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Ecosystem carbon dioxide fluxes after disturbance in forests of North America

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[1] Disturbances are important for renewal of North American forests. Here we summarize more than 180 site years of eddy covariance measurements of carbon dioxide flux made at forest chronosequences in North America. The disturbances included stand-replacing fire (Alaska, Arizona, Manitoba, and Saskatchewan) and harvest (British Columbia, Florida, New Brunswick, Oregon, Quebec, Saskatchewan, and Wisconsin) events, insect infestations (gypsy moth, forest tent caterpillar, and mountain pine beetle), Hurricane Wilma, and silvicultural thinning (Arizona, California, and New Brunswick). Net ecosystem production (NEP) showed a carbon loss from all ecosystems following a stand-replacing disturbance, becoming a carbon sink by 20 years for all ecosystems and by 10 years for most. Maximum carbon losses following disturbance ($\text{g C m}^{-2}\text{y}^{-1}$) ranged from 1270 in Florida to 200 in boreal ecosystems. Similarly, for forests less than 100 years old, maximum uptake ($\text{g C m}^{-2}\text{y}^{-1}$) was 1180 in Florida mangroves and 210 in boreal ecosystems. More temperate forests had intermediate fluxes. Boreal ecosystems were relatively time invariant after 20 years, whereas western ecosystems tended to increase in carbon gain over time. This was driven mostly by gross photosynthetic production (GPP) because total ecosystem respiration (ER) and heterotrophic respiration were relatively invariant with age. GPP/ER was as low as 0.2 immediately following stand-replacing disturbance reaching a constant value of 1.2 after 20 years. NEP following insect defoliations and silvicultural thinning showed lesser changes than stand-replacing events, with decreases in the year of disturbance followed by rapid recovery. NEP decreased in a mangrove ecosystem following Hurricane Wilma because of a decrease in GPP and an increase in ER.

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1. Introduction

[2] Disturbances are an important feature of North American forests, renewing forest stands or changing the vegetation dynamics following less severe disturbances. Wildland fires burn an average of about 40,000 km² in Canada and the U.S. annually [Stocks *et al.*, 2003; U.S. National Interagency Forest Fire Centre, http://www.nifc.gov/fire_info/fires_acres.htm, accessed 25 March 2010] with large interannual variability. About 50,000 km² of forested land is harvested annually in Canada and the U.S., with about half of this as clear-cut harvest [Kurz and Apps, 1999; Birdsey *et al.*, 2006]. Moderate to severe insect infestations are highly variable among years but can affect a greater area than either fire or harvesting [Kurz and Apps, 1999; Birdsey *et al.*, 2006]. Hurricanes and tornados are estimated to affect about 17,000 km² annually in the U.S. [Dale *et al.*, 2001] and there are many additional less severe storms that cause windthrow in forests. These disturbances have a large effect on the carbon (C) balance of North American forests. For example, analyses for Canadian forests showed clearly that insects and fire have caused a net forest C loss that fluctuates annually, but has a lasting legacy [Kurz and Apps, 1999; Kurz *et al.*, 2008a]. Disease and storms also affect the C balance, but their impacts are often difficult to quantify because they result in decreased growth without initial catastrophic removals of C. The net C effects of disturbances have been modeled extensively with some of the model outputs being compared to direct eddy covariance measurements of C flux over daily to annual scales [e.g., Grant *et al.*, 2007]. These direct determinations of net ecosystem exchange (NEE) of carbon dioxide (CO₂) have helped us understand the processes controlling C exchange at individual sites following fire [e.g., Goulden *et al.*, 2006; Welp *et al.*, 2007; Dore *et al.*, 2008; Mkhabela *et al.*, 2009], harvesting [e.g., Chen *et al.*, 2002; Schwarz *et al.*, 2004; Misson *et al.*, 2005; Giasson *et al.*, 2006; Noormets *et al.*, 2007; Krishnan *et al.*, 2009; Zha *et al.*, 2009], insect infestations [Cook *et al.*, 2008; Clark *et al.*, 2010; Brown *et al.*, 2010], and storms [Barr *et al.*, 2010].

[3] In North America, there has been collaboration among researchers making eddy covariance measurements [e.g., Baldocchi *et al.*, 2001] through the AmeriFlux and Canadian Carbon Program (Fluxnet-Canada Research Network) networks. In particular, the Canadian network had a disturbance focus [Margolis *et al.*, 2006]. The North American Carbon Program (NACP) [Wofsy and Harriss, 2002] provides a framework for bringing some of these measurements together to investigate some general relationships between disturbance and forest C exchange across North America. Eddy covariance flux towers have not yet been established along disturbance chronosequences in Mexico. Our goal in the present paper is to synthesize the measurements for locations where tower clusters have been used to measure NEE of forest chronosequences after different types of disturbances.

[4] One option to investigate the effects of disturbance is to measure an ecosystem for several years prior to the disturbance, and then follow with long-term continuous observations to understand the ecosystem response and recovery following the disturbance. Such experiments are not always possible, especially considering the very long times needed

to measure ecosystem development over decades or centuries. Hence investigators often study sites of different ages in parallel to infer the status of an ecosystem as a function of age (time since disturbance). This chronosequence approach is a practical design to acquire age-related data in a short period of time. This is important when employing eddy covariance because we do not have an archive of comparative measurements taken over several decades to study the effects of forest development on the net CO₂ flux. However, there are now some relatively long-term eddy covariance sequences that have run well over a decade at mature forest sites [Barr *et al.*, 2007; Dunn *et al.*, 2007; Urbanski *et al.*, 2007].

[5] A conceptual trajectory of C flux following a disturbance, based on vegetation development [Odum, 1969] and dynamics of decomposition, is that the predisturbance ecosystem is fixing C at some rate, and then there is an immediate C loss as a result of the disturbance, with subsequent recovery over some period [e.g., Kashian *et al.*, 2006]. This loss is caused by death of photosynthesizing vegetation, biomass combustion in the case of fire, harvest removals, or insect herbivory. In cases where insects kill trees (e.g., bark beetles) or a storm causes tree defoliation and mortality, there is usually minimal initial export of C from the ecosystem. However, following most disturbances, changes to the ecosystem have the potential to alter NEE. This could be driven by changes to heterotrophic respiration when forest C pools change, coupled with decreased photosynthesis because of less leaf area. The ecosystem can change quite quickly as new growth follows the disturbance [Chen *et al.*, 2002; Gough *et al.*, 2007]. These generalizations also depend on the severity of the disturbance, with stand-replacing disturbances having different trajectories than less severe partial disturbances (e.g., stand thinning). A fundamental difference between harvesting and fire is that harvesting removes the coarse woody material, whereas fire removes the fine materials (forest floor and fine fuels). Such a difference likely impacts the postdisturbance respiration. Fire may also mineralize nutrients more rapidly, making them available for vegetation uptake. Insect infestations usually do not totally replace forest stands although there are exceptions in single-species forests [e.g., Kurz *et al.*, 2008b]. Similarly, some storms can be catastrophic causing high immediate losses of C [Lindroth *et al.*, 2009]. Typically, shorter disturbance intervals result in lesser C stocks [Gough *et al.*, 2008].

