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Jeffrey A. Hicke

University of Idaho, jhicke@uidaho.edu

Craig D. Allen

U.S. Geological Survey, Los Alamos

Ankur R. Desai

University of Wisconsin - Madison

Michael C. Dietze

University of Illinois at Urbana-Champaign

Ronald J. Hall

Canadian Forest Service

See next page for additional authors

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Authors

Jeffrey A. Hicke, Craig D. Allen, Ankur R. Desai, Michael C. Dietze, Ronald J. Hall, Edward (Ted) H. Hogg, Daniel M. Kashian, David Moore, Kenneth F. Raffa, Rona N. Sturrock, and James Vogelmann

REVIEW

Effects of biotic disturbances on forest carbon cycling in the United States and Canada

JEFFREY A. HICKE*, CRAIG D. ALLEN†, ANKUR R. DESAI‡, MICHAEL C. DIETZE§, RONALD J. HALL¶, EDWARD H. (TED) HOGG¶, DANIEL M. KASHIAN**, DAVID MOORE††, KENNETH F. RAFFA‡, RONA N. STURROCK‡‡ and JAMES VOGELMANN§§

*University of Idaho, Moscow, ID 83844, USA, †U.S. Geological Survey, Los Alamos, NM 87544, USA, ‡University of Wisconsin, Madison, 53706, WI 53706, USA, §University of Illinois at Urbana-Champaign, Urbana, IL 61801, USA, ¶Natural Resources Canada, Canadian Forest Service, Edmonton, T6H 3S5, AB T6H 3S5, Canada, **Wayne State University, Detroit, MI 48202, USA, ††University of Arizona, Tucson, AZ 85721, USA, ‡‡Natural Resources Canada, Canadian Forest Service, Victoria, BC V8Z 1M5, Canada, §§U.S. Geological Survey, Sioux Falls, SD 57198, USA

Abstract

Forest insects and pathogens are major disturbance agents that have affected millions of hectares in North America in recent decades, implying significant impacts to the carbon (C) cycle. Here, we review and synthesize published studies of the effects of biotic disturbances on forest C cycling in the United States and Canada. Primary productivity in stands was reduced, sometimes considerably, immediately following insect or pathogen attack. After repeated growth reductions caused by some insects or pathogens or a single infestation by some bark beetle species, tree mortality occurred, altering productivity and decomposition. In the years following disturbance, primary productivity in some cases increased rapidly as a result of enhanced growth by surviving vegetation, and in other cases increased slowly because of lower forest regrowth. In the decades following tree mortality, decomposition increased as a result of the large amount of dead organic matter. Net ecosystem productivity decreased immediately following attack, with some studies reporting a switch to a C source to the atmosphere, and increased afterward as the forest regrew and dead organic matter decomposed. Large variability in C cycle responses arose from several factors, including type of insect or pathogen, time since disturbance, number of trees affected, and capacity of remaining vegetation to increase growth rates following outbreak. We identified significant knowledge gaps, including limited understanding of carbon cycle impacts among different biotic disturbance types (particularly pathogens), their impacts at landscape and regional scales, and limited capacity to predict disturbance events and their consequences for carbon cycling. We conclude that biotic disturbances can have major impacts on forest C stocks and fluxes and can be large enough to affect regional C cycling. However, additional research is needed to reduce the uncertainties associated with quantifying biotic disturbance effects on the North American C budget.

Keywords: carbon cycling, disturbances, insects, pathogens

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Introduction

Atmospheric CO₂ is a key driver of past and predicted future climate change (IPCC, 2007). In addition to anthropogenic emissions of carbon (C) from fossil fuel burning and other activities, exchange of C with the biosphere is crucial for governing the amount of CO₂ in the atmosphere (CCSP, 2007; Le Quere *et al.*, 2009). Biogenic fluxes of C occur mainly through the interplay of CO₂ uptake by plants (photosynthesis) and release of C back into the atmosphere via autotrophic and heterotrophic respiration (decomposition). Both of these

processes are strongly mediated by abiotic and biotic disturbance processes (Kurz & Apps, 1999; Ciais *et al.*, 2005; Amiro *et al.*, 2010).

There is considerable interest in quantifying the North American C budget that has, in part, been driven by national and international reporting obligations (Chapin *et al.*, 2008; Kurz *et al.*, 2008b). North American terrestrial ecosystems are thought to have been functioning as a carbon sink during the past few decades as a result of forest regrowth following harvest in past centuries, woody encroachment, and sequestration by wetlands and agricultural soils (CCSP, 2007). The First State of the Carbon Cycle Report estimated a North American sink of 0.5 Pg C yr⁻¹ (1 Pg C = 10¹⁵ g C) in 2003, though with large uncertainty (CCSP, 2007).

Correspondence: Jeffrey A. Hicke, tel. + 208 885 6240, fax + 208 885 2855, e-mail: jhicke@uidaho.edu

Reducing this uncertainty to increase confidence in future predictions of C dynamics and to support climate change adaptation and mitigation activities will require research to quantify the magnitude of C sources and sinks and their spatial patterns and controls (Denning, 2005).

Forests play major roles in the global carbon cycle through their influence on the dynamics of the terrestrial carbon cycle (Bonan, 2008; Canadell & Raupach, 2008). Forests contain 422 Pg C, 76% of the C in terrestrial vegetation and about the same amount as in the atmosphere (Houghton & Skole, 1990). In the Northern Hemisphere, forests are major carbon sinks, taking up 0.6–0.7 Pg C yr⁻¹ (Goodale *et al.*, 2002), about 12% of the annual emission of CO₂ by humans (Schimel *et al.*, 2001). Human-caused and natural changes to forests and environmental conditions have resulted in significant effects on the global carbon cycle. For example, large releases of carbon to the atmosphere have been reported from tropical deforestation (Canadell *et al.*, 2007), fire (Turetsky *et al.*, 2011), and insect outbreaks (Kurz *et al.*, 2008b).

Insects and pathogens are agents of significant disturbance in North American forests. Many outbreaks are highly localized, but some range across millions of hectares and may affect up to 45 times the area of wildfire (Dale *et al.*, 2001). These disturbances cost an average of \$1 500 000 000 annually in the United States, five times that of wildfire (Dale *et al.*, 2001). Wood volume lost to insects and disease in Canada from 1977 to 1987 (103 Mm³ yr⁻¹, equally split between insects and disease) was nearly 2/3 of harvest volume and greatly exceeded that from fire (36 Mm³ yr⁻¹) (Fleming, 2000). The large areas of tree mortality or reduced tree growth resulting from major epidemics imply substantial impacts to the North American carbon cycle.

Climate is an important driver of insect and disease outbreaks through direct impacts on the disturbance agent as well as increased susceptibility to potential host trees in times of drought (e.g., Ayres & Lombardero, 2000; Raffa *et al.*, 2008). Future climate change, principally warming, is expected to alter insect and pathogen epidemics (Bentz *et al.*, 2010; Sturrock *et al.*, 2011). Thus, important potential feedbacks exist between climate change and biotic disturbances through the carbon cycle.

Here, we review and synthesize the effects of forest insect and disease disturbances on carbon cycling in the United States and Canada. We focus on major biotic disturbance events, which we define as large (>100 km²) areas of forest affected by insects or disease over time scales less than a decade. We do not consider smaller disturbance events or background herbivory or disease, which we recognize as important, but instead

concentrate on those outbreaks with significant, discrete impacts to US and Canadian carbon cycling. Our review is written for carbon cycle scientists interested in learning more about biotic disturbances and for scientists and land managers familiar with insects and pathogens who want to learn more about how these agents affect carbon stocks and fluxes in forests. We first describe the major insect and pathogen disturbance agents in US and Canadian forests and their extent in the region, then discuss interactions with other disturbance agents. We review the impacts to the carbon cycle, including expected responses as well as studies that document the influence of insects and pathogens on carbon cycling. We end by identifying gaps in knowledge and describing tools available for closing these gaps.

Major forest insect and pathogen species

Types and extent

Recent outbreaks of insects and diseases have affected vast areas of forest in North America (Figs 1 and 2). Here, we discuss the major insects (Table 1) and pathogens (Table 2) of deciduous and coniferous forests in the United States and Canada that have substantial impacts on forests and thus large implications for forest carbon cycling.

Insects. Aerial survey records of forest damage by major insect species (Fig. 1) illustrate the large temporal variation in annual areas affected over the past few decades, both in Canada (Natural Resources Canada, 2009b) and the United States (USDA Forest Service, 2000, 2002, 2003a,b, 2004, 2005, 2006, 2007, 2009a; Natural Resources Canada, 2009b). The records show that there have been substantial differences in the timing, extent, and geographic location of outbreaks among species. At times, major outbreaks have affected a greater total area than fire (Kurz & Apps, 1999). The carbon impacts of these outbreaks differ based on the type of insect and whether or not outbreaks lead to tree mortality.

