The Carbon Balance of an Old-growth Forest: Building Across Approaches

Christopher B. Field* and Jörg Kaduk†

Department of Plant Biology, Carnegie Institution of Washington, Stanford, California 94305, USA

ABSTRACT

The carbon budget of the Wind River old-growth forest is being addressed from a variety of perspectives and with a range of approaches. The goal of this comprehensive analysis is developing a thorough, general, and validated understanding of the carbon balance, as well as the processes controlling it. The initial results from studies addressing annual carbon (C) balance with ground-based methods, eddy flux, leaf-based models, and ecosystem models are consistent in some, but not all, respects. Net primary production is 500–600 g C m^{-2} y^{-1} (5–6 Mg C ha^{-1} y^{-1}), consistent with estimates based on climate alone. The site appears to be close to carbon equilibrium, as a multiyear average, using ground-based methods but a sink of approximately 150–190 g C m^{-2} y^{-1} from eddy flux for a single year. An overview of the mechanisms that can drive forest carbon sinks illustrates why methods emphasizing different temporal and spatial scales, as well as different processes, can come to different conclusions, and it highlights opportunities in moving toward a truly integrated approach.

Key words: old-growth forest; carbon balance; net primary production; eddy flux.

FOREST CARBON BALANCE IN THE GLOBAL CARBON CYCLE

Over the last several decades, the increase in atmospheric carbon dioxide (CO_2) equals only about half of the carbon emitted through human activities. Carbon (C) sinks in the oceans and on land have sequestered the remainder, a quantity that has averaged more than 3 Pg C y^{-1} over the last decade (Battle and others 2000). Carbon sequestration on land can be constrained, at the continental scale, by measurements of atmospheric CO_2 (Tans and others 1990), ^{13}C in CO_2 (Francey and others 1995), and the O_2/N_2 ratio (Bender and others 1996), as well as directly, from forest

inventories (Goodale and others 2002). These large-scale techniques all indicate substantial carbon sequestration in the temperate and boreal latitudes of the Northern Hemisphere, but the locations, mechanisms, and persistence of these carbon sinks are poorly known (Schimel and others 2001). Because terrestrial carbon sinks have a significant influence on the future trajectory of atmospheric CO_2, investments in understanding and potentially managing them should be a scientific priority (Falkowski and others 2000).

A carbon sink in the forest sector can result from fundamentally different processes, on a range of temporal and spatial scales. A photosynthetically active leaf can have a net carbon uptake, whether it is on a tree that is growing or declining. A forest regrowing after harvest or fire is typically a carbon sink for a century or more, as trees accumulate biomass, yet the fact that some forests are accumulating carbon provides no information about

regional patterns, where the overall carbon balance is controlled by the balance between rates of re-growth and rates of disturbance (Schulze and others 2000). Increased rates of tree growth can drive a forest sink, but an increase in growth rates is not a prerequisite for a sink, even at the regional scale. A large-scale sink can also be a result of decreased disturbance, through, for example, successful fire suppression or decreased harvesting (Houghton and others 1999).

One of the central challenges in carbon-cycle research is effectively spanning the range of processes and scales that control forest carbon balance. Integrative techniques tend to have limited power for quantifying small-scale mechanisms. Methods at the scale of the leaf or the small plot of soil provide access to a range of physiological processes but do not extrapolate directly to the scale of entire forests or regions. Across temporal scales, the challenges are similar. Techniques that measure carbon balance on the time scale of minutes provide access to the role of environmental factors like light, temperature, and soil moisture, but they do not necessarily provide useful information about the controls on the dynamics of pools like coarse woody debris and recalcitrant soil organic matter, which change on a time scale of decades to centuries.

