and trails), forest fragmentation and harvesting intensity. Montoro Girona et al. [108•] reported that 60% of residual trees were dead in seed-tree treatments, compared to 30% for shelterwood cuts. These results showed that experimental uniform shelterwood cuttings with 50% harvest intensity successfully reduced the proportion of tree loss compared to the seed-tree system that is employed in Québec's boreal forest. Shelterwood and seed-tree harvesting followed by scarification promotes regeneration through the creation of uniform openings in the canopy, while limiting the growth of competing vegetation [93•].

With respect to SOC, CC might reduce total SOC stocks relative to the effects of PC [65••]. Despite this potential difference, harvesting (PC and CC) exerts a more limited effect on SOC than it does on biomass [23], [65••]. After CC, soil C stocks appeared in many cases to remain relatively constant, with their variation being linked to C transfer from

the litter (Fig. 3) (e.g. leaves, lifted branches after the cut) and to the site conditions (mainly temperature) [18]. The meta-analysis that was conducted by Nave et al. [117] for temperate forests worldwide shows that harvesting generally results in a small reduction (−8%) in total soil C stocks, whereas the mineral horizons showed no significant change overall. In other cases though, forest harvesting had a critical effect on SOC. Covington's [107] results described SOC dynamics following forest harvesting in northern hardwood forests (New Hampshire, USA), showing a decline of 50% within 20 years following harvest. This decrease was attributed to accelerated decomposition and changes in litter inputs after harvest [118] and to changes in depth distribution of plant roots, altered soil water regimes and temperature regimes that accelerate decomposition [30], [87], [107]. SOC responds to the harvesting methods that have been applied: cut-to-length (short-wood), tree length and full tree (Supplementary Information). Cut-to-length and tree length contribute to the build-up of the SOC pool [94], while the full tree method increases ecosystem respiration and decreases total ecosystem and SOC stocks [[110]]. Soil respiration rates increase following harvesting but are substantially higher after full-tree harvest [119]. Johnson and Curtis [58] reported that harvest residues left on site after cut-to-length and tree length treatments increased SOC by +18%, while full tree harvest caused a decrease (−6%) over the long term. Post-harvest SOC dynamics are thus highly variable and depend not only upon silvicultural treatments, but also on a myriad of abiotic and biotic factors (e.g. soil texture and moisture, temperature, precipitation, species, stands). For instance, in three contrasting climatic zones (e.g. cool temperate, warm temperate and subtropical), Sun et al. [120] report that the total SOC of the 0–20-cm soil layer decreased with increasing mean annual temperature. Climate affects forest SOC by shaping both SOC inputs (changing plant productivity) and outputs (affecting soil fauna metabolism) [121].

Rotation Length

Another factor to consider in FMS at the stand level is rotation length, which is an effective way of managing the forest C budget [122]. Shorter rotation lengths are used in IFM, while long rotations are favoured in EFM. Rotation length is commonly used to manage timber yield, but it may also affect forest CSS depending upon tree species and management goals [123]. For instance, Scots pine (*Pinus sylvestris* L.) stands stored the largest total amount of C when applying the longest rotation length, which has a duration that can extend beyond 300 years [123]. Boisvenue et al. [122] have stated that C stocks were lowest in even-aged stands with lower rotation length (100 years), while it was higher in high rotation lengths with 400-year fire return intervals.

Pérez-Cruzado et al. [124] asserted that increasing rotation length from 10 to 20 years for southern blue gum (*Eucalyptus globulus* Labillardière) in a humid temperate region (Galicia, Spain) could increase the C sequestration rate from 7.73 to 10.93 Mg ha⁻¹ year⁻¹ and mineral soil C from -0.24 Mg ha⁻¹ year⁻¹ (lost) to 0.18 Mg ha⁻¹ year⁻¹ (gained). On the one hand, shortening the rotation length generally decreased the C stock in living biomass, but increased the C stock of soil, because the production of litter and harvest residues increased [125]. On the other hand, lengthening rotation not only retains more C by increasing average stem size, but also delays emissions that occur during harvesting [126].