Two major groups of native insects are known to significantly impact carbon cycling. First, bark beetles (Coleoptera: Curculionidae: Scolytinae) feed within phloem and kill trees. Most important bark beetle species in North America are native. A few bark beetle species such as mountain pine beetle (*Dendroctonus ponderosae* Hopkins) can kill healthy, unstressed trees and exert landscape-scale impacts. All of these tree-killing bark beetles have close associations with tree-infecting fungi, and most are host-specific at the level of tree genus.

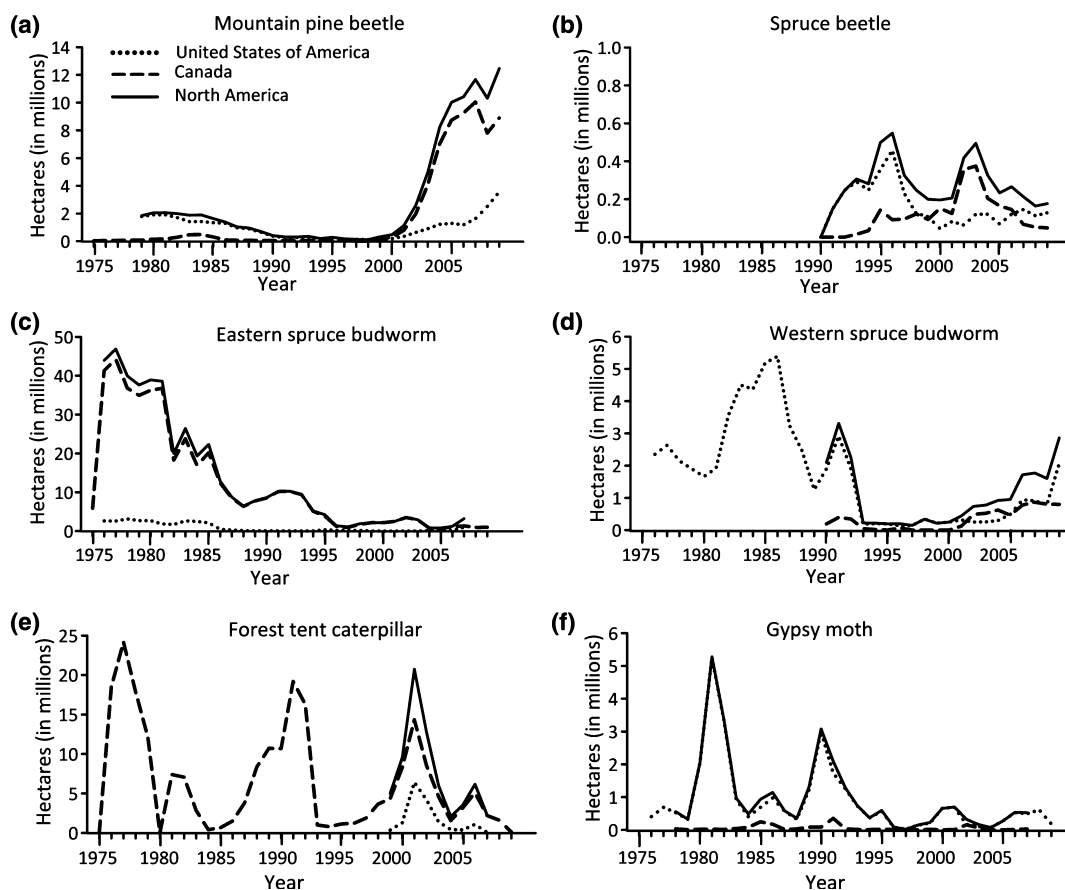


Fig. 1 Annual areas affected by major forest insect species from US (dotted line) and Canadian (dashed line) aerial survey databases and their total (solid line). Example species chosen to illustrate variability among species, through time, and between regions. 'Affected area' includes live and dead trees. Note that impact on carbon cycle varies across species depending on whether insect is a tree-killing bark beetle (a, b) or a defoliator (c–f), which may or may not kill trees. Data sources: National Forest Database, Canadian Forest Service, Natural Resources Canada (Hall *et al.*, 1998), proceedings from the Forest Pest Management Forum (e.g., Natural Resources Canada, 2009a) of Canada, and forest insect and disease conditions in the US reports from the USDA Forest Service (e.g., USDA Forest Service, 2009b).

Notable bark beetle species include mountain pine beetle, which attacks pines across western North America (Table 1). Major outbreaks have occurred in the recent past, with extensive epidemics ongoing in British Columbia, Alberta, and Colorado, among other locations (Kurz *et al.*, 2008a; Natural Resources Canada, 2009a; USDA Forest Service, 2010). Large outbreaks are expected in the future as a result of stands that are in highly susceptible conditions and climate change that leads to a more suitable environment (Hicke *et al.*, 2006; Krist *et al.*, 2007; Kurz *et al.*, 2008a; Bentz *et al.*, 2010). Likewise, spruce beetle (*Dendroctonus rufipennis* Kirby) is considered the most important insect of spruce-fir forests in western North America and is one of the major biotic disturbance agents in Alaska (Berg *et al.*, 2006; USDA Forest Service, 2009a). Southern pine beetle (*Dendroctonus frontalis* Zimmermann) occurs across the southeastern United States, attacking multiple species

of pines over large areas, and is predicted to cause large losses (54 Mm²) of basal area in the next 15 years based on stand conditions (Krist *et al.*, 2007). Various *Ips* species in combination with severe drought were responsible for a major mortality event in piñon pine (*Pinus edulis* Engelm.) in the southwestern United States in the early 2000s (Breshears *et al.*, 2005). Western balsam bark beetle (*Dryocoetes confusus* Swaine) has recently killed large numbers of subalpine fir [*Abies lasiocarpa* (Hook.) Nutt.] across the western United States (USDA Forest Service, 2010).

A second group, defoliators, also exerts substantial impacts on tree growth and mortality, but their effects on carbon cycling may differ substantially from those of bark beetles. The most common effects of folivory are reduced growth and reallocation of carbon, although repeated severe defoliation may cause tree mortality, resulting in similar modifications to C

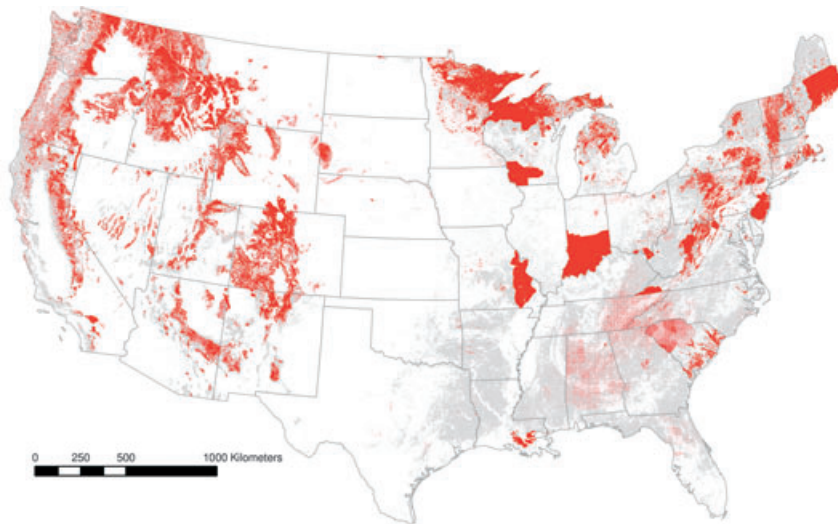


Fig. 2 Locations with insect and disease damage (black) mapped by the USDA Forest Service Aerial Detection Survey, 1997–2010. Affected areas include damaged as well as undamaged trees. Gray indicates forest area (Zhu & Evans, 1994).

cycling as tree-killing bark beetles (Elkinton & Liebhold, 1990; Candau *et al.*, 1998). Most leaf-feeders are host-specific at the level of tree genus, but in North America, two major species, forest tent caterpillar (*Malacosoma disstria* Hubner) and the introduced gypsy moth (*Lymantria dispar* L.; discussed below), have very broad feeding ranges (Table 1). Forest tent caterpillar is a major defoliator of several deciduous trees, include aspen (*Populus* spp.), and has a wide distribution in North America. There have been relatively few reports of widespread mortality following defoliation by this insect (Volney & Fleming, 2000) except in areas experiencing unusually frequent, multi-year defoliation such as northeastern Ontario (Candau *et al.*, 2002; Man & Rice, 2010). Severe defoliation in combination with climatic factors such as drought has also been implicated as a major cause of increases in the decline of aspen (Hogg *et al.*, 2002, 2008) and other forest types in parts of North America (Allen *et al.*, 2010). Hemlock looper [*Lambdina fiscellaria* (Guen.)] undergoes intermittent outbreaks in the United States and Canada (Iqbal *et al.*, 2011) and can cause 32–100% mortality after only a few years of defoliation (MacLean & Ebert, 1999).