WIND RIVER OLD-GROWTH FOREST: A COMPREHENSIVE APPROACH TO LOCAL CARBON BALANCE

To address the challenges of scale and the diversity of processes at the different scales, the Western Regional Center of the National Institute for Global Environmental Change (WESTGEC) program at the Wind River old-growth forest (WROGF) initiated a comprehensive program of studies examining carbon balance and the controls on carbon balance at a range of temporal and spatial scales (Suchanek and others 2004). This coordinated program provides the opportunity to accomplish three important objectives. First, the application of multiple approaches provides the possibility of validation, of using results from one approach to check results of others. Second, information from a range of scales can help link phenomena with underlying causes. Third, the availability of data from multiple processes at a range of spatial and temporal scales provides a context for explicitly testing techniques for scaling.

The WESTGEC program at the WROGF also provides opportunities for scaling across forest ecosystems. The central old-growth stand is different in many respects from the young, rapidly growing forests nearby and those that form the majority of the flux networks, including Fluxnet (Running and others 1999), and Euroflux (Valentini and others 2000). A comprehensive understanding of forest carbon balance will require information about not only a range of forest types but also a range of forest ages.

All of the ongoing studies at the WROGF address phenomena related to carbon balance (Suchanek and others 2004). Here, we consider initial results from four studies of the old growth that explore annual carbon balance at the level of the entire forest. Our purpose is to provide a conceptual background for the nature of carbon balance in an old growth forest, to explore the relationship between this background and the measurements, to summarize the strengths and uncertainties of each method, and to suggest options for further progress in building on the intrinsic complementarity among approaches.

All four of the approaches addressed here involve a combination of techniques and data sources. Many of the uncertainties within as well as between approaches result from challenges in interfacing diverse data sets. The multitechnique nature of each approach also means that the brief names used here are not entirely accurate. The four approaches are

1) *Eddy flux.* Paw U and colleagues (2004) have deployed above-canopy and below-canopy eddy-flux systems at the WROGF since 1998. The above-canopy system provides a direct measure of the CO_2 flux across the horizontal plane of the sensors (Baldocchi and others 1988). It is the only one of the techniques used here that is a direct measure of CO_2 balance at the ecosystem scale. The accuracy of the eddy-flux approach is limited by two kinds of factors. First, the system does not detect all of the flux under all conditions. This includes fluxes in very small turbulent eddies, as well as fluxes that somehow bypass the tower in, for example, spatially confined downdrafts. Fluxes carried by advection (horizontal winds) are not measured with eddy flux, but they are estimated, using additional data sources (Paw U and others 2000), by Paw U and colleagues (2004). The second class of limits concerns the fact that the system does not always provide useful data. Sometimes, this is because wind speeds are too low for accurate measurements. Other times, it is because the system is measuring flux from an area that

Table 1. Estimates of Components of the Annual Carbon Balance at the Wind River Old-growth Forest from Five Methods

	GPP g C m^{-2} y^{-1}	NPP g C m^{-2} y^{-1}	NEP g C m^{-2} y^{-1}
Harmon and others 2004 (ground based)	1906	597	20
J.K. (ecosystem model)	1300	535	
Lieth 1975 (NPP model)		581	
Paw U and others 2004 (eddy flux)	1570		150–190
Winner and others 2004 (leaf model)	2459		

C, carbon; GPP, gross primary production; NPP, net primary production; and NEP, net ecosystem production.

extends outside the old-growth study site at the WROGF. Overall, more than 30% of the measurements at the WROGF cannot be considered reliable (Paw U and others 2004) and need to be replaced with estimates based on a gap-filling procedure (Falge and others 2001).

2) *Ground based.* Harmon and colleagues (2004) quantified WROGF carbon balance as the difference between net primary production (NPP) and heterotrophic respiration. NPP is determined from observed changes in stocks. Heterotrophic respiration is calculated from measured stocks and decomposition rates per unit of carbon stock in each of several pools. The foundation in measured stocks makes this method close to direct and enables a variety of integrative tests that become more powerful as the time scale of the measurements extends to several years or decades. The accuracy of this method is limited by the accuracy with which the stocks, the stock changes, and the decomposition rates are known. Because this approach uses decomposition rates with low time resolution, it is most powerful at quantifying carbon balance on the time scale of a decade, and it has limited ability to determine year-to-year variations. This approach could be modified to include fluxes due to harvesting, fire, or other kinds of off-site transport, but that was not done for this analysis.