[6] Here, we synthesize eddy covariance tower-based CO₂ flux data from forest disturbance chronosequence studies across Canada and the U.S. We have included ecosystems affected by fire, harvesting, and major insect and storm (hurricane) events. There are many more chronosequence studies that have measured C fluxes using chambers [e.g., Bond-Lamberty *et al.*, 2003; Irvine *et al.*, 2007] or biometric sampling [e.g., Bond-Lamberty *et al.*, 2004; Campbell *et al.*, 2004, 2009; Gough *et al.*, 2008]. However, our synthesis of only tower-based eddy covariance data allows us to compare whole ecosystem fluxes using similar methodologies and footprints. Further, we have only included studies where annual Net Ecosystem Production (NEP) has been measured. This excludes many studies where data are only available from short (usually summer) field campaigns or partial years. We have used data from

forested sites that are less than 100 years old to concentrate on younger ecosystems. We recognize that this period is less than the disturbance cycle in some areas (e.g., the boreal fire cycle tends to be slightly longer than this on average) so that we are not integrating to estimate the net C budget for a full disturbance cycle. Also, there have been several previous syntheses that have concentrated on the C dynamics of old-growth forests [Carey *et al.*, 2001; Luysaert *et al.*, 2008]. We have not included the C removals during the disturbance event, such as biomass combustion, harvest removals, or insect migration, and only measure the postdisturbance effects. In this paper we focus on the following broad hypotheses to reconcile the responses of a broad range of forests to disturbance using the existing eddy covariance tower flux data: (1) Disturbances decrease NEP because of decreased Gross Primary Production (GPP) with little effect on Ecosystem Respiration (ER); (2) NEP recovers similarly following stand-replacing fire and harvesting (null hypothesis); (3) Non-stand-replacing disturbances such as insects, storms, and silvicultural thinning have very short-term effects on NEP.

2. Methods

2.1. Site Descriptions

2.1.1. Fire Chronosequences

[7] There are four major fire chronosequences included in this synthesis (Table 1). Three are located in the boreal forest in Alaska, Saskatchewan and Manitoba. The Alaska and Manitoba sites represent more northerly parts of the boreal forest dominated by black spruce (*Picea mariana*), whereas the Saskatchewan sites are at the southern fringe and have components of black spruce, jack pine (*Pinus banksiana*) and trembling aspen (*Populus tremuloides*). The Manitoba and Saskatchewan locations correspond to the northern and southern study areas, respectively, and were investigated during the BOREAS experiment [Sellers *et al.*, 1997]. However, the fire chronosequences were established in the late 1990s following the completion of BOREAS. At both of these chronosequences, long-term flux towers at mature sites anchor the longer-term flux record [Dunn *et al.*, 2007; Kljun *et al.*, 2006]. At all the boreal fire chronosequences, different forest stand ages were selected in a reasonably close geographic area, typically within 100 km. However, despite attempts to match site conditions, some of the variability among sites within a chronosequence will be caused by local environmental factors such as differences in soil type and hydrology. The fire chronosequence in Arizona captured the effects of a stand-replacing wildfire in a high-elevation semiarid ecosystem dominated by ponderosa pine (*Pinus ponderosa*).

2.1.2. Harvest Chronosequences

[8] Most of our harvest chronosequences were stand replacing, involving harvest with most of the larger trees removed and perhaps some protective vegetation left for regeneration [e.g., Giasson *et al.*, 2006]. However, slash may also have been left at the site, depending on local harvesting practices (e.g., New Brunswick site). In the boreal forest, harvest chronosequences were measured in Saskatchewan and Quebec. In both cases, mature (control) forests were fire generated because harvesting is a relatively new activity. The Saskatchewan site represents a southern

boreal condition with jack pine, whereas the Quebec site is a northern boreal black spruce site. These sites also differ by longitudinal gradient with the more eastern Quebec site receiving greater annual precipitation.

[9] In temperate forests, we have harvest chronosequences from several sites in the Wisconsin-Michigan northern hardwoods forest area. These sites are part of the larger ChEAS experiment [Chen *et al.*, 2008]. Essentially all stands less than 100 years old in this area regenerated following harvesting. There are several different forest stand types, ranging from jack pine to aspen and maple-basswood-ash (*Acer-Tilia-Fraxinus spp.*) deciduous species mixes. There are two temperate forest chronosequences on the west coast, located on Vancouver Island and in Oregon, representing Douglas fir (*Pseudotsuga menziesii*) and ponderosa pine forests, respectively. The clear-cut site in New Brunswick is a balsam fir (*Abies balsamea*) forest. The Florida chronosequence is a fast-growing slash pine (*Pinus elliottii* var. *elliottii*) plantation managed on a rotation of 20–25 years.

[10] Thinning treatments were conducted in a balsam fir forest in New Brunswick and ponderosa pine forests in Arizona and California. Measurements were made prior to thinning and then followed after the treatment. These thinnings are part of local forest management and represent treatments that are employed routinely. In Arizona, the slash from thinning was piled and burned the first year following thinning; this was undertaken to reduce forest fuels and the risk of an intense fire.

2.1.3. Insect Chronosequences

[11] There are three insect chronosequences where infestations have been sufficiently severe to cause major defoliation or tree death. The mountain pine beetle (*Dendroctonus ponderosae*) site in British Columbia was established specifically to measure the effects of the beetle, which has been killing large areas of lodgepole pine (*Pinus contorta*) forest [Kurz *et al.*, 2008b]. The affected areas have almost 100% tree mortality, but there is new growth by early successional species. The site in New Jersey experienced a severe defoliation by gypsy moth (*Lymantria dispar*) in 2007. Several forest types were measured that represented various mixtures of pine (*Pinus rigida*, *P. echinata*) and oak (*Quercus velutina*, *Q. prinus*, *Q. alba*, *Q. marilandica*, *Q. ilicifolia*). The Willow Creek site in Wisconsin, although established as part of a harvest chronosequence, experienced a severe defoliation by forest tent caterpillar (*Malacosoma disstria*) in 2001. This allowed an opportunity to study the effects of defoliation of hardwoods (*Tilia americana*, *Fraxinus pennsylvanica*, *Quercus rubra*), although there was a second growth of leaves following defoliation (i.e., most trees were not killed).