Even-Aged Versus Uneven-Aged System

Considering industrial purposes and ease of operations, forests are managed conventionally as even-aged systems under IFM [99••]. However, silviculture systems affect forest CSS differently. Even-aged forests sequester and store more C in biomass than do uneven-aged systems that are used mainly in EFM, but these store more C in soils [126], [127]. For instance, Nilsen and Strand [127] found that long-term timber production in the uneven-aged stand was estimated to be 95% of the even-aged stand, and the difference in net C sequestration was 37 Mg ha⁻¹ in 81 years in favour of the even-aged stand. Over 81 years, there was an increase in mineral soil C (21 Mg ha⁻¹) in an uneven-aged stand compared to an even-aged stand, which was linked mainly to differences in the O horizon. In fact, the C content in the humus layer in the uneven-aged stand was 20% higher compared to that in the even-aged stand [127]. Moreover, based on model simulations, several studies have shown that uneven-aged systems may be the better alternative strategy. This should be taken into consideration when increasing C storage and sequestration rates over the long term. Indeed, Seidl et al. [128] concluded that a transition to uneven-aged forestry has considerable potential with regard to increasing C storage in forest ecosystems and achieving multiple management objectives. Taylor et al. [109], through a simulation that compared management effects of CP and CC in the Canadian boreal forest, found that total ecosystem C increased in uneven-aged stands. Similarly, in temperate forests, Nunery and Keeton [129] reported that C sequestration capacity was greater in uneven-aged systems.

Ruiz-Peinado et al. [99••] noted that uneven-aged stands have continuous litter inputs, thereby ensuring permanent soil and watershed protection, whereas in even-aged stands, there will be periods with no soil cover or only partial soil cover, which could lead to C losses. Laiho et al. [130] reported a 48% higher diameter increment in uneven-sized Norway spruce forests compared to that in even-sized forests over a 15-year period where the uneven-sized forest was

treated with selection cuttings and the even-sized forest with thinning from below. Also, in Finnish forest stands, Pukkala et al. [131] found that uneven-aged systems were more profitable than even-aged plantations when other management objectives (timber and C) were considered. Nevertheless, designing silvicultural approaches that aim to establish an uneven-aged stand structure requires a deep understanding of the competition process. Harvesting intensity should also be considered. In fact, high harvesting intensities could decrease NEP and increase C emissions; in contrast, lower intensities could increase CSS in the long term, regardless of stand age structure [132].

Tree Species Compositions: Mixed Versus Pure Forest Stands

Tree species richness promotes productivity and affects nutrient and light availability [133], [134]. According to the facilitation and niche complementarity theories (Supplementary Information), mixed stands have higher C sequestration potential than do pure stands [72•]. Several studies have shown that ecosystems with high tree species diversity are more productive and sequester more C than low-diversity ecosystems [133], [134]. Erskine et al. [135] found that throughout the tropics, plantations with mixtures were more productive than monocultures, leading to a 55% increase (on average) in mean tree basal area. Litter production, nutrient return and leaf litter decomposition are higher in mixed plantations than in monocultures [136], which can increase the mobilization of nutrients in the soil and increase the productivity of the mixture considerably [137]. In Scots pine (*Pinus sylvestris* L.) and European beech (*Fagus sylvatica* L.) plantations, tree volumes (+12%), stand density (+20%), basal area growth (+12%) and stand volume growth (+8%) of the species were higher in mixture compared to the weighted mean of neighbouring pure stands [72•]. Tree species richness also could increase soil C stocks, through alterations to litter quality, nitrogen fixation and rooting patterns [99••]. For instance, Dawud et al. [138] found that mixed forests (combinations of *P. sylvestris*, *Betula pendula* Roth, *Carpinus betulus* L., *Quercus robur* L. and *Picea abies* [L.] H. Karst) had higher SOC stocks in samples that were taken from deeper layers of the soil profile (20 cm and 40 cm), compared to topsoil (0–10 cm). Generally, the ratio C/N in deeper layers is significantly and positively related to species diversity [138].