3) *Leaf model.* Winner and colleagues (2004) made extensive measurements of leaf-level CO_2 exchange on the major species at the WROGF and used a model to scale from these short-term leaf-level measurements to annual net photosynthesis at the ecosystem scale. Their approach estimates net photosynthesis only but provides a useful reference point for the whole-ecosystem carbon balance from the other techniques. This approach has great strength in clearly documenting differences among species and the sensitivity of CO_2 uptake to environmental variables, including light, temperature, and humidity. The limitations to the accuracy of the integrated numbers come mainly from the scaling. Uncertainty in the spatial distribution of leaf area, photosynthetic characteristics, and environmental factors can be reduced through studies from the canopy crane, but they are still substantial.

4) *Ecosystem model.* J.K. (Table 1) used a comprehensive ecosystem model to explore the balances of energy, water, and carbon at the WROGF. This approach facilitates multifactor validation in which, for example, energy balance closure is used to test aspects of the water balance, and the water balance is used to test aspects of the carbon balance. This approach simulates all of the carbon pools and fluxes in the ecosystem, but it has not, so far, incorporated the starting-condition data on carbon stocks that are critical for quantifying sources and sinks. Without a direct measure of the carbon stocks in all of the pools at the start of the study, this approach requires running the model to equilibrium, insuring that the approach will not detect carbon sources or sinks. Limitations to the accuracy of this technique come from uncertainty about starting stocks, uncertainty about the values for particular parameters, and uncertainty about the model structure. The failure to include all important controls on ecosystem dynamics, including, for example, nutrient dynamics (Cannell and Thornley 2000), also limits accuracy.

All four of the techniques create a picture of an active forest (Table 1). Gross primary production (GPP) is more than 1000 g C m^{-2} y^{-1}, with estimates ranging from 1300 g C m^{-2} y^{-1} from the ecosystem model to 2459 g C m^{-2} y^{-1} from the leaf model (Table 1). This places the ecosystem near the high end of GPP for temperate forests, though substantially below the estimates for many tropical
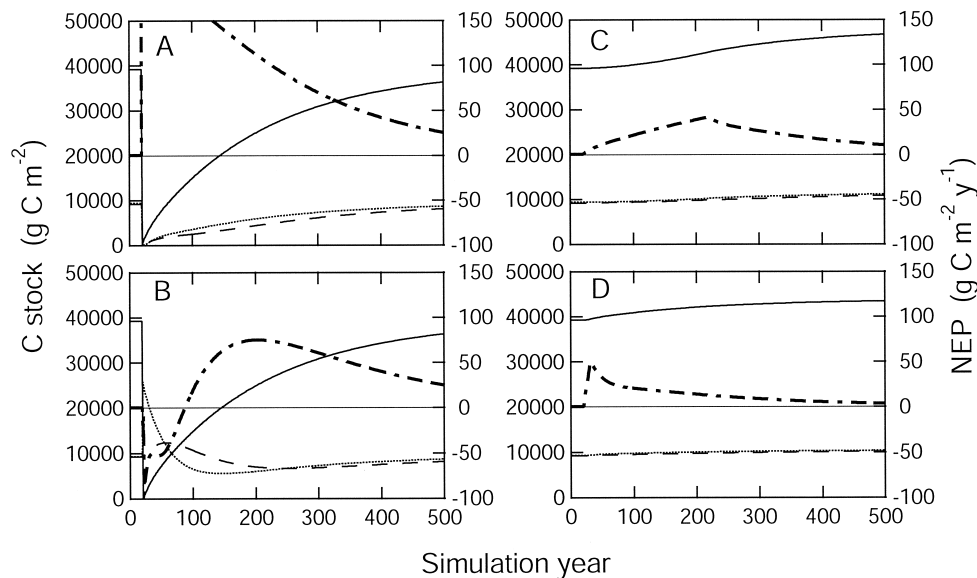
Figure 1. Simulated carbon stocks and fluxes for a simple carbon model (Figure 2) tuned to produce the Wind River old-growth forest stocks, given the net primary production (NPP) (597 g C m^{-2} y^{-1}) observed by Harmon and colleagues (2004). In each panel, the *left axis* is for carbon stocks (g C m^{-2}) and the *right axis* gives net ecosystem production (NEP; g C m^{-2} y^{-1}). The traces are total tree carbon (*solid line*), total detritus carbon (*dotted line*), total carbon in soil organic matter (*dashed line*), and NEP (*dashed-dotted line*). **A:** A forest beginning with all pools empty at year 20. **B:** As in A but starting with all pools in equilibrium. A fire in year 20 removes all of the live biomass pool and transfers 70% of the slow wood pool to the pool of coarse woody debris. **C:** A simulation starting with all pools in equilibrium, with a 0.1% per year increase in NPP starting in year 20 and ending in year 120. The final NPP is 720 g C m^{-2} y^{-1}. **D:** As in C but with an NPP increase of 1% per year in years 20–30. The final NPP is 658 g C m^{-2} y^{-1}.