2.1.4. Storm Chronosequence

[12] Although severe storms take a toll on North American forests through tree windthrow, there have been few opportunities to measure the effects using flux towers. A study in a mangrove ecosystem in southwest Everglades National Park, Florida quantified the impact of Hurricane Wilma (October 2005) on mangrove forest NEE. Species included red (*Rhizophora mangle*), black (*Avicennia germinans*), and white (*Laguncularia racemosa*) mangroves. The storm was severe enough to defoliate the forest crown and destroyed about 30% of the mangrove trees. Flux tower instruments

Table 1. Description of Sites^a

Chronosequence	Location (Latitude, Longitude)	Vegetation Type ^b	Year of Most Recent Disturbance	Years Measured	Annual Mean Air Temperature (°C)	Annual Total Precipitation (mm)	Reference for Data	Site Name Used in Reference	
Alaska	63.9N, 145.7W	ground vegetation	1999	1999, 2002	-1.9	300	<i>Randerson et al.</i> [2006]; <i>Welp et al.</i> [2006, 2007]	Bn3	
	63.9N, 145.4W	bs, ta, willow	1987	2002–2004				Bn2	
	63.9N, 145.7W	bs	1920	2002–2004				Bn1	
	53.9N, 106.1W	jp, bs, ta	1998	2001–2006	0.4	470	<i>Amiro et al.</i> [2006]; <i>Mitchella et al.</i> [2009]	F98	
Saskatchewan	54.3N, 105.9W	jp, ta	1989	2002–2005				F89	
	54.5N, 105.8W	jp	1977	2004–2006				F77	
	53.9N, 104.7W	jp	1919	2000–2007				OJP	
	56.6N, 98.2W	ta, willow, bs	2003	2004–2005	-3.2	520	<i>Kijun et al.</i> [2006] <i>Goulden et al.</i> [2006]; <i>McMillan et al.</i> [2008]	NSA2003	
	56.6N, 98.2W	ta, willow, bs	1998	2003–2005				NSA1998	
	55.9N, 99.0W	ta, willow, bs	1989	2003–2005				NSA1989	
Manitoba	55.8N, 98.4W	ta, willow, bs	1981	2002–2005				NSA1981	
	55.8N, 98.4W	bs, jp, ta	1964	2002–2005				NSA1964	
	55.8N, 98.5W	bs	1930	2002–2004				NSA1930	
	35.1N, 111.8W	pp	1996	2006–2008	7.9	580	<i>Dore et al.</i> [2010] <i>Dore et al.</i> [2008, 2010]	Fwf	
	35.1N, 111.8W	pp	1919	2006–2008				Fuf	
	Saskatchewan	53.9N, 104.6W	ground vegetation, jp	2002	2004–2005	0.4	470	<i>Kijun et al.</i> [2006]; <i>Mitchella et al.</i> [2009]; <i>Zha et al.</i> [2009]	HJP02
		53.9N, 104.7W	jp	1994	2004–2005				HJP94
		53.9N, 104.6W	jp	1975	2004–2005				HJP75
53.9N, 104.7W		jp	1919	2000–2007				OJP	
Quebec	49.3N, 74.0W	ground vegetation, bs	2000 harvest, 2003 scarified	2002–2008	0	960	<i>Giasson et al.</i> [2006]; <i>Bergeron et al.</i> [2008]	HBS00	
	49.8N, 74.6W	bs	1975	2008			H. A. Margolis, personal communication, 2009	HBS75	
Vancouver Island	49.7N, 74.3W	bs	1915	2004–2008			<i>Bergeron et al.</i> [2007, 2008]	EOBS	
	49.9N, 125.2W	df	2000	2001–2008	8.6	1450	<i>Humphreys et al.</i> [2006]; <i>Krishnan et al.</i> [2009]	HDF00	
New Brunswick	49.5N, 124.8W	df	1988	2002–2008				HDF88	
	49.4N, 125.3	df	1949	1998–2008				DF49	
	46.5N, 67.1W	bf	2004	2005–2008	3.4	1190	M. B. Lavigne, personal communication, 2009	NL-CC	
	46.5N, 67.1W	bf	1975, thinned in 1991 and 2005	2004–2008				NL-CT	

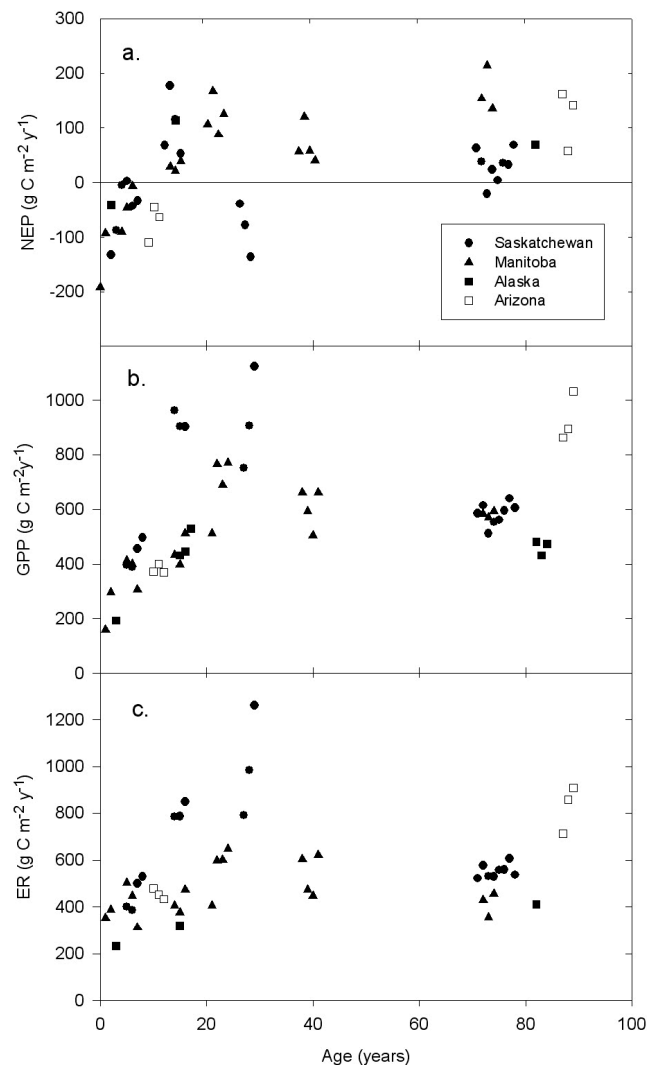


Figure 1. Annual (a) NEP, (b) GPP, and (c) ER for the fire chronosequences.

and data acquisition were also destroyed by the storm. Researchers reestablished the study field site in October 2006. Hence, measurements here are a true sequence with predisturbance and postdisturbance measurements.