Several avenues of research have shown that pure and mixed stands do not differ in terms of the aboveground standing volume that they attain. Examples include Norway spruce (*Picea abies*) and European beech mixtures in Northern Europe or mixtures of black spruce and trembling aspen (*Populus tremuloides* Michaux) in Canada [139•], [140]. In the Canadian boreal forest, Légaré et al. [141] reported that

aspen exerted a positive effect on black spruce productivity, but only when the aspen constituted < 40% of stand basal area. It seems that increasing NPP in mixedwoods requires a balance between species that are used and their densities, and should consider the spacing and spatial arrangement of the stands [141], [142]. Therefore, it is important to emphasize that the effects of mixtures on productivity vary with stand development stage, stand density and site conditions [72•].

Old-Growth Forest Conservation

Old-growth and intact forests are critical in stabilizing terrestrial C storage, maintaining biodiversity and providing other ecosystem functions [17••], [22]. These forests represent 22% of the world's forested land surface (12 M km²), of which three countries (Russia, Brazil and Canada) account for nearly two-thirds of that area. Furthermore, Canada represents 25% of the world's remaining primary forest, while tropical South America (including Amazon rain forest) represents 35%, but with a high rate of reduction or loss (7.1% during 2000–2013), compared to the boreal (0.3% in North America) and temperate (0.9% in South America temperate forest) forests [17••]. However, the extent of the world's intact forests has been reduced by 7.2% (a reduction of 919,000 km²) since 2000; the primary global cause of this loss is industrial timber extraction that has resulted in forest landscape alteration and fragmentation [17••], [143].

Old-growth forests alone sequester about 1.36 Pg year⁻¹ of C [144••]. The older trees (and stands) may exhibit reduced uptake rates, but the C that is stored in soils and biomass within them can greatly exceed that of younger stands [18], [144••], [145]. McGarvey et al. [146•] found that total C density is 30% higher (154 Mg ha⁻¹), and deadwood C density is 1800% higher (120 Mg ha⁻¹) in old-growth forests than in surrounding younger stands (5 Mg ha⁻¹). Old-growth forests contribute considerably more to increased soil C from accumulated deadwood than do IFM and EFM [146•]. On the one hand, stand age correlates positively with tree biomass and C accumulation until an advanced age where net C uptake is thought to be balanced by respiration and increased mortality [147]. Therefore, older tree cohorts store C less efficiently in live woody tissues, although they can continue accumulating C [144••]. On the other hand, numerous studies expect that much of this C will move back to the atmosphere if these forests are disturbed or replaced with younger forests [148]. Current deforestation emissions are about 1.2 ± 0.6 Pg year⁻¹ of C, but only 12% of the global intact forest area is protected [17••], [143]. During the period 2000–2013, the tropical regions are responsible for 60% of the total reduction of the intact forest; tropical South America lost 322,000 km², whereas Africa lost 101,000 km². The temperate and southern boreal regions contributed 21%

to the global area loss [17••]. Consequently, the old-growth conservation strategy must be promoted by reducing deforestation and degradation. The latter problems need to be addressed in the short term, especially in the tropics.

Discussion

C stocks and fluxes in temperate, tropical and boreal forests are considered to be promising mitigation strategies for addressing climate change. This review aims to better understand the effects of management on C among forest ecosystems to maximize their potential as mitigation tools. The purposes of forest management could be classified as follows: (a) conservation or restoration of natural areas (e.g. conservation of old-growth forest), (b) EFM where productivity and other services are balanced by maintaining native ecosystems and biological diversity and (c) IFM using plantations (generally as mono-specific, even-aged systems) and intensive silviculture (e.g. mainly planting, MSP, fertilization, CC). Yet, the challenge is to link disturbances regimes (e.g. harvesting, wildfires, windthrow) to the climatic and site conditions, which affect their severity and extent, together with forest regeneration and tree growth.

This review determined the potential for applying different management practices, in terms of their effects on CSS (Table 1). The MSP and fertilization used in IFM are two practices that could increase forest C sequestration capacity and SOC in the long term. However, MSP could decrease SOC in the short term, so lower-moderate MSP techniques (scarification, mounding or disc trenching) are suggested to reduce these negative effects [63], [64•], [66]. Jandl et al. [65••] emphasize that the selected technique of MSP is important and will determine whether net C effects of the activity are positive or negative. MSP methods may lead to multiple interactions among soil physical and chemical properties that influence forest CSS; their long-term impacts on soil C are still a matter of research, while their positive effects on living biomass are well known. Thinning-from-below as a pre-commercial treatment could increase forest CSS in IFM and EFM [96], [101], [102]. In commercial treatments, extensive ones (PC, thinning and selective cutting) are highly recommended to increase forest NPP and SOC [23], [65••], [92]. When timber quality is the goal of IFM, upper and middle pruning could be used to promote C sequestration in soil and biomass [85]. Nevertheless, little is known about the effects of management on C sequestration and storage in soils; work published over the last two decades encourages extensive treatments rather than intensive ones [58], [65••], [114], [118], since SOC reduction is expected under climate change [27]. All practices should be avoided that would accelerate this reduction.