forests (Cramer and others 1999). NPP is also high. The estimates between 500 and 600 g C m^{-2} y^{-1} also place the forest at the active end of temperate forest ecosystems. This high level of primary production is consistent with the site's high leaf-area index (8.6) (Parker and others 2004), abundant precipitation (2467 mm y^{-1}) (Shaw and others 2004), and absence of extremely cold winters. It is also consistent with the NPP estimated from the widely used Miami model, which predicts 581 g C m^{-2} y^{-1} for a site with the climate of the WROGF forest (Lieth 1975). These estimates of substantial primary production are somewhat difficult to reconcile with the hypothesis that NPP falls as a forest ages (Ryan and others 1997). All of the proposed mechanisms for restricting NPP in old-growth forests (autotrophic respiration, nutrient limitation, and hydraulic limitation) could impact the WROGF forest. Perhaps NPP has dropped from very high initial values, or perhaps the age-dependent declines in NPP have been no more than modest.

NEP and net ecosystem exchange (NEE) should both estimate annual carbon storage or loss at the WROGF. NEP is traditionally defined as the net change in stocks (with a positive number indicating

a sink), whereas NEE is the time integral of the atmospheric fluxes (often with a negative value indicating a sink). In general, the concept of old growth implies a forest where all of the pools are operating close to equilibrium and where NEP is close to zero (Waring and Running 1998).

Estimated NEP is close to zero in the ground-based analysis reported by Harmon and colleagues (2004). They estimate NEP at 20 g C m^{-2} y^{-1} (a small sink), with a likely uncertainty range of −116 to +156 g C m^{-2} y^{-1}. The estimate based on eddy flux is substantially higher, with values of 150 and 190 g C m^{-2} y^{-1} (a substantial sink), depending on the method selected to calculate the fluxes for time periods when the wind speed is too low for eddy flux to be reliable (Paw U and others 2004). To evaluate these numbers, it is important to look broadly at the kinds of factors that can create a carbon sink in forest ecosystems.