2.2. Field Measurements and Data Processing

[13] The details of each individual field measurement and annual data processing protocol are given in the references listed in Table 1. Note that for this synthesis, each investigator supplied their best estimates of their annual totals of C fluxes for each site. This makes these measurements consistent with previous publications from each site. NEE was calculated every 30 min using the covariance of a fast-response infrared gas analyzer for CO_2 and a three-dimensional sonic anemometer for wind velocity. The gas analyzers were either closed-path or open-path systems. Although there was some variability among researchers, typical data processing included corrections for nonzero mean vertical wind velocity, tubing losses (closed-path analyzers) and density effects (especially for open-path analyzers). Known problems with sensor heating of open-path analyzers [Burba

et al., 2008] were either corrected, or were compensated by excluding cold weather data [Welp *et al.*, 2007] or filling cold-weather periods with modeled respiration [Mkhabela *et al.*, 2009].

[14] NEP was calculated as the gap-filled annual sum of NEE, defined so that a downward flux is positive (i.e., terrestrial ecosystem gain is positive). ER (positive flux is upward) was calculated based on nighttime NEE measurements combined with regression and modeling. GPP (downward flux is positive) was calculated as the sum of NEP and ER, sometimes combined with light-response modeling to fill gaps [e.g., Moffat *et al.*, 2007].

[15] In a multiple-site synthesis, variability among individual field techniques, annual data processing, and algorithms for GPP and ER contribute additional uncertainty [Desai *et al.*, 2008]. We appreciate the general need for a greater degree of homogeneity in postprocessing flux data, however the site investigators are contributors to either the AmeriFlux or Canadian Carbon Program networks, and some standardization has been achieved through these collaborations. Annual NEP is likely to be estimated within about $\pm 25 \text{ g C m}^{-2} \text{y}^{-1}$ based on uncertainty in gap-filling techniques [Moffat *et al.*, 2007]. However, there is some additional uncertainty caused by random error of about $\pm 20 \text{ g C m}^{-2} \text{y}^{-1}$ [Richardson and Hollinger, 2005]. Typically, we would expect annual NEP to be estimated to better than $\pm 50 \text{ g C m}^{-2} \text{y}^{-1}$ at most sites, with better estimates at certain sites. Baldocchi [2008] gives a good review of the potential issues that affect flux tower measurements.

3. Results and Discussion

3.1. Fire Chronosequences

[16] NEP, GPP and ER showed similar trends with time since disturbance for all of the four fire chronosequences (Figure 1). All sites that are less than 10 years of age were C sources. The three boreal chronosequences (Saskatchewan, Manitoba, Alaska) became net C sinks after about 10 years. During this period of positive NEP, there was substantial interannual variability at any given site, often ranging about $100 \text{ g C m}^{-2} \text{y}^{-1}$. This magnitude of interannual variability seemed to be similar at any given location, even when there were only three site years. Considering this variability, the NEP response with time for sites older than 10 years of age was relatively invariant with time. The Saskatchewan chronosequence at about 70 years of age included data from the southern old jack pine site, which tended to have lower NEP than at the nearby old aspen site [Kljun *et al.*, 2006], and likely does not fully represent the successional endpoint of the young postfire forests. At about 30 years of age, the Saskatchewan chronosequence showed three site years with consecutive negative NEP. This site had visibly decaying coarse woody debris lying on the surface contributing to ER. The Arizona site at about 10 years of age had similar NEP to the slightly younger boreal sites. Trees had still not regenerated at the Arizona site, and a sparse grassland had succeeded (seasonal maximum leaf area index = 0.6) with a large amount of coarse woody debris present [Dore *et al.*, 2008]. We do not have intermediate-aged forest data for Arizona, so the comparative trajectory is not clear even though the older Arizona site (about 90 years of age) had a similar positive NEP to the boreal sites. However, the postfire

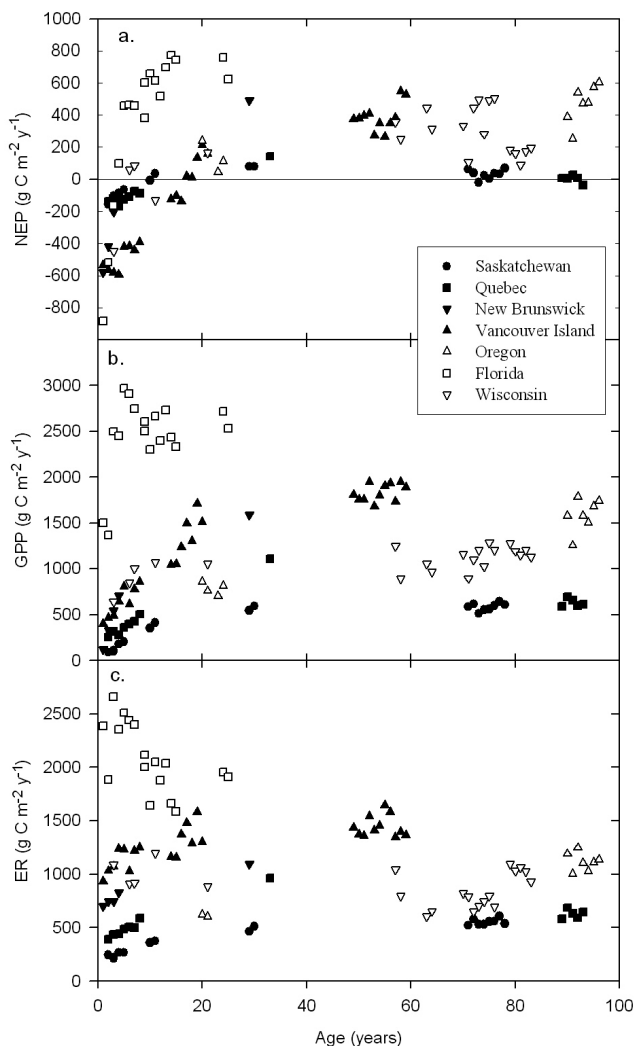


Figure 2. Annual (a) NEP, (b) GPP, and (c) ER for the harvest chronosequences.

vegetation dynamics are very different at the Arizona site compared to the boreal sites, and it could take many years to reach positive NEP following fire at the Arizona site.