Budworms are defoliating insects that feed primarily on the buds of new conifer needles. Eastern spruce budworm (*Choristoneura fumiferana* [Clem.]) causes more damage than any other insect in North America's boreal forests (Volney & Fleming, 2000). Western spruce budworm (*Choristoneura occidentalis* Freeman) is considered the most widely distributed and destructive conifer defoliator in western North America (Fellin & Dewey, 1982). Extensive jack pine budworm (*Choristoneura pinus* Freeman) outbreaks occur in jack pine

forests in Canada and the US east of the Rocky Mountains (Volney, 1994; Natural Resources Canada, 2009b), with reductions in growth reaching 75% in severely infested stands (Gross, 1992) and affected trees becoming predisposed to subsequent lethal attacks by bark beetles (Wallin & Raffa, 2001).

Additionally, nonnative invasive insects from all feeding guilds have become increasingly important during the last century (Aukema *et al.*, 2010). There is increasing evidence that invasive insects have a large impact on forest carbon cycling by altering disturbance regimes, nutrient cycling, and other processes in ecosystems where they have not co-evolved (Peltzer *et al.*, 2010). Carbon cycle consequences have been studied for two important invasive insects. Gypsy moth is a defoliator that was established in the middle of the 19th century and spread throughout the eastern United States (USDA Forest Service, 2009a) and eastern Canada (Régnière *et al.*, 2009). Hemlock woolly adelgid (*Adelges tsugae* Annand) is a major disturbance agent in forests of the eastern United States, attacking hemlocks (*Tsuga* spp.) and feeding on tree fluids. Hemlocks in this region have poor natural defenses against or tolerance of hemlock woolly adelgid, leading to high mortality probability from outbreaks.

Pathogens. A plant disease is defined as 'any malfunctioning of host cells and tissues that results from continuous irritation by a pathogenic agent or environmental factor and causes symptoms' (Agrios, 2005). Here, we focus on pathogens, including infectious diseases (Table 2). Forest pathogens are taxonomically diverse and include fungi, bacteria, viruses, nematodes, and

Table 1 Insect species that cause major impacts to the North American carbon budget

Insect type	Insect species	Host tree species	Origin	Major outbreak examples (see also Fig. 1)	US basal area risk ^a (million m ²)
Bark beetles	Mountain pine beetle (<i>Dendroctonus ponderosae</i> Hopkins)	Pines of western North America (<i>Pinus</i>)	Native	<ul style="list-style-type: none"> • 1930s: 200 000 ha, Idaho^b • 1970s–1980s: 2 Mha, western United States^c • 2000s: 12 Mha, western Canada^d 	69
	Spruce beetle (<i>Dendroctonus rufipennis</i> Kirby)	Spruces of western and northeastern North America (<i>Picea</i>)	Native	<ul style="list-style-type: none"> • 1990s: 1.5 Mha, Alaska^e • Current: 112 000 ha, Alaska^c 	18
	Western balsam bark beetle (<i>Dryocoetes confusus</i> Swaine)	Subalpine fir [<i>Abies lasiocarpa</i> (Hook.) Nutt.]	Native	<ul style="list-style-type: none"> • Ongoing: 216 000 ha, western United States^c 	5
	Southern pine beetle (<i>Dendroctonus frontalis</i> Zimmermann)	Pines of the southern United States (<i>Pinus</i>)	Native	<ul style="list-style-type: none"> • Mid-1980s: 10.5 Mha^c (different system for area; see ^j) • Early 2000s: 5 Mha^{c,e} 	54
	Conifer engraver species (<i>Ips</i> spp.)	Pines and spruces throughout North America (<i>Pinus</i> and <i>Picea</i>)	Native	<ul style="list-style-type: none"> • 2000s: 1.2 Mha, southwestern United States^g 	33
	Fir engraver beetle (<i>Scolytus ventralis</i> LeConte)	True firs (<i>Abies</i>)	Native	<ul style="list-style-type: none"> • Ongoing: 20 000 ha, western United States^e 	25
Defoliators	Eastern spruce budworm (<i>Choristoneura fumiferana</i> [Clem.])	Firs (<i>Abies</i>), spruces (<i>Picea</i>)	Native	<ul style="list-style-type: none"> • 1940s: 16 Mha, eastern Canada^h • 1970s–1980s: 20 Mha, eastern Canada^h 	8
	Western spruce budworm (<i>Choristoneura occidentalis</i> Freeman)	Firs (<i>Abies</i>), spruces (<i>Picea</i>), Douglas-fir [<i>Pseudotsuga menziesii</i> (Mirb.) Franco]	Native	<ul style="list-style-type: none"> • 1980s: 5 Mha, western United States^e • Ongoing: 769 000 ha, western United States^e 	0.5
	Gypsy moth (<i>Lymantria dispar</i> L.)	Multiple trees species throughout northeastern United States; primarily angiosperms but also <i>Larix</i> and <i>Pinus strobus</i> L.	Invasive	<ul style="list-style-type: none"> • Early 1980s: 5.3 Mha, northeastern United States^e • Ongoing: 60 000 ha, northeastern United States^e 	41
	Forest tent caterpillar (<i>Malacosoma disstria</i> Hubner)	Broadleaf species in North America	Native	<ul style="list-style-type: none"> • Early 2000s • Central United States: 2.8 Mhaⁱ • Canada: 14 Mha^d 	1
Fluid feeders	Hemlock woolly adelgid (<i>Adelges tsugae</i> Annand)	Hemlock (<i>Tsuga</i> spp.)	Invasive	<ul style="list-style-type: none"> • Ongoing and expanding; in 17 states in eastern United States^e 	2

Table 1 (continued)

Insect type	Insect species	Host tree species	Origin	Major outbreak examples (see also Fig. 1)	US basal area risk ^a (million m ²)
Wood borers	Emerald ash borer (<i>Agrilus planipennis</i> Fairmaire)	Ash spp. (<i>Fraxinus</i> spp.)	Invasive	• Introduced in 2002; ongoing outbreak threatening species extirpations ^j	5
Root feeders	Weevils (<i>Curculionidae</i> spp.)	Maple (<i>Acer</i>), birch (<i>Betula</i>)	Invasive	• 15% of fine root biomass of northern hardwood forests in upper Midwestern United States consumed annually ^k	N/A

^aEstimates of basal area loss in the next 15 years for the United States (table 3 in Krist *et al.*, 2007); similar standardized estimates not available for Canada or Mexico.

^bhttp://www.usu.edu/beetle/databases_bark_beetle.htm.

^cUSDA Forest Service (2009b).

^dNatural Resources Canada (2009b).

^eUSDA Forest Service (2009a).

^fFor southern pine beetle, all acres within a county were counted if that county contained a single infested tree.

^gBreshears *et al.* (2005).

^hCandau *et al.* (1998).

ⁱUSDA Forest Service (2005).

^jPoland & McCullough (2006).

^kCoyle *et al.* (2008).

parasitic plants. Fungal pathogens, which are the most common causes of forest diseases, are primarily in the phyla Basidiomycota and Ascomycota (Durall *et al.*, 2005). Many forest pathogens are specific to a host genus (e.g., *Cronartium ribicola* J.C. Fisch on *Pinus* spp.), others have a wide host range including both coniferous and deciduous species (e.g., *Armillaria* spp.), and a few are host species specific (e.g., most dwarf mistletoes).

The effects of some forest pathogens on carbon cycling may be similar to those of defoliating or fluid-feeding insects, i.e., reductions in tree growth (Tkacz & Hansen, 1982; Hansen *et al.*, 2000; Woods *et al.*, 2005), and some pathogens kill stressed or weakened trees. However, other pathogens, especially root pathogens, are able to kill vigorous, dominant trees (Hansen & Goheen, 2000). Most wood decay organisms, predominately fungi, generally do not cause major disturbance events in forested landscapes, but they play an important role in carbon cycling in forests through decomposition.

Estimates of plant pathogen extent in North America are not well documented, but some figures are available. Harausz & Pimentel (2002) reported that pathogens have affected ca. 17.4 million ha and 6% of total annual production in the United States. Average Canadian losses in 1982–1986 have been estimated at

45 million m³ per year, which is ca. 16% of production (Singh, 1993).