Table 1 A summary of the expected effects of different practices that are applied in extensive forest management (EFM) and intensive forest management (IFM) on carbon sequestration (NPP) and soil organic carbon (SOC)

Practices	FMS	Expected effects on CSS	
		NPP	Soil C storage
MSP	IFM	Increase	Decrease ^a
Fertilization	IFM	Increase	
Pre-commercial treatments			
Upper and middle pruning	IFM	Increase	
Lower pruning		Decrease	Increase
Thinning-from-below	Both IFM and EFM	Increase	
Other thinning methods		Decrease	
Commercial treatments			
CC + cut-to-length or tree length	IFM ^b	Decrease	Increase
CC + full tree	IFM	Decrease	
PC < 2/3 + full tree	EFM ^b	Increase	Decrease
PC < 2/3 + cut-to-length or tree length	EFM	Increase	
Long rotation	EFM	Increase	
Short rotation	IFM	Increase	Decrease
Uneven-aged stands	EFM	Increase	
Even-aged stands	IFM	Increase	Decrease
Mixed forest	IFM or EFM	Increase ^c	
Monoculture	IFM	Increase	Decrease
Old-growth forest conservation	Conservation	Decrease	Increase

MSP mechanical soil preparation, CC clear-cutting, PC partial cuts

^aMSP effect depends upon the technique that is used and its intensity; it decreases the SOC only in the short term

^bWe assumed that CC is used only in IFM as final commercial cutting, while PC are used in EFM

^cRequires balancing among species that are being used. However, C accumulates in biomass and in the litter layer, which provides slow build-up of the C pool in the mineral soil

Conservation strategies maintain more C storage in soils than do EFM and IFM [146•]. EFM increases forest C sequestration capacity in the long term [129], while IFM (e.g. planting + MSP + fertilization) has the highest C rate capacity in the short and medium terms (Fig. 4) [65••]. EFM compromises between NPP and SOC, both being an intermediate between conservation and IFM (Fig. 4). In EFM, we recommend the application of thinning-from-below in the early stages of stand development [88], [99••]; then, in the final harvest, PC (intensity, as defined by managers must be less than 2/3 of the volume harvested) will maintain both C sequestration and storage, preferably combined with cut-to-length or tree-length to maintain SOC in the medium and long terms [58], [92], [109]. EFM will eventually replace the biomass that is lost in the harvest in favour of the residual trees, and the pool will equal or exceed its pre-treatment storage if post-cutting mortality is managed [23], [95], [108•]. Following PC, post-cutting mortality could be alleviated by selecting the adequate PC treatment and harvest intensity for each stand (e.g. uniform shelterwood cuttings in boreal forest) [108•]. Yet, extensive treatments increase structural diversity and support uneven-aged systems and natural regeneration, enhancing aboveground

C storage capacity [109], [128]. Indeed, extensive treatments (selection or partial cutting) maintain complex forest structures, which allow for greater light infiltration and promote more efficient resource use by trees [149]. They likewise maintain C stock stability and reduce vulnerability to natural disturbances, mainly wildfires, by reducing fuels and crown density [76], [150]. With the application of a conservation strategy, maintaining a high stand density (old-growth forest) would maximize the soil C pool [65••], [144••]. Consequently, encouraging such a strategy would likely improve the climate change mitigation benefits of forests. In the Canadian boreal forest, a conservation strategy that aims to maintain 50% of old-growth forests could then have a positive impact on the C budget, mainly in soil pools.