[17] Separation of NEP into the GPP and ER components helps to identify the relative driving forces. GPP clearly increased with stand age for the first 20–30 years (Figure 1b). The Saskatchewan sites had the highest GPP in the 15–30 year age range. These sites had a warmer climate than the Manitoba or Alaska sites and had a fast-growing deciduous component of trembling aspen. After 30 years, the three boreal chronosequences tended to show similar GPP. The Arizona site had similar GPP to the boreal sites at about 10 years, but greater GPP at about 90 years. A possible explanation is that the Arizona chronosequence was more moisture limited for vegetation establishment following fire but the older stand benefited from the warmer climate, compared to the boreal sites.

[18] Ecosystem respiration had a less well-defined trajectory with age than either NEP or GPP, although it is slightly lower at very young ages (Figure 1c). With the exception of the Saskatchewan sites at 15 and 30 years, and

the 90 year old Arizona site, ER did not vary much with age. The high ER at the Arizona site and at some Saskatchewan sites is consistent with the high GPP at these sites. However, the negative NEP at the 30 year old site indicates that heterotrophic respiration is an important factor, likely because of decaying coarse woody debris. It is important to note that the Saskatchewan sites at 15 and 30 years used open-path gas analyzers that have known problems with sensor heating [Burba *et al.*, 2008]. Use of these analyzers without heating corrections will underestimate ER. In this study, data collected when temperatures were below 0°C were excluded and replaced using respiration estimated as a function of soil temperature. Although this increases the uncertainty in ER, the high ER was mostly caused by summertime losses at these sites, likely enhanced by decomposition of coarse woody debris [Mkhabela *et al.*, 2009].

3.2. Harvest Chronosequences

[19] NEP trajectories following harvesting showed similar temporal changes to those after fire, although there was more variability caused by location (Figure 2a). In particular, sites in warmer climates had higher NEP, and the Florida trajectory clearly showed faster recovery following harvest. The greatest C loss in the early years following harvesting was also at warmer sites, which caused a greater dynamism in the C flux than at colder sites. The boreal sites (Saskatchewan, Quebec) had reduced amplitude throughout the trajectory. The scale of Figure 2a used to accommodate all ecosystems diminishes the relative interannual variability of the boreal sites. This comparison showed greater absolute interannual variability in C flux for warmer sites than colder sites in North America. However, the overall interannual variability effect needs to be integrated spatially over all North American forests to evaluate its importance.

[20] Similarly to NEP, GPP showed clear ecosystem differences among geographic locations (Figure 2b). The much larger fluxes for Florida, Vancouver Island and Oregon dwarfed the boreal trajectories. However, for all chronosequences, a clear GPP recovery occurred within about the first 20 years following harvest. The boreal, Wisconsin, and Florida GPP values were relatively flat after 20 years, whereas the west coast (Vancouver Island, Oregon) ecosystems showed an increase over time. This western forest increase is consistent with continued C accumulations observed in biometric and inventory data [Law *et al.*, 2004; Hudiburg *et al.*, 2009]. Lower photosynthetic assimilation fluxes were also documented by Buchmann and Schulze [1999] for forest stands less than 20 years of age. As in the case of fire, ER had a relatively flat trajectory, with some reduction in ER in the very first years following harvest at some sites (Figure 2c).

3.3. Respiration Components for Fire and Harvest Chronosequences

[21] The large differences in C fluxes among geographic regions are largely climate driven. Process models can help explain these differences, but there is no simple climate scaling variable such as normalization by annual temperature alone when we consider the chronosequence. For example, at very young (<4 years old) harvested sites, there were similar values of NEP and GPP for sites with different annual temperatures, although ER was much better sepa-

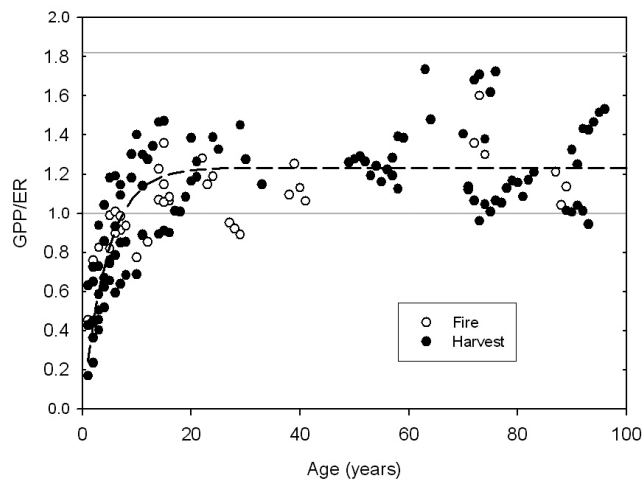


Figure 3. The ratio of annual GPP/ER with stand age for fire and harvest sites. The horizontal line at GPP/ER = 1.82 corresponds to a constant autotrophic respiration value of $0.55 \cdot \text{GPP}$ and no heterotrophic respiration. The dashed line is the regression for all data points where $y = 1.23 (1 - e^{-0.224x})$, $r^2 = 0.60$, and $n = 162$.

rated (Figure 2, Table 1). However, we would expect C allocation to scale in some fundamental ways. For example, the ratio of GPP to ER clearly showed low values at early years following disturbance (Figure 3) for both postfire and postharvest sites. As discussed for NEP, GPP/ER became greater than unity (i.e., $\text{NEP} > 0$) by 20 years for all chronosequences and by 10 years for most. More importantly, GPP/ER did not vary much with age following this initial increase for sites generated by either harvest or fire, and had an asymptote of 1.23. This is consistent with a global analysis of flux data where most of the forested sites were mature, which gave an average ratio of $\text{GPP/ER} = 1.2$ [Law *et al.*, 2002].