We briefly describe some of the most important functional groups of pathogens (Table 2). Cankers occur as localized wounds or dead areas in the bark of stems or branches and reduce tree growth and occasionally girdle trees completely (Agrios, 2005). Foliar pathogens can defoliate trees, thereby reducing photosynthetic capacity and causing concomitant growth loss. In some cases, foliar pathogens damage trees by causing branch and stem deformation. The hyphae of vascular wilt and some blue-stain or sapstain fungi kill trees by plugging their hosts' water- and nutrient-conducting tissues (Six & Wingfield, 2011). These fungi are often vectored by insects, such as in the case of Dutch elm disease, a pathosystem that includes species of *Ophiostoma* and two species of bark beetles. Root disease fungi such as *Armillaria* spp. and *Heterobasidion* spp. initiate infection mostly underground on roots, often originating from inoculum residing on intact, infected stumps. Many of these pathogenic root fungi have long-term impacts on tree growth and survival and on overall forest productivity (Klepzig *et al.*, 1991; Cruickshank, 2000; Cruickshank *et al.*, 2009). Rust fungi require live hosts and usually two taxonomically unrelated hosts to complete their life cycle. To date, the most important rusts in North American forests are the stem and cone rusts of

Table 2 Pathogens that cause major impacts to the North American carbon budget

Pathogen type	Disease name (pathogen species)	Host tree species	Origin	Examples of major epidemics and/or long-term perturbations and impacts	US basal area risk ^a (million m ²)
Canker	Chestnut blight [<i>Cryphonectria parasitica</i> (Murrill) Barr.]	American chestnut [<i>Castanea dentata</i> (Marshall) Borkhausen]	Invasive	<ul style="list-style-type: none"> • 1920s: 3.5 billion trees infected^b • 1950s: 3.6 Mha dead or dying^c • <i>C. dentata</i> extirpated from its original range^d 	Host extirpated
	Beech bark disease (<i>Neonectria</i> spp.)	American beech (<i>Fagus grandifolia</i> Ehrh.)	Invasive	<ul style="list-style-type: none"> • 1970: most of the NE United States and SE Canada affected^e • 1977: Vermont lost 708 000 cubic m^f 	7
Foliar	Red band needle blight (<i>Dolhistroma septosporum</i>)	Pines (<i>Pinus</i>) and other conifers	Native	<ul style="list-style-type: none"> • 2002–2004: 38 000 ha impacted, mortality of 2700 ha in NW BC^g • Extensive mortality in plantations in BC^h • 2010: 160 000 ha affected in Oregonⁱ • 2000: stands with the most severe SNC had volume growth loss of ca. 52%^j 	N/A
	Swiss needle cast [<i>Phaeocryptopus gäumannii</i> (Rohde) Petrak]	Douglas-fir [<i>Pseudotsuga menziesii</i> (Mirb.) Franco]	Native	<ul style="list-style-type: none"> • 1930–1973: widespread loss of large trees across NA^{d,k} 	1
Root	Dutch elm disease [<i>Ophiostoma ulmi</i> (Buisman) Nannf and <i>O. novo-ulmi</i>]	Elms (<i>Ulmus</i> spp.)	Invasive	<ul style="list-style-type: none"> • Responsible for volume losses of 2–3 Mm³ yr⁻¹ in Canada's Pacific NW^l • In some forests of western NA, 35% of annual tree mortality caused by <i>Armillaria</i>^m • Infections range from 10% to 50%; in severe cases 30% of a stand may be killedⁿ • 12.5% of CA commercial forest land is infested, annual losses of 262 000 cubic m^o 	48 (all root diseases)
	Armillaria root disease (<i>Armillaria ostoyae</i>)	Mainly conifers	Native	<ul style="list-style-type: none"> • Infections range from 10% to 50%; in severe cases 30% of a stand may be killedⁿ • 12.5% of CA commercial forest land is infested, annual losses of 262 000 cubic m^o 	48 (all root diseases)

Table 2 (continued)

Pathogen type	Disease name (pathogen species)	Host tree species	Origin	Examples of major epidemics and/or long-term perturbations and impacts	US basal area risk ^a (million m ²)
Stem rust	Fusiform rust [<i>Cronartium quercium</i> (Berk.) Miyabe ex Shirai]	Loblolly (<i>Pinus taeda</i>), slash (<i>Pinus elliotii</i> var. <i>elliottii</i>) pines	Native	<ul style="list-style-type: none"> • 1930s: recognized as problem in MS and LA, regionally up to 30% of seedlings infected^b • 1960–1970s disease incidence: 5.5 Mha affected >10%, 1 Mha >50%^{b,c,d} • In northern Idaho, trees decreased 90% where previously dominant^e • 0.6 Mm³ estimated mortality loss in Canada, 1976^f 	2
Dwarf mistletoe	<i>Arceuthobium</i> spp.	Five-needle pines (<i>Pinus</i> spp.)	Invasive	<ul style="list-style-type: none"> • In Canada, 3.5 Mm³ loss to growth reduction and mortality in 1981 and 1987 • In United States, 3.8 Mha, 11 Mm³ (10–50% of annual commercial harvest) lost/year in growth, mortality^{g,h} • 1990s: in CA, caused mortality of >3 million oaks (<i>Quercus agrifolia</i> Née) and tanoaks [<i>Lithocarpus densiflorus</i> (Hook. & Arn.) Rehd.]ⁱ 	6
Phytophthora	Sudden oak death (<i>Phytophthora ramorum</i> sp. nov.)	Pinaceae and Cupressaceae	Native	<ul style="list-style-type: none"> • Numerous spp. identified as potential hosts 	5

^aEstimates of basal area loss in the next 15 years for the United States (table 3 in Krist *et al.*, 2007); similar standardized estimates not available for Canada or Mexico.

^bAgrios (2005).

^cAnagnostakis (1987).

^dLoo (2009).

^eGriffin *et al.* (2003).

^fHouston (1994).

^gWatt *et al.* (2008).

^hWoods *et al.* (2005).

ⁱ<http://www.cof.orst.edu/coops/sncc/2010Results.htm>.

^jMainwaring *et al.* (2005).

^kFarrar (1995).

^lMorrison & Mallet (1996).

^mSinclair *et al.* (2005).

ⁿLittle & Browning (1989).

^oMarosy & Parmeter (1989).

^pPowers *et al.* (1981).

^qSchmidt *et al.* (1986).

^rAnderson *et al.* (1986).

^sNeuenschwander *et al.* (1999).

^tSingh (1993).

^uGill (1954).

^vDrummond (1982).

^wGoheen *et al.* (2006).

pinus (Sinclair *et al.*, 2005). *Phytophthora* species infect a wide variety of hosts and have been responsible for severe forest epidemics worldwide, such as the recent sudden oak death epidemic in California and Oregon caused by *Phytophthora ramorum* sp. nov. Dwarf mistletoes (*Arceuthobium* spp.) are parasitic vascular plants causing significant impacts to a range of conifer species in North America (Hawksworth & Wiens, 1970; Loomis *et al.*, 1985; Singh, 1993; Geils *et al.*, 2002; Brandt *et al.*, 2004). Dwarf mistletoes reduce host growth and increase tree mortality and susceptibility to other damage agents.

Invasive pathogens tend to have more pronounced acute impacts than native species, and, when combined with invasive insects, pose a greater threat than native species to forest ecosystems stability in some areas (Lovett *et al.*, 2006). For example, invasive pathogens causing such diseases as white pine blister rust, chestnut blight, and butternut canker are responsible for some of the most significant long-term changes to North American forests observed, including the functional extinction of a number of keystone taxa across all or most of their range (Loo, 2009).

Climate change and outbreaks

Climate is a major driver of insect and pathogen outbreaks. Temperature influences these disturbance agents in multiple ways. For insects, life stage development rates increase with temperature, potentially leading to a switch from a 2- or 3-year life cycle to a 1-year life cycle that results in faster population growth (Bentz *et al.*, 1991, 2001) and population synchrony for mass attack, often required to overcome tree defenses (Raffa & Berryman, 1987; Logan & Powell, 2001). Other insects undergo an intrinsic resting state called diapause, which is triggered by low temperatures or shortened photoperiod and acts to maintain populations in life stages most suited for withstanding cold conditions (Tauber *et al.*, 1986). Winter temperatures also affect population levels of insects through mortality of overwintering life stages in cold conditions (Wygant, 1940; Régnière & Bentz, 2007). Pathogens similarly require temperatures above a minimum to grow and survive. However, pathogens are more directly affected by moisture (Desprez-Loustau *et al.*, 2006); for most pathogens, moisture is necessary for reproduction and dispersal (Agrios, 2005).

Climate also influences outbreaks through the condition of potential host trees. Some insects and pathogens prefer or have easier access to stressed or low vigor trees, which may be less well defended against attack (Raffa *et al.*, 2008). Hosts predisposed to attack by drought, caused by either lower precipitation and/or

higher temperatures, often lead to population increases of bark beetles and latent pathogens (Raffa *et al.*, 2008; Kliejunas *et al.*, 2009; Bentz *et al.*, 2010; Sturrock *et al.*, 2011).

Anthropogenic emissions of greenhouse gases have resulted in a warming climate that has facilitated outbreaks in recent decades. Changes in both temperatures (e.g., Logan *et al.*, 2003; Carroll *et al.*, 2004; Manter *et al.*, 2005; Berg *et al.*, 2006) and moisture or drought (e.g., Breshears *et al.*, 2005; Hebertson & Jenkins, 2008; Jung, 2009) have been associated with insect and pathogen outbreaks. Future projections predict warming and enhanced drought associated with climate change (IPCC, 2007), and thus patterns of insect and pathogen outbreaks are likely to change in response to projected climate change (e.g., Hicke *et al.*, 2006; Venette & Cohen, 2006; Kliejunas *et al.*, 2009; Bentz *et al.*, 2010; Sturrock *et al.*, 2011).