Forest soils are considered to be a potential C sink. Post and Kwon [151] reported that the average rate of soil C sequestration was 0.3 tonnes ha⁻¹ year⁻¹ (range: 0–3 t ha⁻¹ year⁻¹) across different climatic zones. Furthermore, soils store 68% of the world's forest C (32% in vegetation) considering only soil and vegetation pools (see Fig. 2), and 44% when considering all pools [2•]. Consequently, strategies that increase soil C sequestration and storage should be promoted. C inputs to the soil come from roots, dead trees

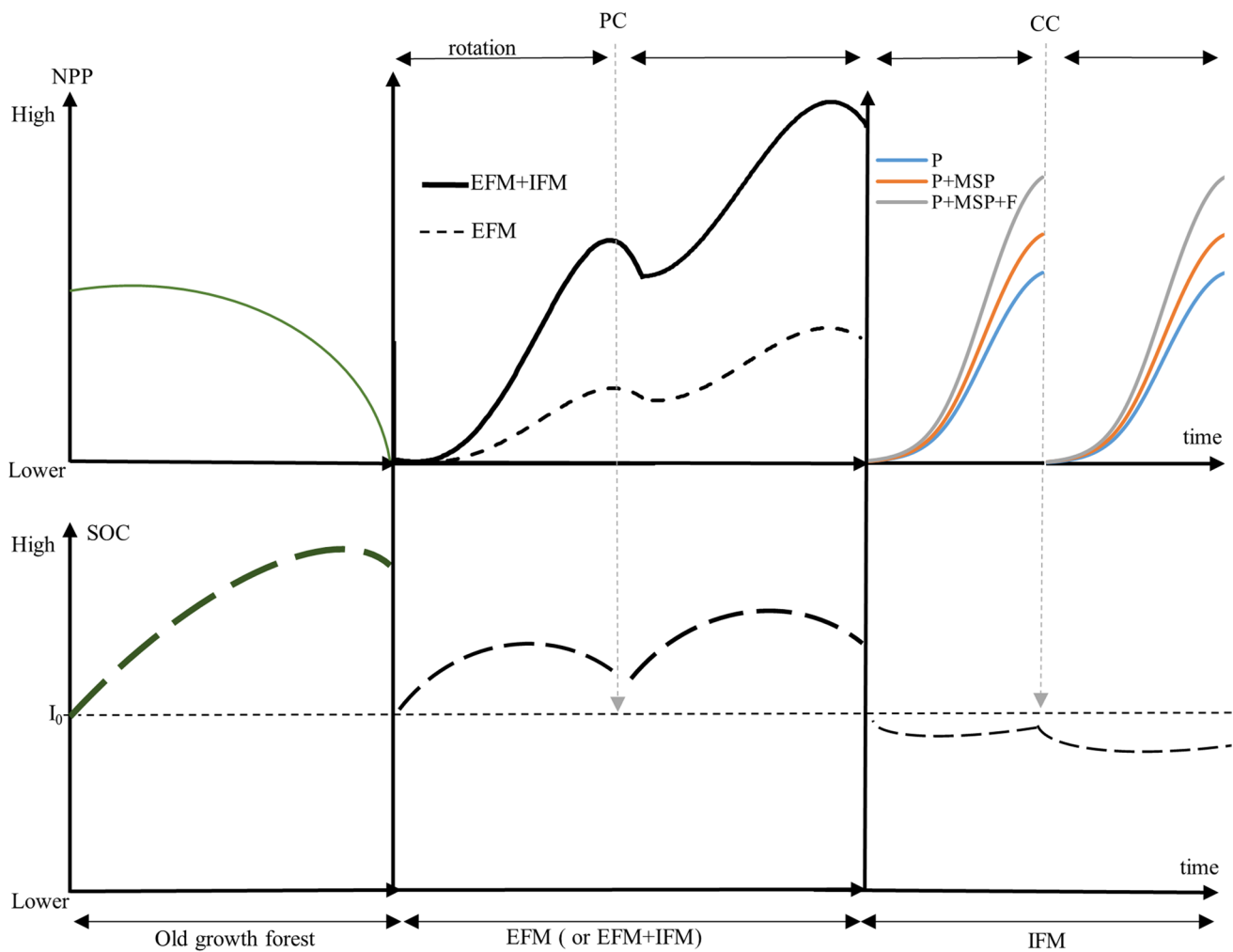


Fig. 4 The theoretical pattern of carbon sequestration capacity and soil carbon storage (SOC) in three systems, where we assumed that SOC starts with an initial stock value I_0 ; intensive forest management (IFM), extensive forest management (EFM) and old-growth forest conservation strategies. EFM strategy compromises carbon sequestration and carbon storage, both being intermediate between the conservation and IFM strategies (legend: P, plantation; F, fertilization; and