[22] ER can be separated into autotrophic (R_a) and heterotrophic (R_h) respiration components. Although we usually do not have independent measures for each of these, it is instructive to examine the chronosequence data by assuming some relationship between R_a and GPP. We recognize that the R_a/GPP ratio can vary [DeLucia *et al.*, 2007; Piao *et al.*, 2010], especially among our large range of ecosystem types and climates. However, a range of studies estimate R_a to be about $0.55 \cdot \text{GPP}$ [e.g., Landsberg and Waring, 1997; Jassal *et al.*, 2007], which would yield $\text{GPP/ER} = 1.82$ if $R_h = 0$ (horizontal line in Figure 3). All points were below this maximum because $R_h > 0$, and the relative effect of R_h was clearly greatest in the first 10–20 years following disturbance (i.e., R_a is low). When $\text{GPP} = \text{ER}$ (i.e., $\text{NEP} = 0$), $R_h = 0.45 \cdot \text{ER}$. At the lowest measured value of GPP/ER of about 0.2 in Figure 3, R_h was about 90% of ER. This corresponded to the sites where GPP was low immediately following harvest (Figure 2b), with most of this GPP likely being from ground vegetation contributions before new trees were established.

[23] We can carry the respiration analysis further, again assuming a constant fraction of R_a to GPP (0.55), recognizing that this may change with forest age and species [DeLucia *et al.*, 2007]. In Figure 4, we plot the derived R_h as

a function of age. Here we have normalized the R_h for each site by the mean value for all sites in the local chronosequence (e.g., each Saskatchewan fire site year R_h is divided by the mean value of all Saskatchewan fire site years) to allow comparison on the same scale. Although there were some higher R_h values at young sites, there was no significant regression relationship with age ($y = 0.98 + 0.0004x$; $r^2 = 0.003$). Splitting the sites into groups of > 10 and ≤ 10 years of age also showed no statistical difference (Student's t test $P = 0.5$). Hence, it appears that R_h is largely invariant with age for the full data set, even though there are likely trends in some of the individual chronosequences. This is evident for some of the youngest harvested sites and for the 30 year old Saskatchewan fire site, which had high R_h .

[24] The data support the hypothesis that disturbances decrease NEP mostly because of decreased GPP. Fire and harvesting slightly decreased ER soon after the disturbance, but ER then either increased over time or did not vary. Figure 3 also supports the hypothesis that NEP recovery is similar following stand-replacing fire and harvesting, at least in a broad sense. However, there are differences at any given location, as has been demonstrated for individual chronosequences [Mkhabela *et al.*, 2009].

3.4. Insects, Storms, and Thinning

[25] The studies of insects, storms, and thinning followed a true sequence of years that encompass the disturbance at a given site. The strength of these measurements is that there is no spatial variability when a true chronosequence is followed. However, interannual variability caused by climate fluctuations needs to be assessed using a control site [e.g., Dore *et al.*, 2010]. Although the time period (i.e., age effect) was shorter, the continuous measurements demonstrated the nature of the disturbance effect. NEP following gypsy moth and forest tent caterpillar infestations showed a decrease in the year of infestation, with a clear recovery in subsequent

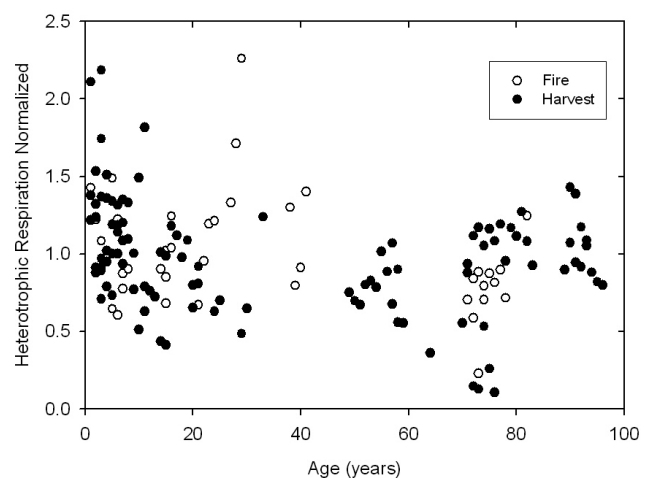


Figure 4. Estimated heterotrophic respiration with stand age. We assume that heterotrophic respiration = $\text{ER} - 0.55 \cdot \text{GPP}$. Heterotrophic respiration values for each site are normalized by the mean value for the local chronosequence for comparison on the same scale. There is no trend with age ($r^2 = 0.003$).

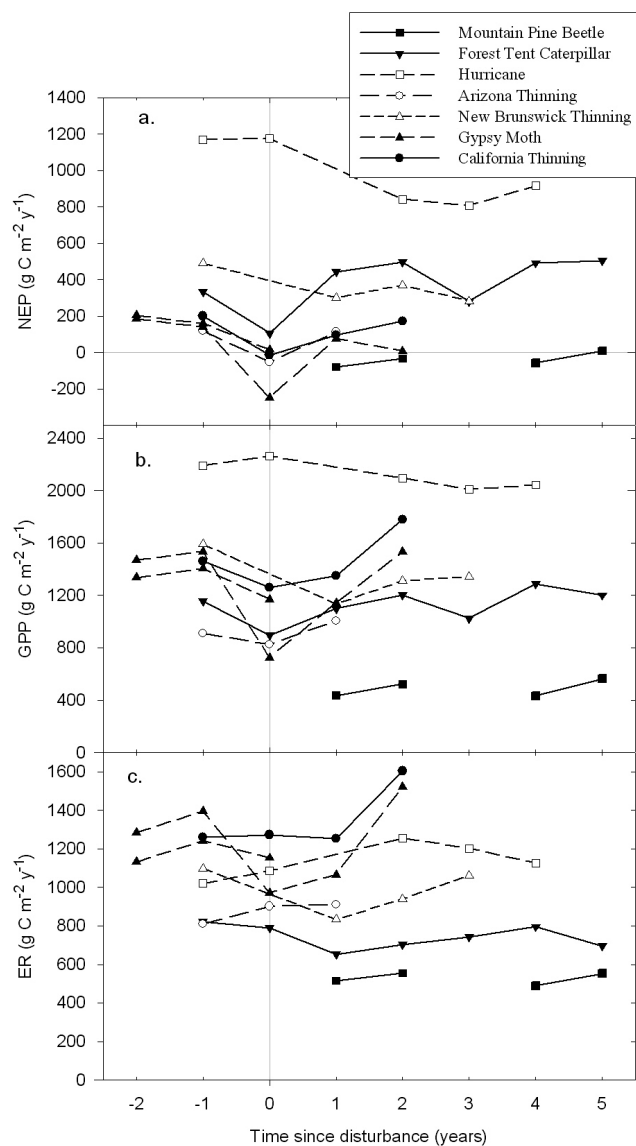


Figure 5. Annual (a) NEP, (b) GPP, and (c) ER for insects, storms, and thinning. The zero year is the year of disturbance.