Disturbance interactions

Insect or pathogen impacts are best understood within the context of interactions with other biotic and abiotic agents. Predators and pathogens of biotic agents reduce population levels, and competition among species can affect populations. Symbiotic interactions also occur. Root pathogens, root herbivores, and defoliators can predispose trees to attack by bark beetles and wood borers (Wallin & Raffa, 2001), and defoliators can release latent pathogens such as some species of *Armillaria*. Insects are frequently the vectors for pathogen dispersal, e.g., symbioses between fungi [*Ophiostoma montium* (Rumbold) von Arx, *Grosmannia clavigera*] and *Dendroctonus* bark beetles (Bleiker & Six, 2007), and conversely trees whose defenses are compromised by pathogens or fire also become more susceptible to insects (Klepzig *et al.*, 1995; Lombardero *et al.*, 2006).

The term 'forest decline' describes stands and/or landscapes where trees, typically of a single species, progressively lose vigor and often die, frequently due to a complex of abiotic and biotic factors (Klepzig *et al.*, 1991; Manion & Lachance, 1992). Although declines are not solely caused by biotic agents, insects and pathogens may amplify the effects of the predisposing stress factors (McDowell *et al.*, 2008; Raffa *et al.*, 2008). A current example is the increasing area of sudden aspen decline in western North America, which appears to be caused by a combination of drought stress and defoliation and stem damage by insects and pathogens (Worrall *et al.*, 2008, 2010), and can result in widespread, cumulative mortality (Michaelian *et al.*, 2011).

Insects and pathogens interact with several abiotic disturbances. Over the past few decades there have been significant, increasing trends in reports of

drought- and heat-related forest die-off events (Allen *et al.*, 2010) as well as in background tree mortality rates (van Mantgem *et al.*, 2009; Dietze & Moorcroft, 2011) in which biotic agents played a role. Outbreaks interact with wildfire in two ways (Parker *et al.*, 2006; Romme *et al.*, 2006; Jenkins *et al.*, 2008). First, outbreaks may kill trees, thereby modifying fuels and fire characteristics in complex patterns that vary with time since outbreak (e.g., Fleming *et al.*, 2002; Jenkins *et al.*, 2008; Bentz *et al.*, 2009). Second, fires may affect the likelihood and severity of insect and pathogen outbreaks by altering species composition or stand structure in the long term as well as by injuring surviving trees in the short term and predisposing them to secondary host infection (Parker *et al.*, 2006; Simard *et al.*, 2008). Interactions also occur between biotic disturbances and wind. Windthrow (and other disturbances) provide a source of stressed trees that allow bark beetles such as Douglas-fir beetle to build to epidemic levels (Schmitz & Gibson, 1996). Nonhost tree species may be more exposed to wind during large-scale defoliator outbreaks. Pathogens can also increase the risk of wind damage by weakening stems or roots (Papaik *et al.*, 2005).

Expected responses of carbon stocks and fluxes

In this section, we describe general patterns of carbon cycle responses following biotic disturbances based on direct impacts on trees as well as understanding of forest processes following different disturbance types (Odum, 1969; Fleming *et al.*, 2002; Hicke *et al.*, 2003; Litvak *et al.*, 2003; Kashian *et al.*, 2006) (Fig. 3). Documented C cycle impacts then describes studies that support these responses. First, biotic disturbances reduce gross primary productivity (GPP; see Table 3 for C cycle definitions) of stands through defoliation or other growth reductions or tree mortality. Second, trees killed by aggressive bark beetles or repeated growth reductions alter carbon cycling through increases in heterotrophic respiration (R_h). Growth reductions over several years reduce carbon transfer to dead organic matter pools, which subsequently reduces R_h . In addition, killed trees generate a large amount of dead organic matter, some of which begins to decay immediately. Carbon in more labile structures such as leaves is released to the atmosphere first, although in killed conifers, needles remain on the dead trees for 1–3 years

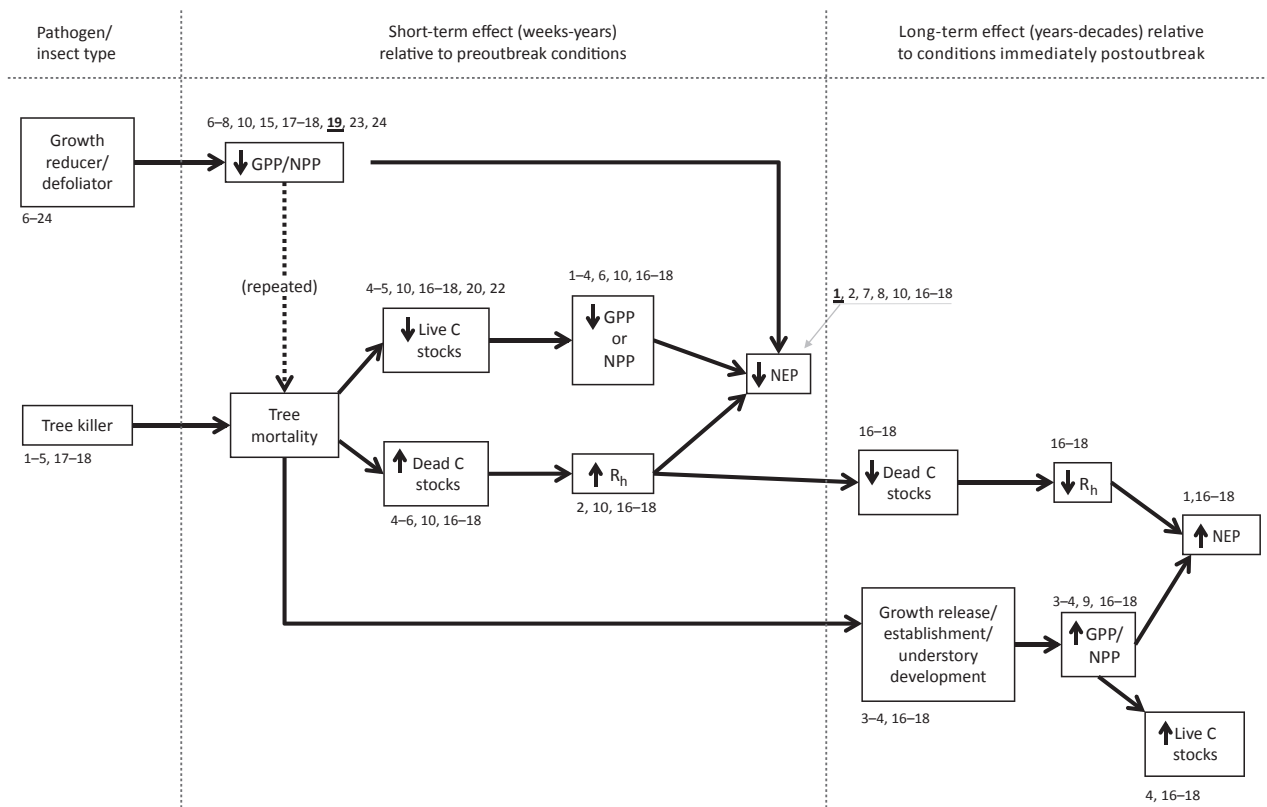


Fig. 3 Conceptual diagram showing impacts of insect and pathogen outbreaks on carbon budgets. Numbers outside of boxes reference studies in Tables 4 and 5 that provide evidence. Studies that provide evidence counter to that indicated in diagram noted in bold underlined text (two cases).

Table 3 Carbon cycle terms and definitions. See also Chapin *et al.* (2006)

Variable	Units	Definition
Carbon stocks	g C or g C m ⁻²	Reservoirs of carbon in various tree and soil pools such as stem, foliage, roots, and soil organic matter
Carbon fluxes	g C m ⁻² yr ⁻¹	Transfers between pools of carbon, including those in the ecosystem and the atmosphere
Gross primary production (GPP)	g C m ⁻² yr ⁻¹	Total amount of atmospheric C fixed by plants
Autotrophic respiration (R_a)	g C m ⁻² yr ⁻¹	Release of C to the atmosphere by plants
Heterotrophic respiration (R_h)	g C m ⁻² yr ⁻¹	C released by microbes through decomposition
Net primary production (NPP)	g C m ⁻² yr ⁻¹	GPP - R_a ; the net amount of carbon fixed by plants and available for subsequent use by heterotrophs
Net ecosystem production (NEP)	g C m ⁻² yr ⁻¹	NPP - R_h ; positive when ecosystems are sinks of C
Net ecosystem exchange (NEE)	g C m ⁻² yr ⁻¹	Exchange of carbon between the ecosystem and the atmosphere; positive when there is a net transfer of C to the atmosphere and is often the same as (but opposite in sign to) NEP
Net biome production (NBP)	g C m ⁻² yr ⁻¹	Flux of C to/from ecosystems; includes NEP as well as losses of C through such processes as combustion or leaching

following bark beetle attack, delaying this decomposition. Snags remain standing for decades following tree death (e.g., Mielke, 1950), further delaying decomposition. As a result of these processes as well as the long decay time of wood, the release of carbon through decomposition following disturbance occurs over a period of decades to centuries (Harmon *et al.*, 1986; Busse, 1994).