A Bucket Model for Forest Carbon Balance

To understand the processes that drive forest carbon balance, it is useful to start from an analogy
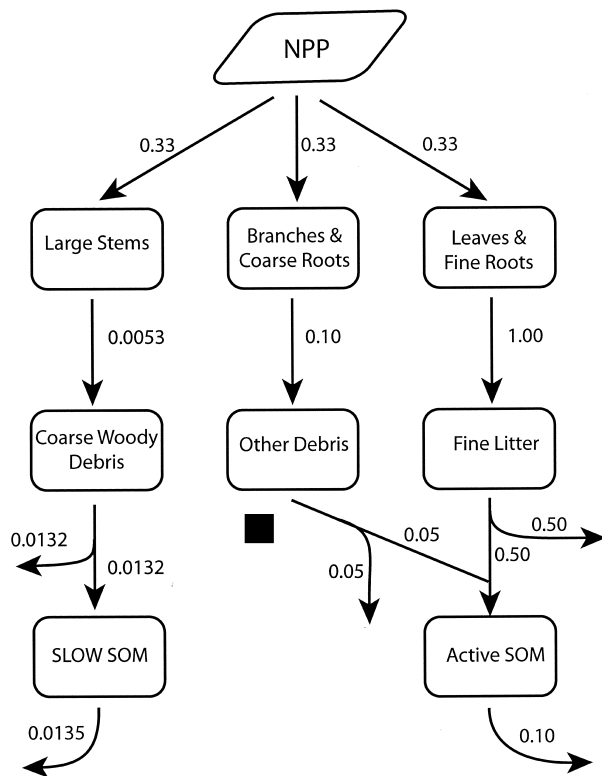
Figure 2. Structure and parameters for a simple eight-pool carbon model. For all of the pools, the number on the *outward arrow* is the proportion of the donor pool that moves outward from the pool in any year. The parameters for large stems, coarse woody debris, and slow soil organic matter (SOM) were adjusted to produce the pools reported by Harmon and colleagues (2004). NPP, net primary production.

organic carbon in streams and groundwater are examples of the second. In a temperate forest without recent major fires, these fluxes are small, almost certainly not significant factors in the overall carbon balance.

With the leaky bucket, as with the forest, four kinds of mechanisms can raise the water level or generate carbon storage. One class of mechanisms concerns the distinction between an old-growth forest and an aggrading forest. The other three are equally relevant to old-growth and aggrading forests. It is important to consider these separately, because each has very different implications for regional and global carbon balance.

First, the water level will rise after the bucket is emptied. A disturbance like logging or fire results in a loss of organic matter, effectively reducing the pressure behind the leak (Figure 1A). This decrease in pressure or, for the forest, decomposition rate means that inputs exceed outputs for some period. A simple eight-box model tuned to reproduce the stocks measured by Harmon and colleagues (2004) (Figure 2) suggests that the time required to fill the bucket can be substantial. Starting from the extreme assumption of empty carbon pools in vegetation, detritus, and soils, NEP drops below 100 g C m^{-2} y^{-1} (1 Mg C ha^{-1} y^{-1}) only after 207 years. The time required for NEP to fall below 10 g C m^{-2} y^{-1} is 664 years (Figure 1A). With more realistic starting conditions, the approach to equilibrium is quicker. Consider the case immediately following a major fire, where all of the trees are killed and a large fraction of the biomass is transferred to a pool of coarse woody debris. In this case, NEP is smaller, reaching a peak of about 75 g C m^{-2} y^{-1} after 180 years and falling to about 37 g C m^{-2} y^{-1} after 400 years (Figure 1B). But in contrast to the example of starting from empty pools, NEP can follow a complex trajectory, with a phase of several decades when the forest is a carbon source, followed by a phase when it acts as a substantial sink.

Recovery from past disturbance could account for a larger sink if part of the forest were disturbed recently or if the equilibrium organic matter content of the ecosystem were substantially above the 58,000 g C m^{-2} reported by Harmon and colleagues (2004). We can explore the latter option in the leaky-bucket model by halving the turnover rates of carbon in the large stem, coarse woody debris, and slow soil organic matter (SOM) pools (Figure 2). With this assumption, the forest gains carbon over more than a millennium, reaching levels of total organic matter over 110,000 g C m^{-2}. Even this unrealistically massive forest, however,

with a leaky bucket. NPP is adding water to the bucket, and decomposition is removing the water. With a leak at the bottom, the rate of water loss is proportional to pressure, or the amount of water in the bucket, just as decomposition is typically proportional to the amount of organic matter in the decomposing pools. The carbon storage in the forest is the water level. As long as NPP and the size of the leak do not change through time, the water level (or total carbon storage) will eventually stabilize at the point where NPP and the leak rate are equal (Figure 1A). This point of carbon equilibrium essentially defines an old-growth forest and underlies the concept that an old-growth forest should not be a major carbon sink.

