

Opinion

Are old forests underestimated as global carbon sinks?

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Abstract

Old forests are important carbon pools, but are thought to be insignificant as current atmospheric carbon sinks. This perception is based on the assumption that changes in productivity with age in complex, multiaged, multispecies natural forests can be modelled simply as scaled-up versions of individual trees or even-aged stands. This assumption was tested by measuring the net primary productivity (NPP) of natural subalpine forests in the Northern Rocky Mountains, where NPP is from 50% to 100% higher than predicted by a model of an even-age forest composed of a single species. If process-based terrestrial carbon models underestimate NPP by 50% in just one quarter of the temperate coniferous forests throughout the world, then global NPP is being underestimated by 145 Tg of carbon annually. This is equivalent to 4.3–7.6% of the missing atmospheric carbon sink. These results emphasize the need to account for multiple-aged, species-diverse, mature forests in models of terrestrial carbon dynamics to approximate the global carbon budget.

Keywords: carbon sequestration, carbon sink, coniferous forests, missing carbon, net primary productivity, old-growth forests

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Forested areas, particularly in the Northern Hemisphere, have been proposed as possible sinks of atmospheric carbon that are currently not accounted for by global carbon cycle models (Tans *et al.* 1990; Ciais *et al.* 1995; Francey *et al.* 1995; Keeling *et al.* 1996; Fan *et al.* 1998). Several factors have been hypothesized to contribute to this missing carbon sink, including increased productivity by forests as a result of nitrogen deposition and greater atmospheric CO₂ concentrations, interannual climate variability (favouring either increased photosynthesis or decreased respiration), longer growing seasons, and regrowth of forests harvested in the early and middle parts of the 20th Century (Sedjo 1992; Schimel 1995; Goulden *et al.* 1996a; Myneni *et al.* 1997; Battle *et al.* 2000; Schimel *et al.* 2000). While young and recovering forests have obvious potential as carbon sinks, carbon exchange between old forests and the atmosphere is thought to be at equilibrium. The vague

term 'old forest' is used intentionally because, with the exception of canopy gap and hybrid models, specific forest ages are rarely incorporated into either conceptual or process-based forest growth models (Waring & Running 1998). However, forests older than approximately 100 years are generally considered to be insignificant carbon sinks (Jarvis 1989; Melillo *et al.* 1996a).

The perception that old forests are not carbon sinks is based on two simple but interconnected assumptions about how forests grow: (i) age-related growth trends of individual trees and even-aged, monospecific stands can be extended to natural forests; and (ii) respiration of tree stems and branches in old forests uses so much photosynthate that these forests can no longer accumulate carbon as biomass.

These assumptions are fundamental components of the simple conceptual model for forest growth, biomass allocation, assimilation, and respiration proposed by Kira & Shidei (1967) in the late 1960s and further popularized by Odum (1969, 1971). The basic premise of the model is that as forests age, the decrease in biomass of photosynthetic leaves relative to respiring sapwood forces an inevitable decline in NPP (Fig. 1). Ultimately, it is

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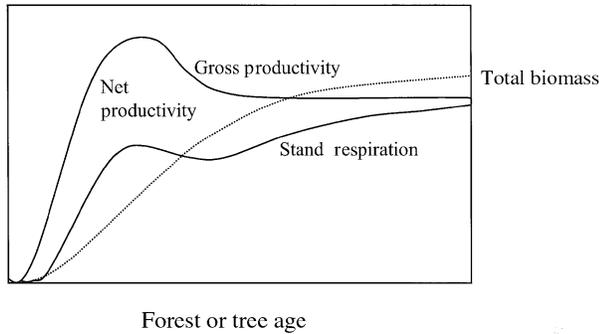


Fig. 1 Gross primary productivity (GPP), stand biomass, and stand respiration as a function of increasing forest or tree age. The difference between GPP and stand respiration is net primary productivity (NPP). Redrawn from (Kira & Shidei 1967; Odum 1969).

assumed, 'old' or 'mature' forests reach a steady state with respect to carbon cycling (i.e. photosynthetic gross primary productivity, GPP, is equal to autotrophic respiration) and they sequester little, if any, atmospheric carbon (Jarvis 1989; Melillo *et al.* 1996a). These assumptions are also inherent in many process-based models of forest growth (Ryan *et al.* 1996), and they are reinforced by widely accepted theory that basic biogeochemical cycles are conservative properties of ecosystems that do not vary much over a wide variety of species mixtures (Shaver *et al.* 1997; Waring & Running 1998).