Reductions in net primary productivity (NPP) and increases in decomposition of dead organic matter affecting heterotrophic respiration (R_h) result in large reductions of net ecosystem productivity (NEP). The amount of change of these individual fluxes and therefore of the net C flux is determined by the magnitude of an outbreak's impact on stands. For severe outbreaks, the magnitude of the effect may be large enough to cause a stand to switch from a carbon sink to a carbon source in a manner similar to the effects of wildfire (Fleming *et al.*, 2002; Kurz *et al.*, 2008a; Dymond *et al.*, 2010).

Other impacts to C cycling beyond reductions in productivity and increases in decomposition exist. During outbreaks, defoliators consume C in leaves and release large fluxes of nitrogen, carbon, and other nutrients into forest ecosystems through leaf fragments, frass, and exuviae (Frost & Hunter, 2004). Moderate to severe

outbreaks alter functional attributes of the ecosystem (e.g., light regime, water availability and loss, nutrient cycling) in a way that affects the trajectory of succession and recovery. Outbreaks severe enough to modify soil moisture and nutrients, for example, cause changes in tree density or species composition such that long-term carbon storage or the rate of carbon cycling is also altered. At longer temporal and broader spatial scales, carbon loss to the atmosphere and altered hydrologic processes following severe outbreak areas may drive climate feedbacks that could affect the frequency and severity of future insect or pathogen outbreaks, although such feedbacks have yet to be quantified. Finally, killed trees resulting from insect and pathogen outbreaks interact with other disturbances to affect carbon cycling, particularly with fire and wind damage (see discussion above).

Biotic disturbances that cause extensive tree mortality may be comparable to fires in terms of impacts to carbon cycling (Fleming *et al.*, 2002; Kashian *et al.*, 2006). Many biotic disturbances have less immediate impacts than fires, such as defoliation events that kill trees only after several consecutive years of attack (Fleming *et al.*, 2002). Other outbreaks, such as those of some bark beetles, can kill many trees within a stand within 1 year, acting more similar to fire. Differences exist, however:

fires result in an immediate release of some carbon to the atmosphere via combustion; severe fires kill non-host species, understory trees, shrubs, and herbs in addition to host trees; and although outbreaks modify some soil properties such as biogeochemical cycling (e.g., le Mellec & Michalzik, 2008; Morehouse *et al.*, 2008), fires can also cause microbial mortality through heating, increase weathering rates, reduce surface albedo, and modify infiltration and runoff rates (Nearby *et al.*, 2005).

Documented C cycle impacts

Characteristics of studies

To facilitate comparison and synthesis, studies were summarized by insects (Table 4) and pathogens (Table 5) and organized along key factors (Figs 3 and 4) that included the type of insect or pathogen (especially whether or not the damage agent killed trees); the severity of disturbance in terms of the number of trees attacked within a stand and the amount of tree mortality; the time since disturbance; the methods of the study and the C variable(s) studied; and the existence and type of study controls that illustrate effects relative to unaffected stands or preoutbreak conditions. We identified 19 studies that assess impacts to US and Canadian carbon cycling by insect outbreaks (Table 4) and six studies that documented impacts by pathogens (Table 5). The insect studies were roughly divided among bark beetles, defoliators, and hemlock woolly adelgid, a fluid feeder. Multiple studies of mountain pine beetle, spruce budworm, forest tent caterpillar, gypsy moth, and hemlock woolly adelgid have been published. Two studies included multiple species (of insects) (Kurz & Apps, 1999; Stinson *et al.*, 2011).

Most studies were field observations of productivity or carbon cycling (Romme *et al.*, 1986; Jenkins *et al.*, 1999; Kizlinski *et al.*, 2002; Forrester *et al.*, 2003; Morehouse *et al.*, 2008; Nuckolls *et al.*, 2009; Pfeifer *et al.*, 2011), including eddy covariance tower measurements (Cook *et al.*, 2008; Hadley *et al.*, 2008; Brown *et al.*, 2010; Clark *et al.*, 2010). As such, there was an emphasis on tree to stand scales. Analyses of eddy covariance tower observations were opportunistic (i.e., unplanned) (Cook *et al.*, 2008; Clark *et al.*, 2010), although in one case, study sites were selected specifically to investigate mountain pine beetle impacts (Brown *et al.*, 2010). The pathogen studies addressed leaf to plot scales.

Several investigations used carbon cycle models informed by or parameterized with field observations and concentrated on recent times since outbreak (Cook *et al.*, 2008; Schäfer *et al.*, 2010). A few studies estimated regional impacts using upscaling of finer scale results,

simulation modeling, or remote sensing (Kurz & Apps, 1999; Hicke *et al.*, 2002; Kurz *et al.*, 2008a; Albani *et al.*, 2010; Clark *et al.*, 2010; Dymond *et al.*, 2010; Hennigar & MacLean, 2010; Stinson *et al.*, 2011), and several assessed effects on time scales of decades to centuries (Hogg, 1999; Kurz & Apps, 1999; Kurz *et al.*, 2008a; Dymond *et al.*, 2010; Hennigar & MacLean, 2010; Pfeifer *et al.*, 2011).

Fifteen studies addressed some aspect of tree growth. Nine studies quantified responses of the net carbon flux, through eddy covariance methods or simulation modeling. Several studies investigated other aspects of carbon cycling, such as C stocks or soil respiration. Overall, the studies summarized in Tables 4 and 5 identified the types and levels of impact that can be expected from insect and pathogen outbreaks to C. These studies also illustrated the difficulty in drawing definitive broad-scale conclusions regarding specific species as a result of the varying spatial extents, time since disturbance, severity of outbreak, and diversity of carbon variables analyzed to date (Fig. 4).

Carbon cycle responses

Immediately following attack, insects and pathogens often caused reductions in tree- and stand-level primary productivity or C stocks (Romme *et al.*, 1986; Hogg, 1999; Forrester *et al.*, 2003; Manter *et al.*, 2003; Meinzer *et al.*, 2004; Cook *et al.*, 2008; Morehouse *et al.*, 2008; Nuckolls *et al.*, 2009; Clark *et al.*, 2010; Dymond *et al.*, 2010; Hennigar & MacLean, 2010; Lovett *et al.*, 2010; Schäfer *et al.*, 2010; Busby & Canham, 2011; Pfeifer *et al.*, 2011), although one study of beech bark disease reported no change in aboveground NPP across a gradient of impact (Hancock *et al.*, 2008). Productivity decreased by over 50% in some outbreaks of bark beetles, defoliators, and fluid feeders. Variability occurred as a result of outbreak severity (number of affected trees) within a study, suggesting that this factor was a major contributor to the reported range of decreases. Other factors such as type of disturbance agent, forest type, and consecutive years of disturbance also influenced responses.

Net ecosystem productivity decreased from stronger positive values (C sinks) to weaker positive values or switched to negative NEP values (C sources) (Kurz & Apps, 1999; Cook *et al.*, 2008; Kurz *et al.*, 2008a; Albani *et al.*, 2010; Brown *et al.*, 2010; Clark *et al.*, 2010; Dymond *et al.*, 2010; Stinson *et al.*, 2011). Major NEP reductions occurred across biotic disturbance types, even for a very short-term defoliation event (Cook *et al.*, 2008). Variability in NEP reduction immediately after attack was related to factors that cause a range of NPP responses (described above), the amount of killed

Table 4 Summary of studies that report effects of insect outbreaks on carbon budgets