It is possible, at least in principle, that carbon could be allocated to some pool where it decomposes exceedingly slowly or where it is transported off site before decomposing. Charcoal is an example of the first class of pool, and dissolved inorganic and
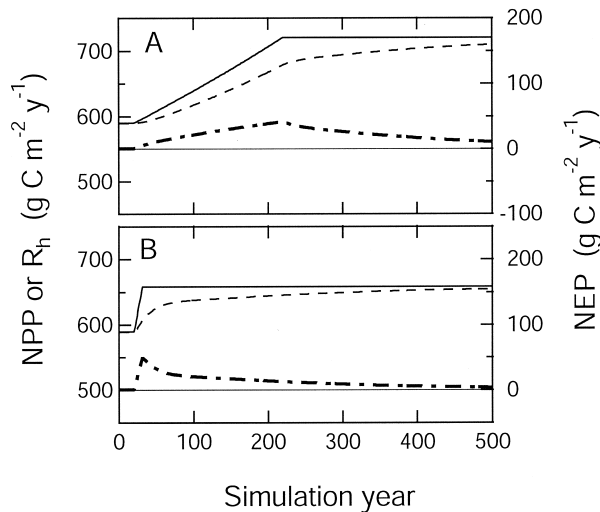
Figure 3. Simulated carbon fluxes for the simple carbon model (Figure 2) [net primary production (NPP; *solid line*), heterotrophic respiration (R_h, *dashed line*), and [net ecosystem production (NEP, *dashed-dotted line*)] with **(A)** an initial carbon balance and an NPP increase of 0.1% per year in years 120–220, and **(B)** an initial carbon balance and an NPP increase of 1.0% per year in years 20–30. These results are from the same simulations used to generate Figure 1C and D.
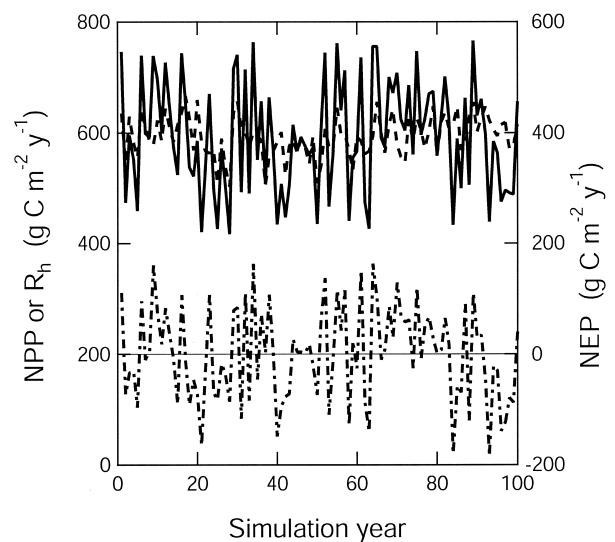

Figure 4. Simulated carbon fluxes for the simple carbon model (figure 2) (NPP (solid) heterotrophic respiration (R_h, dashed), and NEP (dash-dot)) with an initial carbon balance and a randomly varying NPP and heterotrophic respiration (each with a ±30% range).

starting with all pools empty, is a sink of only 105 g C m^{-2} y^{-1} after 400 years.

Second, the pool size will increase if NPP increases. After NPP increases, there will be a lag until the carbon in the decomposable pools increases enough so that decomposition balances the increased input. The resulting sink is a consequence of NPP keeping ahead of decomposition, and it can persist as long as NPP keeps increasing. When NPP stops increasing, the sink eventually disappears. The magnitude of any sink from an NPP increase depends on the rate of increase and on the turnover time of the carbon in the ecosystem (Thompson and others 1996). At present, evidence for widespread increases in NPP from changes in the climate or in the atmosphere is mixed (Caspersen and others 2000; Hicke and others 2002), but we can explore the possible range with two scenarios.