The validity of the first assumption (that even-aged stands can predict NPP of natural forests) was examined by measuring growth rates, sapwood:leaf ratios, and biomass accumulation in natural, but structurally simple, subalpine forests in the northern Rocky Mountains that range in age from 67 to 458 years (see Note 1 at end of article). These stands are dominated by two species, whitebark pine (*Pinus albicaulis*, Engelman) and subalpine fir (*Abies lasiocarpa*, Nuttall), with the former dominating early successional stands and the latter dominating late-successional stands. Biomass allocation, aboveground net primary productivity (ANPP), and total aboveground biomass in these forests were compared to modelled values for simple, even-aged stands composed of 100% whitebark pine (see Note 2 at end of article).

It was found that sapwood:leaf mass ratios of modelled even-aged stands steadily increase with age as described by other simple forest-growth models (Fig. 2a). In contrast, sapwood:leaf mass ratios of the natural forests diverge from those predicted from modelled stands at approximately 175 years and remain 25–50% lower for the next 300 years. This difference is a consequence of continuous recruitment of both species in natural stands of all ages and the disproportional increase in the abundance of late-successional subalpine fir which has much lower sapwood:leaf ratios for trees of all ages.

Differences in ANPP are even more striking (Fig. 2b). As described for other even-aged stands, ANPP of modelled stands reaches its maximum at approximately 250 years and decreases thereafter. ANPP in 200-y-old natural stands is almost twice that in modelled stands, and the difference between natural and modelled stands increases steadily throughout our sampled age range. Differences in stand aboveground biomass range from approximately 30% at 200 years to over 40% at 400 years (Fig. 2c). These results indicate that long-term recruitment and late-successional species may have significant effects on stand productivity and that growth and carbon acquisition in old natural forests cannot be extrapolated from the productivity of even-aged stands. The patterns in NPP and biomass in these whitebark pine and subalpine fir stands can be generalized to other coniferous forests where changes in biomass allocation from early to late successional species result in much lower sapwood:leaf area ratios in mixed stands than in single species stands. Although whitebark pine and subalpine fir forests cover only 8–14% of the landscape in the Northern Rocky Mountains, the successional processes and the sapwood:leaf area dynamics in these two species are similar in boreal and temperate coniferous forests worldwide (Waring & Schlesinger 1985; Kimmins 1987; Margolis *et al.* 1995; Pfister *et al.* 1977).

The second assumption (that high respiration costs of sapwood in old forests preclude carbon allocation to growth) is a fundamental component of basic forestry theory and most process-based forest growth models. In these models respiration per unit sapwood remains constant as forests age and sapwood respiration is calculated as an exponential function of temperature and biomass, irrespective of tree size or age, using the equation: $R = aBQ(T)$, where a is a constant, B is biomass, Q is the temperature coefficient of respiration and T is sapwood temperature (Running & Coughlan 1988; EPRI 1993; McGuire *et al.* 1993; Ryan *et al.* 1996; Thornley & Cannell 1996; White *et al.* 2000). This calculation results in modelled forests reaching a steady state in carbon exchange in less than 100 years. In nature, however, neither trees nor forests show constant respiration rates per unit of sapwood or biomass over time (Sprugel 1984; Ryan & Waring 1992). Instead, stem respiration decreases with increasing tree size (Yoda 1967; Carey *et al.* 1997; Lavigne & Ryan 1997). By not including size- or age-dependent decreases in stem maintenance respiration per unit sapwood volume in process-based models of forest growth, respiration in older stands can be overestimated by a factor of 2–5 (estimated from Carey *et al.* 1997; Lavigne & Ryan 1997), and thereby provide an intuitively satisfying, but misleading, mechanism for the first assumption (see Note 3 at end of article). In contrast, the fact that stem respiration decreases with tree size