years (Figure 5a). The gypsy moth-affected sites were slightly more complicated because of 2 years of infestation in the case of one site, and the use of prescribed fire in some stands. The oak-pine site was not defoliated in 2005 and 2006, but was completely defoliated in 2007. The pitch pine-scrub oak site was not defoliated in 2005 and 2006, and understory oaks and some shrubs were defoliated in 2007. In Figure 5a, we have included data from the oak-pine and pitch pine-scrub oak stands [Clark *et al.*, 2010]. We have not included the data in the year following infestation at the pitch pine-scrub oak site, which experienced prescribed fire in March 2008 and could have complicated the response due to insect disturbance.

[26] The mountain pine beetle sequence included two sites: one site had data for the first 2 years following infestation, whereas the other was measured 4 and 5 years after. For all four site years, NEP was slightly negative becoming neutral by year five, whereas we would expect

these 80 to 100 year old lodgepole pine stands to have been net C sinks (there is no pre-effect measurement site). During the year of gypsy moth and forest tent caterpillar infestations, both GPP (Figure 5b) and ER (Figure 5c) decreased. GPP increased following the infestation year, however ER continued at a lesser rate than it was prior to the forest tent caterpillar infestation. We recognize that differences can also be caused by interannual variability in climate, which is difficult to assess with a single sequence.

[27] The effect of Hurricane Wilma in Florida is shown where a complete year (2004) and a partial year (2005, with November and December gapfilled) were measured before the October 2005 event [Barr *et al.*, 2010], and then measurements resumed in 2007. A decrease in NEP was mostly attributed to an increase in ER, presumably because of more woody debris available for decomposition. Also, an increase in soil temperature of 1 to 3°C resulting from increased radiation penetration to the surface may have contributed to higher heterotrophic respiration following the storm. The high NEP values at this Florida mangrove site were driven by a high GPP without a correspondingly high ER. This was likely caused by a net lateral efflux of particulate and dissolved organic C that was not available for local respiration. In addition, a portion of the respired CO₂ was exported with the outgoing tide as dissolved inorganic C and released to the atmosphere outside of the tower flux footprint.

[28] The thinned site in Arizona showed a decrease in NEP during the treatment year, recovering in the following year. ER at this site increased through the 3 years of measurement and GPP decreased in the year of thinning and then increased in the following year. The California site, which was also ponderosa pine, showed a similar NEP and GPP trajectory to the Arizona site, being carbon neutral in the thinning year. ER increased 2 years after the thinning treatment. This site was quite young, having been planted in 1990. The New Brunswick site had some thinning conducted 14 years prior to the commercial thinning. Following the commercial thinning, NEP, GPP and ER all decreased. The short period of record is insufficient to know the longer-term effect. More measurements are needed on the effects of forest operation treatments, especially over longer periods [e.g., Gough *et al.*, 2008]. In summary, the results on the effects of insects and thinning support the hypothesis that the C impact is relatively short-term, with the greatest decrease in the year of disturbance. However, the hurricane effects appear to be longer lasting.

3.5. Implications for Modeling and Further Measurements

[29] The observed fluxes exhibited a trajectory characterized initially by C losses occurring immediately after the disturbance, followed by a recovery phase of positive NEP. However, the speed of the recovery was important, and all trajectories showed a positive NEP at 20 years following disturbance and most were positive at 10 years. Once the young forests became net C sinks, NEP quickly reached a fairly stable value that remained relatively constant with age, at least for the 100 year limit of the trajectories presented here. The exceptions to this trend were the west coast sites (Vancouver Island, Oregon) which tended to have an increase in NEP over the period of our data sets. This was caused by steadily increasing GPP with relatively little

change in ER. The relatively time-invariant trajectories of NEP in boreal, southern pine and deciduous forests after 20 years were caused by little change in either ER or GPP. For many chronosequences, leaf area index did not change much for forests greater than 20 years of age [e.g., *McMillan et al.*, 2008]. The GPP/ER stayed approximately constant at between 1 and 1.5 once $NEP > 0$ for both fire and harvest chronosequences (Figure 3). Heterotrophic respiration was invariant with age (Figure 4), suggesting that this process can be modeled as close to being constant for a chronosequence at a given geographical location, similar to that reported by *Law et al.* [2003] and *Luyssaert et al.* [2008].

[30] Integration of the NEP trajectories over time gives the net C sequestration. When considering the effects of disturbance, this integration should be over the period between disturbance events. However, there was sufficient interannual variability and differences among sites to make a simple integration of any of the NEP figures difficult. For example, a regression of NEP versus age for the boreal fire chronosequences (Figure 1a) yielded a best fit of $NEP = -99.5 + 42.27 \cdot \ln(\text{age})$ with $r^2 = 0.34$. We also included three site years at about 160 years of age at the Manitoba site in this regression. Removing the three negative NEP points at about 30 years (the Saskatchewan F77 site) only improved the regression slightly to $r^2 = 0.42$. Using this regression of all the boreal fire sites, the NEP crossover time to a positive value was 10.5 years. However, the potential to have a secondary period of negative NEP caused by woody debris decomposition was evident and should be considered in process models. This is because postfire decay requires the woody material to be wet and support microbial decomposers, typically through contact with the ground, which lags the disturbance event. Such a lag may not occur with whole-tree harvest when the finer slash materials left on the postharvest site would have the opportunity to start decomposing without lag. It was difficult to gauge this process in the flux trajectories, but the boreal fire and harvest sites did not appear much different in the very early years, and the most negative NEP was seen at the warmer sites in Florida, New Brunswick, Vancouver Island and Wisconsin (Figure 2a). However, a closer comparison of harvest and fire on an expanded scale show some differences when closely located sites were compared. For example, the fire-generated sites had higher GPP and ER than harvest-generated sites in Saskatchewan [*Mkhabela et al.*, 2009], whereas in Arizona, the thinned sites had higher GPP and ER than the postfire sites [*Dore et al.*, 2010].