MSP: mechanical soil preparation). This figure also shows the theoretical effects of clear-cuts (CC) and partial cuts (PC) on forest carbon sequestration and storage during a rotation period; we have assumed that post-mortality is managed in EFM by using an adequate PC form and intensity (for details, see text in the section “Harvesting Treatments: Clear-Cuts Versus Partial Cuts”)

and litterfall and are lost through R_h [34•]. Soil C storage is generally sustained by a continuous input of organic matter, meaning that the conservation strategy of old-growth forests could increase this pool [144••], [146•]. Regarding extensive or intensive treatments (PC vs. CC), several studies found conflicting results; some research indicated that harvest decreases soil C sinks, whereas others reported positive effects. Indeed, it has been suggested that harvesting reduces soil C [117], but others showed an increase [152], and some studies found no effect [18], [23], [30], [58]. In a meta-analysis of 112 publications from around the world, harvesting reduced soil C stocks by an average of 11.2%, with the greatest losses being occurred in organic horizons (–30.2%), lower losses occurring in the uppermost mineral

soil (0–15 cm depth; –3.3%) and significant losses in deep soil layers (60–100+ cm; –17.7%) [20••]. However, this variation is likely related to differences among studies in terms of harvest intensity, tree composition, stand ages and the length of time following harvest [152–154]. Rannik et al. [154] and Strukelj et al. [155] found that 5 to 9 years after CC, the soil pool remained a significant C source. In selective cuts, Pötzelsberger and Hasenauer [152] found that soil C was a significant C sink, increasing by 11%.

Assessment of the forest sector’s contribution to climate change mitigation must be at the sector level, and not only within the ecosystem, which means that HWP contributions must be considered. The HWP pool stores the C beyond the ecosystem and participates in reducing greenhouse

gas (GHG) emissions through its long-term storage of C, which depends upon its uses and life cycle (Figs. 1, 2) [19]. An additional benefit occurs by substituting materials that generate more greenhouse gases through their production with HWP or by substituting fossil fuel energy with renewable sources, such as biomass energy [19]. Yet, the global demand for industrial wood is expected to double over 2030–2050 [156]; consequently, harvesting pressures on world forests will increase significantly. According to our review, an EFM strategy is a promising approach to fulfill this demand, particularly if it is combined with some IFM practices (MSP and fertilization) in localized areas (Table 2, Fig. 4). In fact, combining IFM and EFM practices result in an increase in landscape productivity and soil C storage in both the short and long terms compared to IFM (Fig. 4).

An adaptive FMS to maximize CSS at the landscape scale is important since it is considered a political concern; forests are not managed on a single stand basis, but at the landscape scale [94], [95], [157]. Indeed, landscape-scale C stock changes are the sum of stand-level changes, and the effects of forest management on C stocks ultimately must be evaluated at the landscape scale [157]. Therefore, managers could diversify FMS at the landscape scale, given that this approach could increase CSS and harvested volumes. This approach was developed by Seymour and Hunter [158] and denoted “functional zoning” (TRIAD approach). It has been used in parts of boreal Canada as a potential strategy for achieving diverse objectives by dividing the landscape into three zones: conservation zone, IFM zone and EFM zone. The IFM zone is characterized by high-input, production-focused plantation silviculture. The EFM zone, where less-intensive approaches such as ecological silviculture are used, allows non-timber objectives (e.g. biodiversity conservation, aesthetics) to be met, while providing an opportunity for timber production [159]. The conservation zone represents the unmanaged

forest and ecological reserves. The establishment of the TRIAD strategy requires a forest management approach that integrates several spatial and temporal scales, and all zones need to be managed in an integrated fashion to ensure sustainable management [160]. The challenge lies in determining the appropriate proportion for each zone, as large proportions are not recommended for IFM, for instance. The IFM zone could mostly use the productive areas (high site indices). Irland [7•] states that IFM is likely to be attractive to landowners on such sites, and maybe financially unwarranted on the ones with the lowest productivity. Therefore, the TRIAD approach could be guided by the site index and cost-effectiveness. However, at the stand scale, the effects of all the practices that are discussed on forest CSS are very sensitive to site conditions and the climate [161].