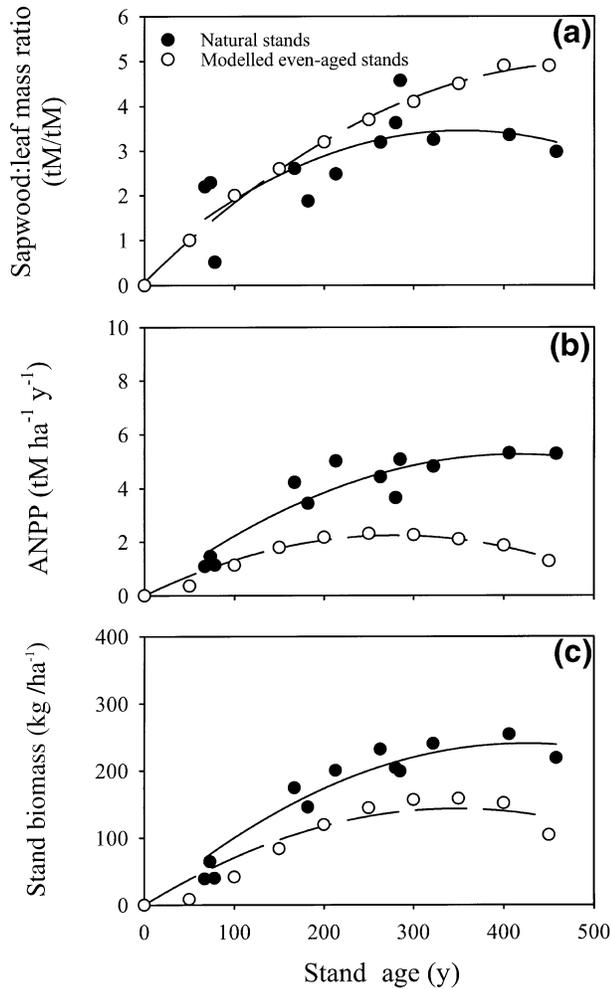


Fig. 2 Whole-stand sapwood:leaf mass ratios (a), annual net primary productivity (b), and biomass (c) for natural subalpine forest stands of different ages in the northern Rocky mountains and simulated whitebark pine stands composed of even-aged stands of whitebark pine without recruitment over time.

provides a potential mechanistic explanation for the lack of growth decline that we found in old subalpine forests [albeit a small fraction as stem maintenance respiration is likely only 5–10% of annual NPP in this cool, water-limited environment (Ryan *et al.* 1995)]. The omission of size- and age-related decline in stem respiration from models of forest productivity could potentially explain why estimates of low net primary productivity in mature stands have been attributed to increasing woody tissue respiration (Odum 1969).

Alternative hypotheses have been proposed to explain reduced productivity as forests age. These include declines in nutrient availability and hydraulic conductivity (thereby reducing photosynthesis) (Ryan & Waring 1992; Yoder *et al.* 1994; Binkley *et al.* 1995; Murty *et al.* 1996; Ryan & Yoder 1997; Ryan *et al.* 1997). Although

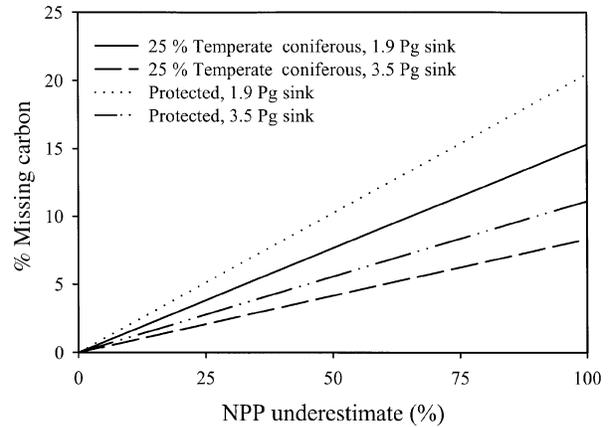


Fig. 3 Percentage of missing carbon sink accounted for if models of forest growth underestimate NPP of coniferous forests in the Northern Hemisphere. Lines illustrate amount of missing carbon accounted for if NPP is underestimated for 25% of temperate coniferous forests (TCF) or for all protected forests (PF) in Europe, North America and the former Soviet Union (Melillo *et al.* 1993; McGuire *et al.* 1996). Values are expressed as percentages of high (3.5 Pg y⁻¹) and low (1.9 Pg y⁻¹) estimates of missing carbon.

these alternative hypotheses for the cause of forest growth decline suggest allocational or physiological mechanisms to explain why growth of individuals or stands decline through time, they do not address the effects that succession and species diversity may have on maintaining long-term productivity and biomass accumulation in natural forests.

In order to estimate the potential of older forests as carbon sinks, the increase in carbon uptake was calculated if annual NPP of temperate coniferous forests [4.65 Mg C ha⁻¹ y⁻¹ (Melillo *et al.* 1993, McGuire *et al.* 1996)] (see Note 4 at end of article) was underestimated by up to 100%. This potential underestimate is based on results from subalpine forests in the Northern Rockies (Fig. 2), and was applied to 25% of temperate coniferous forests globally [i.e. 62.5 × 10⁶ ha of ~250 × 10⁶ ha (Melillo *et al.* 1996b)] (Fig. 3). Assuming a moderate underestimate of 50% and that 1.9–3.4 Pg of C is still missing to balance the global carbon budget in global climate models (Tans *et al.* 1990; Ciais *et al.* 1995; Keeling *et al.* 1996), then 4.3–7.6% of this missing C could be from growth of older temperate coniferous forests (Fig. 3). If this analysis is refined to include only the 137.6 × 10⁶ ha of coniferous forests in Europe, USSR, and North America that are protected (see Note 5 at end of article), then if NPP is currently underestimated by 50%, 5.5–10% of the global carbon sink may be accounted for (Fig. 3). Although the past use of these protected areas is not known, they do provide a conservative estimate of the current area occupied by older, natural stands of mixed-species. In addition to these conifer forests, productivity