One possibility is that NPP is increasing largely as a result of CO_2 fertilization, as a result of the greater than 30% increase in atmospheric CO_2 since the beginning of the industrial revolution. In many wild plants, NPP under controlled conditions increases by something like 20% in response to a CO_2 doubling (Koch and Mooney 1996). With recent increases on the order of 0.5% y^{-1}, a linear assumption suggests that CO_2 fertilization could increase NPP by something like 0.1% y^{-1}. An in-

crease of this magnitude over 120 years in the eight-box model (Figure 2) could drive a modest current sink of approximately 29 g C m^{-2} y^{-1} (Figures 1C and 3A). A much more dramatic increase in NPP [for example, 1% y^{-1} over a decade as suggested by Myneni and colleagues (1997)] could lead to a current sink of 50 g C m^{-2} y^{-1} (Figures 1D and 3B). With either scenario, the carbon sink from an NPP increase fades gradually after NPP stabilizes.

The third bucket analogy concerns the case of fluctuating inputs or outputs. The processes controlling NPP are somewhat distinct from the processes controlling decomposition, at least on an annual basis. Years of high NPP can have low heterotrophic respiration, and vice versa, at both the local scale (Goulden and others 1996) and the regional scale (Braswell and others 1997). As a consequence, interannual variability in climatic conditions can lead to large, though temporary, variations in NEP (Kaduk and Heimann 1996; Potter and others 1999). For example, uncorrelated ±30% year-to-year variation in NPP and heterotrophic respiration leads to NEP of up to ±200 g C m^{-2} y^{-1} in the eight-box model (Figure 4). Even though a 1-year sink through this mechanism is the largest in the examples considered here, it is the least relevant to long-term carbon balance, because the fluctuations are around a mean of zero.

The fourth mechanism that could drive a carbon sink is analogous to an increase in the viscosity of the water in the bucket. If biomass allocation shifts

toward depositing more carbon in a less decomposable pool, the average rate of decomposition will decrease (Field 1999). This mechanism has been discussed as a candidate to account for carbon sinks in scenarios with warming (Shaver and others 1992) and elevated CO_2 (Mooney and others 1999). The consequences and dynamics of a sink driven through this mechanism are similar to those for a sink driven by an NPP increase.

IMPLICATION OF CARBON SINKS FROM DIFFERENT MECHANISMS

Each of these four mechanisms could drive a 1-year to several-year carbon sink at the Wind River Canopy Crane Research Forest. The implications of each for regional, long-term, carbon balance are, however, very different.

A sink due to recovery from disturbance can persist over many decades. Sinks resulting from this mechanism appear to be important, perhaps dominant components of the current carbon sink in the temperate and boreal latitudes of the Northern Hemisphere (Kauppi and others 1992; Houghton and others 1999; Caspersen and others 2000); yet a sink from forest regrowth at a single site provides little information about regional carbon balance, which is determined by a mosaic of forest patches at many different stages of development (Kurz and Apps 1999). In essence, any contribution of regrowth to the measured carbon sink at the WROGF simply indicates that the forest has not yet reached the point of carbon equilibrium. From the carbon-balance perspective, it is not yet old growth.

A carbon sink from increasing NPP could be important for the regional or global carbon budget, especially if the NPP increase is sustained over decades (Thompson and others 1996). It is possible that this mechanism is contributing to a current sink, but the resulting sink is likely to be modest. The combined effects of CO_2 fertilization, nitrogen fertilization from deposition (Townsend and others 1996), and a lengthening of the growing season (Myneni and others 1997) could account for a decade-scale carbon sink in the neighborhood of 50–100 g C m^{-2} y^{-1}.

A 1-year to several-year carbon sink from fluctuating NPP and soil respiration is a good possibility. The climate at the site is quite variable, with substantial year-to-year variation in precipitation, especially with El Niño–Southern Oscillation (ENSO) cycles (Shaw and others 2004). The 1998–99 period was wet, relative to the long-term average. A stimulation of NPP from the extra precipitation could drive a substantial 1-year sink.

Alternatively, a large sink in 1 year could be due to a decrease in respiration. At the WROGF, soil respiration (as measured by the 3-m eddy-flux station) was lower throughout the summer of 1999 than the summer of 1998 (Paw U and others 2004). Of course, a sink from fluctuating NPP or heterotrophic respiration is irrelevant for long-term carbon balance, because negative deviations are as common as positive.