The question that is raised by this review relates to the economic feasibility of the proposed practices to be implemented in IFM and EFM. MSP, fertilization, pruning and thinning-from-below have additional costs. In order to harvest the same volume using PC as with CC, PC must be applied in different places and requires greater access to the forest (operational barriers), compared to CC, thereby making PC more costly. Mixed stands favour C sequestration, but maintaining the balance among the mixed species may be difficult and could be more expensive than monoculture [162]. Nichols et al. [162] assume that the prices and scheduling of silvicultural and harvesting operations remain unchanged between monoculture and mixed stands, but establishment costs could be higher in mixed stands. Yet, these practices improve productivity (more harvested volume). Therefore, they generate more revenue in the long term, but require higher initial investments. IFM is always used because it is more profitable than EFM. We still need to integrate externalities and C offset measures to compare the profits between EFM, IFM and conservation [163].

Table 2 The main broad contrasts between the ends of the spectrum of IFM and EFM strategies, and their expected effects on carbon sequestration, with the possibility of mixing both strategies at the landscape scale

	IFM	EFM	IFM + EFM
Stand establishment	MSP	–	MSP
	Fertilization	–	Fertilization
Rotations	Shorter	Longer	Longer
Stand composition	Single species	Mixtures	Mixtures
Structure	Even aged	Uneven-aged	Uneven-aged
Pre-commercial treatments	Thinning	Thinning	Thinning
Commercial treatments	Clear-cuts	Partial cuts or selective	Partial cuts or selective
Carbon sequestration in the short term	High	Modest to low	High
Carbon sequestration in the long term	Modest to low	High	High

Conclusion

After reviewing several practices that are applied in EFM and IFM, we can conclude that increasing forest C sequestration capacity requires an understanding of the effects of management, climate and industry, together with predictions as to how these effects might change in forest ecosystems over time (long and short terms). Silvicultural practices and systems could be used to convert existing stands to more suitable stand structures and compositions, which may increase C sequestration as well as mitigate and adapt ecosystems to the effects of global change. PC with cut-to-length or tree-length harvesting systems has been identified as one of the major solutions for increasing biomass and soil C content. Yet, their long-term effects are not fully understood, mainly when we consider the form and intensity of PC, which requires further research on this topic. Regarding global strategies, each one has its advantages: conservation increases SOC storage, IFM increases C sequestration capacity in biomass in the short term and EFM is a compromise between conservation and IFM and is more effective in the long term. Consequently, the diversification of those strategies at the landscape scale under the TRIAD zonation approach could be the best direction for increasing forest C sequestration capacity, instead of using only one strategy. On the one hand, the applied proportion of each strategy should depend upon the managed territory as well. On the other hand, natural disturbance regimes and climate change could greatly enhance or reduce C storage capacity and should be considered in subsequent management decisions.

We highlight that all of the practices and strategies that have been discussed in this review are applied in almost all biomes. Moreover, their effects are similar, although the magnitude of these effects differs, mainly in terms of the practices that accelerate R_h . For example, in the boreal forest, CC will increase R_h and reduce SOC, but not to the same magnitude as seen in tropical and temperate forests, where the climate is warm. The warmer climate will substantially increase ecosystem R_h following CC and, therefore, will induce very substantial reductions in SOC compared to the boreal biome. Many knowledge gaps remain, however, given that the long-term effects of these practices on forest C budgets in each biome at regional and global scales are still poorly understood, especially when considering how a changing climate might alter these effects. This review does not aspire to cover all aspects of management and their effects on forest C, nor does it discuss all relevant implications. Instead, it provides forest managers with an overview of promising practices and strategies that can be implemented to mitigate climate change, by increasing forest C sequestration capacity.

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Declarations

Conflict of Interest The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as potential conflicts of interest.

Human and Animal Rights This article does not contain any studies with human or animal subjects that were performed by any of the authors.

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