of temperate broadleaved forests (~10% of forests worldwide, World Resources Institute 1986) may also account for a significant percentage of the missing C sink (Fan *et al.* 1998).

With respect to the two fundamental assumptions for forest productivity, it was found that: (i) if recruitment and succession are accounted for, then growth declines in old forests may be lower in magnitude and occur over much longer periods of time than previously predicted from modelled estimates of even-aged, single-species stands; and (ii) respiration rate per unit sapwood volume decreases with increasing tree or stand age and therefore does not provide an accurate mechanism to model growth decline in forests. The present results also suggest that species composition and diversity matter to ecosystem properties in old forests, and that some basic biogeochemical processes in forests may not be as conservative as previously thought. Forests cover ~28% of Earth's land surface [$\sim 4.1 \times 10^8$ hectares (Dixon *et al.* 1994)] and account for a large proportion of the global terrestrial carbon budget (Lieth 1975; Sedjo 1992; Schimel 1995; Goulden *et al.* 1996a) and global net primary productivity (>60%: Lieth 1975; Melillo *et al.* 1993). Recent long-term eddy-covariance flux measurements of carbon dioxide, water vapour, and energy exchange from a variety of forest ecosystems worldwide have refined estimates of net ecosystem exchange (NEE) for these systems and have advanced understanding of the role of forests as carbon sinks (e.g. Wofsy *et al.* 1993; Sellers *et al.* 1995; Goulden *et al.* 1996a,b; Hollinger *et al.* 1998, 1999; Schulze *et al.* 1999; Valentini *et al.* 2000). However, it is not feasible to measure net primary productivity or net ecosystem exchange directly on a global scale, and therefore models of forest productivity can provide a valuable means to estimate forest carbon fluxes at local, regional and global scales. At local to regional scales, cross validation between measured ecosystem-level carbon fluxes and carbon fluxes scaled-up from stand-level models can lend insight into the physiological basis for daily, seasonal, and interannual variability in net ecosystem exchange (Goulden *et al.* 1996a). Further comparisons, between measured fluxes and broader scale models, and among models differing in scale and complexity, can be used to evaluate model performance (Hunt *et al.* 1996; Pan *et al.* 1998; Cramer & Field 1999). Models that describe stand-level processes accurately are necessary in predicting the role of future forests as carbon sinks. Because of forests' considerable contribution to global carbon exchange, it is crucial to improve modelled estimates of NPP by refining climate and soil databases that are used for model parameterization (Pan *et al.* 1996) and through the incorporation of basic ecological principles and realistic rates of carbon exchange into models of terrestrial carbon budgets.

Notes

¹Trees of each species were selected to represent their typical ranges of diameters at 140 cm above ground (d.b.h.) and cut down at the base. Total tree height and the basal diameter of all live branches were measured on each bole. Disks 3–5 cm thick were cut at 2-m intervals from each bole and cross-sectional areas of sapwood, heartwood, and bark on each disk were traced on clear acetate. The volume (in cubic metres) of each component in each 2-m bole section was calculated using the areas of the disks at each end of the sections in the following equation: volume = $((A_1 + A_2)/2) \times 2$ m, where A_1 = initial area (m²) and A_2 = terminal area (m²). Bole volume was calculated by summing all sections for each tree. The volume of each component was converted to mass using the specific gravity (in kg m⁻³) of the heartwood, sapwood, and bark. A subsample of branches from all trees of each species were used to calculate the regression relationship of leaf mass and sapwood mass to branch diameter and these regressions were used to calculate the leaf mass and branch sapwood mass for each tree.

The widths of the five most recent annual rings (1991–95) were measured for all 23 trees at three different places on each disk section. This width was subtracted from all disk sections and bole biomass was recalculated using the 5-y preharvest estimates of tree size. The 5-y preharvest mass was subtracted from current bole mass for each tree and divided by 5 to estimate current annual aboveground bole productivity. The annual productivity of the bole, as a percentage of current bole mass, was used to estimate branch productivity. Leaves from 10 randomly chosen branches from different trees for each species were separated into the sample year's current growth, and that of all previous years, prior to drying and weighing. Estimates of the proportion of total leaf mass that was a single year's production were developed from these samples. This ratio was applied to the canopies of all trees to estimate an annual rate of leaf productivity for each species. Bole, branch, and leaf productivity were summed as an estimate of total aboveground productivity (ANPP) for each species by d.b.h.