[31] In this synthesis, we examined all the disturbance data on a common scale. This approach helped to show some large generalities, but it is clear that more complete trajectories would help for any given location. The Florida harvest sites were likely the most complete because of their continuity and the relatively quick vegetation growth following a disturbance. The Manitoba sites were the most complete fire chronosequence, but given the relatively long fire cycle (typically over 100 years) [*Stocks et al.*, 2003], missing ages still pose questions about whether the trajectories are relatively smooth. Measurements at more sites in a given geographic area would help account for spatial variability. However, measurements at the Wisconsin group of sites showed that interannual variability at a given site is of the same magnitude as intersite variability [*Noormets et al.*,

2009]. For recently disturbed sites where NEP and GPP recovery was rapid (e.g., boreal fire), both interannual and spatial variability were relatively less important during this early period compared to later in the trajectory, at least on a 100 year timescale. Although we need to consider the length of each disturbance cycle, these results suggest that good modeling of the period beyond about 10 years is important to get the net rotational C balance because of greater variability during this period. The first 10–20 years is also very important where NEP recovery is slower, such as the Arizona fire or Vancouver Island harvest sites, or where the rotational period is quite short (e.g., Florida harvest).

[32] We were fortunate to have some data on the effects of insects and storms, but clearly these were insufficient to understand fully the impacts on C exchange. The continuous sequence data at these sites, and the thinned sites, helped to bracket the nature of the impacts. However, we would expect some of the effects to have a temporal lag. For example, changes in GPP in a given year could affect ER in the following year because of changes to leaf-litter inputs. This is further complicated by potentially different weather conditions in subsequent years. Despite this complication, a short-term decrease in NEP was observed in the year of defoliation (Figure 5a). For insect infestations causing tree death, such as for the mountain pine beetle sites, new vegetation growth appears to be compensating for decomposition of killed trees with the ecosystem being C neutral about 5 years following the attack [*Brown et al.*, 2010]. However, as in the case of fire, it is likely that there will be a second period of enhanced ER when these dead trees fall over and decompose more quickly. Such processes could be documented by selectively measuring annual fluxes in stands where this event has happened.

[33] The thinning sites in Arizona, California and New Brunswick illustrate the potential to investigate C dynamics as a result of silvicultural practices. Given that there are many possible ecosystem management options, it is likely that future eddy covariance measurements need to be employed in a diverse range of practices and sites to capture the range of responses [e.g., *Vesala et al.*, 2005]. Although silviculture usually focuses on tree growth performance or fuel reduction, the ability to determine annual NEP for different forest management options would help establish net C benefits ranging from years to decades. The effect of Hurricane Wilma reduced NEP for at least 4 years following the event, and continued data are needed to evaluate the recovery dynamics of severe storms.

4. Conclusions and Recommendations

[34] Eddy covariance studies following forest disturbance illustrate that C flux trajectories are consistent with a conceptual model of net loss in early years, followed by C gain as the new forest becomes established. The data showed that recovery to a net C sink is relatively rapid in most ecosystems investigated, usually occurring within 20 years. The postfire Arizona site is an exception because of succession to grassland without tree establishment. We had fewer measurements following less severe ecosystem changes, such as insect defoliation or forest silvicultural thinning, and these effects need to be assessed more fully and compared to interannual variability caused by climate. We also recognize

that our chronosequence measurements are essentially a “snapshot” of recent CO₂ fluxes, with older forests having developed under past conditions that had lower ambient CO₂ concentrations and a different climate.

[35] Although the boreal fire and some of the harvest chronosequence sites have been decommissioned, there is a need to learn more about developmental dynamics, such as the decomposition of coarse woody debris following disturbance. It is possible that this is a short-term respiration flux that occurs in a pulse of a few years in favorable climatic conditions, or could be a more continuous process that affects the net flux for several decades as in the semiarid ponderosa pine region [Sun *et al.*, 2004]. We also have poor spatial representation, especially in nonboreal fire-dominated ecosystems. For example, there are many ecosystems where needleleaf evergreen forests regenerate directly after fire without a broadleaf deciduous successional component. We could then expect a more delayed NEP recovery. Alternatively, tree generation can be greatly delayed or absent, as in the Arizona fire chronosequence (Figure 1a). Understory vegetation has shown a compensatory effect on NEP with the thinning of overstory trees [Campbell *et al.*, 2009], so ecosystem studies should include understory measurements to quantify the trajectory of response of ecosystem components after disturbance. Postharvest trajectories only have a small spatial sample. Even in a single geographical area, there are many possible trajectories. For example, the data from Wisconsin showed considerable spatial variability at times less than 20 years, even though we had few points (Figure 2a). Continuity of data at these sites and addition of nearby sites would help address the issue of spatial and temporal variability.

[36] Research opportunities provided by major disturbances, such as Hurricane Wilma, provide valuable data for tracking recovery of ecosystems, as changes in pools and fluxes after such events are difficult to model. More observations in disturbed systems are essential for calibrating models that are used to map C balances across regions. At sites that have been shut down, there is an opportunity to revisit these sites again in the future to fill in gaps in the trajectories. The difficulty is that we will likely miss surprises, either caused by vegetation dynamics (e.g., changes in species mix), climate/weather, or other forcings (storms, insects, disease). An example is the forest tent caterpillar event in Wisconsin [Cook *et al.*, 2008]. Even with a good model, it would be difficult to plan the best period to revisit sites, or to determine how long we would need to make measurements. Given site logistics, a campaign of at least 5 years would likely be needed at a given site. Hence, revisiting sites will likely be opportunistic, and new disturbances (e.g., storms) [Chambers *et al.*, 2007] will also create additional opportunities. In addition to revisiting sites, there are many additional scientific questions that need to be answered. In particular, those tied to a management decision would be a high priority. This involves spending resources for a silvicultural practice, insect and disease control, or suppression or addition of fire. Many of these management options are linked to values other than C, but C is becoming an increasingly valued commodity, and needs to be considered. In addition, experiments should be conducted for each disturbance type to investigate the impacts of climate. This could be done with paired chronosequences with

similar disturbances under different climates, which would provide a partial analog for future climate change and allow us to identify differences in disturbance recovery caused by climate. Whole ecosystem studies of the C consequences of these management options using eddy covariance will continue to provide valuable information to assess C sources and sinks in a biosphere undergoing rapid changes resulting from climatic variations and disturbances.

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