The difference between the carbon budgets estimated by Harmon and colleagues (2004) and Paw U and coworkers (2004) is compatible with a substantial sink due to this mechanism. Year-to-year variation in NPP or soil respiration should not appear as a sink in measures that integrate fluxes over decades, but it should in measurements with annual or finer resolution.

WIND RIVER OLD-GROWTH FOREST CARBON BALANCE: RECONCILING THE NUMBERS

The general picture from all of the approaches used to explore the carbon balance of the WROGF is of a productive forest with high rates of production and decomposition. The NPP estimated from Lieth's (1975) Miami model is remarkably close to the NPP calculated from stem increments and litterfall by Harmon and colleagues (2004). The estimate from the ecosystem model of J.K. is within 10% of this value, within the limits of the uncertainty in any of the approaches. Despite the similarity in NPP estimates, the values for GPP are diverse, spanning a range of nearly twofold. The lowest estimate, from J.K. (Table 1) is approximately 2.5 times NPP, in the standard range for forest ecosystems. The actual ratio could be somewhat higher than this, because the model of Kaduk assumes a low value for the biomass of active roots. The high value, from Winner and colleagues (2004), is more than four times the NPP. A value this high would imply very high rates of autotrophic respiration—higher than consistent with the approaches of Harmon and colleagues (2004) or Paw U and colleagues (2004). It is likely that the high GPP estimate reported by Winner and colleagues (2004) and the low estimate reported by J.K. both reflect the strategy used to integrate photosynthesis through the canopy. The model of J.K. does not account for enhanced light penetration from leaf clumping and diffuse illumination, both of which can increase canopy photosynthesis (Hollinger and others 1994). Winner and colleagues (2004) focused their measurements on the youngest cohort of fully expanded leaves and may have underestimated impacts of leaf aging (Field and Mooney 1983). Both approaches model

GPP as highly sensitive to diurnal and seasonal water stress, but used different methods to estimate the levels of stress.

The estimates of NEP from Harmon and colleagues (2004) and Paw U and coworkers (2004) are, in some respects, quite close. The frustrating aspect of NEP is that it tends to be a small difference between two large numbers. Both the eddy-flux and ground-based methods end up estimating the downward and upward fluxes of CO_2 with fundamentally different approaches. In the study by Paw U and colleagues (2004), the downward flux during the day comes basically from the eddy flux, whereas the upward flux at night involves alternative methods, including either large corrections to the eddy flux or an alternative method calibrated against temperature. Harmon and colleagues (2004) measure NPP directly, but estimate heterotrophic respiration from a combination of local stocks and regional turnover constants. In both methods, the respiration estimate is weaker than the estimate of uptake.

Based on the leaky-bucket model, it is unlikely that the WROGF could represent a sustained carbon sink much greater than 100 g C m^{-2} y^{-1}. It is possible, however, that the forest could be a substantial carbon sink in any given year, as a consequence of fluctuating NPP and decomposition. The leaky-bucket model is not intended as an authoritative representation of the fluxes at the WROGF, but it is based on a series of fundamental constraints. For a forest that has accumulated 58,000 g C m^{-2} over the last 400 years, it is difficult to construct a biogeochemical framework in which sustained net storage still approaches the average rate of about 150 g m^{-2} y^{-1}.

Old-growth forests are not important for their rate of carbon storage. The rates cannot be very high, and the aerial extent of old growth is a depressingly small fraction of the total. Still, old-growth forest has a value for carbon balance that far outstrips its sink activity. First, these forests contain a vast quantity of carbon. Alternative management schemes never match old growth when evaluated based on the time integral of total carbon in live and dead organic matter (Harmon and others 1990). Second, old-growth forest is a wonderful laboratory for understanding the components of carbon balance. It provides unique opportunities to quantify the long-term dynamics of organic matter pools, to explore the year-to-year variability in controls on these pools, and to integrate the biogeochemical fluxes on diverse time scales with the ecological actors driving them.

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