Biomass allocation and ANPP estimates were constructed for forests using empirical data from 12 natural stands in the Bob Marshall Wilderness in Montana, 300–400 km north of the harvest site. These stands varied in age from 67- to 458-y-old, and appeared to have regenerated after stand-replacing fires. In each stand, 400 m² circular plots were located and all tree stems were classified into 5-cm size classes. In each plot 10–20 trees of various sizes, but including the largest trees, were cored as close to the ground as possible and aged by adding the age at the height of the core to regression estimates for the number of years the tree took to reach core height. Over 95% of the basal area in these stands was whitebark pine and subalpine fir. The median d.b.h. for each d.b.h. class (e.g. 7.5 in the 5–10 cm class) were entered into the regression models that were developed using the harvested whitebark pine and subalpine fir to calculate sapwood mass, leaf mass, and ANPP. Sapwood mass, leaf mass, and ANPP of all d.b.h. classes were summed for each plot and scaled to tM ha⁻¹. Time-based models were built using the age of the oldest cored tree in each stand for stand age (Callaway *et al.* 2000).

²In order to provide a simple null model for stands without subalpine fir and without recruitment over time, the biomass allocation and productivity regressions from harvested whitebark pines were used to model biomass allocation and productivity of a theoretical, even-aged, whitebark pine stand. This stand began with 800 3.8 cm d.b.h. stems ha⁻¹ at 50 years (an estimate reached by

doubling the number of whitebark pines in this size class in the two youngest natural stands that were 70–80-y-old, that experienced 30% mortality every 50 years, and wherein all surviving trees grow into the next largest age class every 50 years. These inputs were designed so that modelled stands at 450 y age had similar tree densities in the > 50 cm d.b.h. classes to the natural stands studied here that exceeded 400 y age. Such consistent mortality may be unrealistic for many natural stands, but it is representative of a much larger dataset on stand dynamics in the Bob Marshall Wilderness (Keane & Arno 1993).

³It is likely that live cell volume in sapwood decreases with increasing tree size as trees age. Therefore, models calculating stem respiration as a function of live cell volume are less likely to overestimate stem respiration. For example, see modifications to Forest-BGC in White *et al.* (1998).

⁴An average estimate of NPP of temperate coniferous of $4.65 \text{ Mg C ha}^{-1} \text{ y}^{-1}$ forests was used (from Melillo *et al.* 1993; McGuire *et al.* 1996). This value of NPP was estimated using the process-based terrestrial ecosystem model (TEM) and data sets for climate, elevation, vegetation, and soils at a 0.5° latitude by 0.5° longitude resolution. This estimate ($4.65 \text{ Mg C ha}^{-1} \text{ y}^{-1}$) is ~20% lower than the average NPP of temperate coniferous forests from the IBP Woodlands Data Set if both above- and belowground NPP are included ($5.68 \text{ Mg ha}^{-1} \text{ y}^{-1}$; DeAngelis *et al.* 1981). McGuire *et al.* (1996) derived estimates of potential vegetation cover from existing vegetation maps from regional sources.

⁵Productivity of protected forests is based on areal estimates given in: World Resources Institute (1986). Protected forest areas are: 22.3×10^6 ha in Europe, 36.1×10^6 ha in North America, and 158×10^6 ha in the former USSR. Coniferous forest as a percentage of total forest area in each region is: 50% in Europe, 44% in North America, and 70% in the former USSR. The estimate of average NPP used in calculations for protected European and North American forests was $4.65 \text{ Mg C ha}^{-1} \text{ y}^{-1}$ (temperate coniferous forest), and for forests in the former USSR was $2.38 \text{ Mg C ha}^{-1} \text{ y}^{-1}$ (boreal forest), estimated from Melillo *et al.* (1993) and McGuire *et al.* (1996). This estimate for boreal forest is similar to that for a southern boreal forest in Maine ($2.1 \text{ Mg C ha}^{-1} \text{ y}^{-1}$; Hollinger *et al.* 1999), but is greater than estimated by Schulze *et al.* (1999) for boreal forests in Siberia ($1.23 \text{ Mg C ha}^{-1} \text{ years}^{-1}$). However, the areas we are considering in the former USSR also include Russian Europe where ANPP is higher by a factor of ~3 (Schulze *et al.* 1999).

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