Outbreak characteristics				Study characteristics				Study results			
Insect type	Insect species	Host type	Location	Methods	Spatial extent	Time since disturbance	Outbreak severity	Control	Carbon variable*	Results	Reference
1 [†] Bark beetles	Mountain pine beetle	Lodgepole pine (<i>Pinus contorta</i> Dougl. ex Loud.)	British Columbia	2 years of field measurements 2006–2007	Two stands, MPB-03 and MPB-06	• MPB-03: 4–5 years • MPB-06: 0–1 years	• >95% red- and gray-attack • Year 1: 50% green-attack • Year 2: 73% dead	• None • Year 1: preattack	NEP	• -56 and 4 g C m ⁻² yr ⁻¹ in Years 1 and 2 • -82 and -33 g C m ⁻² yr ⁻¹ in Years 1 and 2	Brown <i>et al.</i> (2010)
2			Regional	Simulation modeling		21 years during and following outbreak	Varies	Years prior to outbreak	NBP	NBP changed from sink to a source; magnitude of source was reduced but >0 after 21 years	Kurz <i>et al.</i> (2008a)
3		Yellowstone area		Field measurements (dendrochronological)	Four attacked stands	Decades before, 10–20 years following infestation	41–67%	Preoutbreak and uninfested control stands	NPP as indicated by bole volume increment	• 20–45% reduction in 5-year NPP • 10 years to recovery to preoutbreak values and values from unattacked stands	Romme <i>et al.</i> (1986)
4		Central Idaho		Field measurements, simulation modeling of recovery	12 stands	100+ years following outbreak	18–52% number of trees	Prior to outbreak and uninfested control simulations	• Aboveground C stocks • Aboveground woody C production	• 18–70% immediate reduction • Recovered to preoutbreak values in 1–25 years and to unattacked simulations in 56–185 years • 25–62% immediate reduction • Never recovered to preoutbreak values; recovered to unattacked simulations in 30–160 years	Pfeifer <i>et al.</i> (2011)
5	<i>Ips</i> and <i>Dendroctonus</i>	Ponderosa pine (<i>Pinus ponderosa</i>)	Southwestern United States	Field measurements	10 infested	0–2 years following infestation	≥ 80%	10 uninfested plots	• Aboveground C stocks • Soil respiration	• 60% in killed trees • Similar among infested and uninfested plots	Morehouse <i>et al.</i> (2008)

Table 4 (continued)

Outbreak characteristics				Study characteristics				Study results			
Insect type	Insect species	Host type	Location	Methods	Spatial extent	Time since disturbance	Outbreak severity	Control	Carbon variable*	Results	Reference
Defoliators 6	Forest tent caterpillar outbreaks (with drought)	Aspen	Two sites in central Canada	Dendrochronology, simulation modeling	Multiple stands	Decades before and after outbreak	70% of leaf area lost per tree (prescribed); 81–97% of trees attacked based on tree-ring analysis	Results in years before and years after outbreak	• Stem growth • Stem C of living trees	• Reduction by 80–90% based on tree-ring analysis • Reduction by 15–25% based on model simulation	Hogg (1999)
7	Forest tent caterpillar outbreaks	Northern hardwood	Wisconsin	Field measurements, eddy covariance tower, simulation modeling	One stand	Year of, year before, year after outbreak	40% of leaf area	Measurements in year before and year after outbreak	• GPP • NEP	• 24% decrease during year of outbreak • Reduction in sink (77 g C m ⁻² yr ⁻¹ vs. 323–422 g C m ⁻² yr ⁻¹)	Cook <i>et al.</i> (2008)
8	Gypsy moth	Pine/oak	New Jersey	Field measurements, eddy covariance tower, modeling upscaling using aerial surveys	Three stands 1588 km ²	2 years during outbreak year of outbreak	Partial to complete defoliation in second and third years 20% of landscape had ≥75% defoliation	Year prior to outbreak estimate without outbreak	• GPP • NEP • Annual NEE	• 25–58% reduction • Reduced sink or switched to C source • 41% reduction; 55% reduction in most impacted stands	Clark <i>et al.</i> (2010) and Schäfer <i>et al.</i> (2010)
9	Eastern spruce budworm	Eastern forests	Canada, United States	Remote sensing, modeling	Regional	5–40 years following defoliation	Unspecified	None	NPP	Recovery indicated by increasing NPP over 17-year period	Hicke <i>et al.</i> (2002)
10			Quebec, Canada	Simulation modeling	Regional (106 000 km ²)	Outbreak and study period 2011–2024	Various: 0–30% mortality per year, 0–86% growth loss per year; 95% of study region experienced defoliation	Simulations without outbreak	• C stocks • NPP • NBP	• Reductions of 11–90% in merchantable C and 2–10% in ecosystem C • Reduction of 3.5% • Switch from sink (4.6 g C m ⁻² yr ⁻¹) to source (–16.8 g C m ⁻² yr ⁻¹) during outbreak	Dymond <i>et al.</i> (2010)
11			New Brunswick, Canada	Simulation modeling	Regional (210 000 ha)		50–100% defoliation	Preoutbreak conditions	• C stocks	• 24% reduction in living biomass	Hennigar & MacLean (2010)
Fluid feeders 12	Hemlock woolly adelgid	Eastern hemlock species	Northeastern United States	Eddy covariance towers	Hemlock and oak stands	N/A; effects estimated by comparing pre- and	N/A; outbreak effects estimated by comparing	N/A	NEE	• Maximum postoutbreak forest (oak) uptake 60%	Hadley <i>et al.</i> (2008)

Table 4 (continued)

Outbreak characteristics				Study characteristics				Study results			
Insect type	Insect species	Host type	Location	Methods	Spatial extent	Time since disturbance	Outbreak severity	Control	Carbon* variable	Results	Reference
13				Field measurements	Six sites	5–6 years after initial infestation	Ranged from 0% to 98% basal area in infested hemlocks	Sites across gradient of damage	Soil C and C:N in total soil, forest floor, or mineral soil	greater than hemlock • Annual NEE similar No differences among sites with different levels of infestation	Jenkins <i>et al.</i> (1999)
14				Field measurements	Six infested sites	Unspecified	43% of hemlock trees killed, 35% of basal area	Four control sites	• Soil C, mineral C:N • Forest floor mass, forest floor C:N	• No differences compared with uninfested stands • Lower in damaged sites	Kizilinski <i>et al.</i> (2002)
15			Southern United States	Field measurements	Plots	3 years of infestation	Unspecified	Year prior to infestation and hardwood plots without infestation	• Basal area increment • Very fine root biomass • Soil CO ₂ efflux	• Decreased by 50–90% • Decreased by 20–40% in 2 years • Decreased by 20% in 1 year	Nuckolls <i>et al.</i> (2009)
16			Eastern United States	Spread and ecosystem modeling	Hemlock locations in eastern United States	Continuous	Linear increase 0–50% for 0–20 years following initial infestation	Simulation without insect outbreak	Regional NEP	For 2000–2040 period, reduction by 8%; for 2040–2100 period, increase by 12%	Albani <i>et al.</i> (2010)
Multiple 17	Eastern spruce budworm, mountain pine beetle, jack pine budworm, hemlock looper	Various	Canadian forests	Simulation modeling	Regional	1920–1989	Various	Years prior to infestation	NEP	Increased disturbance (insect outbreaks, fire) in latter decades contributed to switch from sink to source	Kurz & Apps (1999)
18	Mountain pine beetle, spruce beetle, eastern hemlock looper, forest tent caterpillar, large aspen tortrix	Various	Canadian forests	Simulation modeling	Regional	1990–2008	Various	N/A	Ecosystem C stock change	• 483 Tg C in biomass killed by insects • Peak of 107 Tg C yr ⁻¹ in 2005 associated with mountain pine beetle outbreak	Stinson <i>et al.</i> (2011)

*See Table 3 for explanation of abbreviations.

†Study identifier used in Fig. 3.

Table 5 Summary of studies that report effects of pathogen outbreaks on carbon budgets

Outbreak characteristics		Study characteristics					Results				
Pathogen type	Pathogen species	Host type	Location	Methods	Spatial extent	Time since disturbance	Outbreak severity	Control	Carbon variable*	Results	Reference
	Beech bark disease	American beech	Northeastern United States	Field observations during (1985) and after (2000) outbreak	Eight plots	Unspecified	5–95% live beech by basal area; no information provided about%/beech killed	Gradient of beech bark disease damage	<ul style="list-style-type: none"> • Aboveground NPP • Growing season soil CO₂ efflux 	<ul style="list-style-type: none"> • No differences across disease gradient • Decreased by 40% in infested stands 	Hancock <i>et al.</i> (2008)
20				Field observations during (1985) and after (2000) outbreak	49 plots	15 years	See biomass	Preoutbreak measurements	<ul style="list-style-type: none"> • Aboveground live biomass of beech • Litterfall, % lignin 	<ul style="list-style-type: none"> • 1% reduction in live and 99% increase in dead beech • No change 	Forrester <i>et al.</i> (2003)
21				Field measurements; defined score to indicate disease progression	19 plots	Variable	Variable, most severe plot was 40% killed by basal area	Plots with limited impact	<ul style="list-style-type: none"> • Basal area, decomposition rate • Litter mass, C flux, C in forest floor and soil 	<ul style="list-style-type: none"> • Increased with disease score • No change with score 	Lovett <i>et al.</i> (2010)
22				Field measurements	Inventory plots in Maine, Pennsylvania, and Michigan	Various; earliest attack >50 years prior	Inferred from spatial gradient of initial attack by disease	Uninfected control trees	<ul style="list-style-type: none"> • Aboveground C stocks • Needle net assimilation • Whole-canopy net assimilation 	<ul style="list-style-type: none"> • 11% reduction in locations with earliest attack • Negative needle net carbon balance when pathogen colonization >25% of stomata • Reduced by 85% 	Busby & Canham (2011)
Foliar	Swiss needle cast, <i>Phaeocryptopus gaeumannii</i>	Douglas-fir	Western Oregon, United States	Field measurements and modeling	Trees at three sites	Ongoing	Density of pathogen: 0–70% of needle stomata	Uninfected control trees sprayed		<ul style="list-style-type: none"> • Negative needle net carbon balance when pathogen colonization >25% of stomata 	Manter <i>et al.</i> (2003)
Parasite	Dwarf mistletoe (<i>Arceuthobium</i> spp.)	Western hemlock	Washington State, United States	Field measurements	Eight trees at one site	Ongoing	Five severely infested trees	Three uninfested trees	Maximum photosynthetic rates	In heavily infested trees, photosynthetic rate was half that of uninfested trees	Meinzer <i>et al.</i> (2004)

*See Table 3 for explanation of abbreviations.

†Study identifier used in Fig. 3.

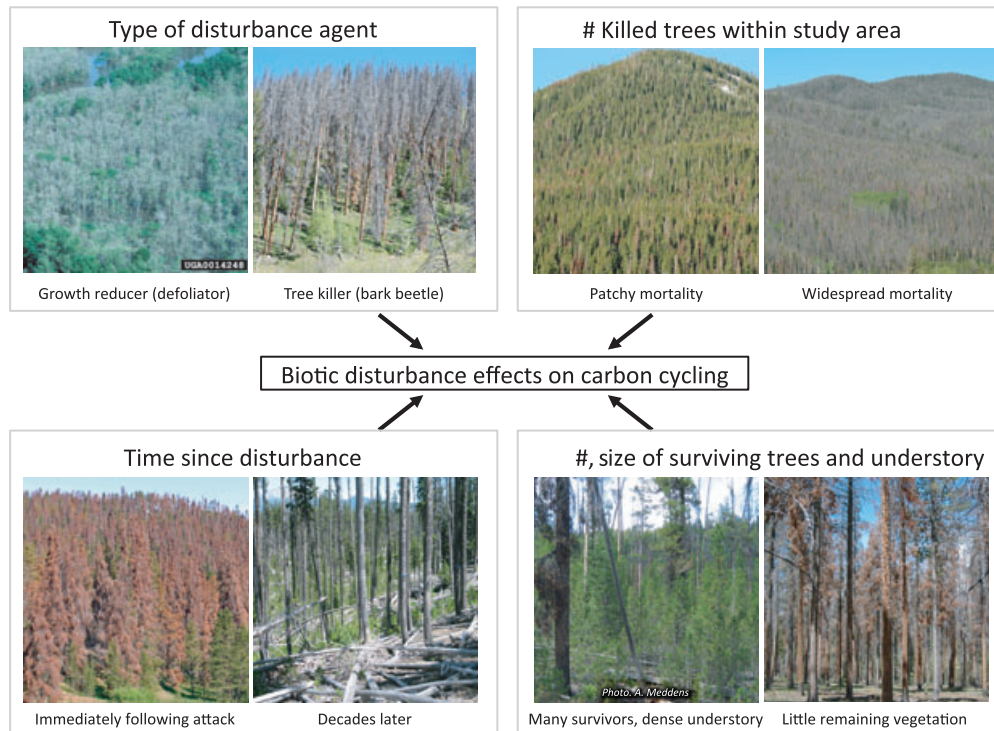


Fig. 4 Processes that influence how biotic disturbances affect carbon cycling. Examples of mountain pine beetle and forest tent caterpillar (upper left) outbreaks illustrate the range of conditions for each process. Photos by J. Hicke except where noted (G. J. Lenhard, Louisiana State University, Bugwood.org, upper left; A. Meddens, U. Idaho).

trees that affect decomposition fluxes, and the contribution of the understory to carbon uptake.

Substantial NEP responses occurred at local scales as well as regional scales during extensive tree mortality. Ecosystems became C sources following outbreaks as observed by eddy covariance towers (Brown *et al.*, 2010; Clark *et al.*, 2010). Epidemics with a substantial fraction of trees killed caused forests to become C sources at regional scales (Kurz & Apps, 1999; Kurz *et al.*, 2008a; Dymond *et al.*, 2010; Stinson *et al.*, 2011). However, epidemics affecting only a minor amount of trees within a study area or epidemics that did not kill trees only reported reductions in sink strength, not a switch to a source (Albani *et al.*, 2010; Clark *et al.*, 2010). Thus, effects were dampened at larger scales as the percentage of affected trees decreased.

Studies' conclusions about soil and forest floor C impacts varied, with some noting decreased carbon stocks, C:N values, and soil CO₂ efflux in attacked stands compared with unattacked stands (Kizlinski *et al.*, 2002; Hancock *et al.*, 2008; Nuckolls *et al.*, 2009; Lovett *et al.*, 2010), and some reporting no change in one or more of these variables (Jenkins *et al.*, 1999; Kizlinski *et al.*, 2002; Morehouse *et al.*, 2008; Lovett *et al.*, 2010).

Insect and pathogen outbreaks can have long-term impacts to carbon cycling, though fewer studies

addressed this. As with immediate effects, long-term dynamics varied by disturbance type. Localized studies indicated recovery of aboveground carbon stocks or NPP to preoutbreak values or unattacked stands within one to several decades (Romme *et al.*, 1986; Forrester *et al.*, 2003; Pfeifer *et al.*, 2011). Following an outbreak, stand productivity can increase if the growth of surviving trees or understory accelerates after release from competition (Romme *et al.*, 1986; Brown *et al.*, 2010). However, this rapid recovery does not occur universally (Pfeifer *et al.*, 2011). The speed and magnitude of the recovery of productivity depend critically on the size of the surviving trees. In particular, stands with large surviving trees (that already dominate light, water, and nutrient resources) and few smaller trees do not exhibit accelerated growth rates (Pfeifer *et al.*, 2011). Recovery rates also are a function of the severity of the outbreak (number of trees affected) and seedling establishment rate (Pfeifer *et al.*, 2011).

Regionally, reductions in NEP can also last decades when significant tree mortality occurs (Kurz *et al.*, 2008a; Albani *et al.*, 2010; Dymond *et al.*, 2010; Stinson *et al.*, 2011). Part of the effect is a result of the long period for growth and decomposition fluxes to return to preoutbreak values, as in the stand-level cases. However, another important aspect is that outbreaks may

last years at landscape and broader scales, with insect or pathogen populations moving across a region of interest, attacking different stands at different times (Kurz *et al.*, 2008a; Albani *et al.*, 2010; Dymond *et al.*, 2010).

Responses of the carbon cycle are highly dependent on type of biotic disturbance. Several examples illustrate this point. A short-term (e.g., 1 month) outbreak of a defoliator can reduce NPP and therefore NEP within the year of the outbreak (Cook *et al.*, 2008). However, defoliation is often followed by the development of new leaves that allow some photosynthesis during that growing season (Churchill *et al.*, 1964; Cook *et al.*, 2008), and trees are not killed, allowing recovery of NEP in subsequent years (Cook *et al.*, 2008). In contrast, a bark beetle epidemic can kill many trees within a stand in 1 year (Morehouse *et al.*, 2008; Brown *et al.*, 2010; Pfeifer *et al.*, 2011), altering carbon cycling for decades to centuries (Romme *et al.*, 1986; Pfeifer *et al.*, 2011). Pathogen and defoliator epidemics that occur over several years can kill trees (Candau *et al.*, 2002; Dymond *et al.*, 2010; Man & Rice, 2010), with similar long-term impacts as bark beetles. However, effects are more muted than bark beetle-caused tree mortality in the first few years during growth reduction (Fleming *et al.*, 2002).

Although the focus of this paper is on the United States and Canada, we include here a brief review of the few relevant studies in other regions. Studies of short-term C cycling impacts based on eddy covariance tower observations reported reductions in photosynthesis and NEP for sap-sucking (Kirschbaum *et al.*, 2007) and defoliating (Allard *et al.*, 2008; Heliasz *et al.*, 2010) insects. Carbon fluxes to the soil and C:N ratios in frass were greatly increased in areas attacked by pine lappet moth (*Dendrolimus pini* L.) (le Mellec & Michalzik, 2008; le Mellec *et al.*, 2009), and a fungal pathogen reduced plant productivity following infection (Luque *et al.*, 1999). These findings from Europe and Australia were consistent with those in North America.

Many studies have assessed responses of growth of trees and stands to insect and pathogen attack. These impacts have been reported in such variables as diameter increment, volume increment, or radial growth (e.g., Gross, 1992; Filip *et al.*, 1993; Mayfield *et al.*, 2005; Fischer *et al.*, 2010; Collins *et al.*, 2011; Cruickshank *et al.*, 2011; Iqbal *et al.*, 2011). Similarly, studies have reported on the amount of mortality following epidemics, but results are variously described in terms of number of trees, volume, or basal area (e.g., Roe & Amman, 1970; Gross, 1992; Filip *et al.*, 1993; Singh, 1993; Fleming, 2000; Harausz & Pimentel, 2002). Such studies improve our understanding of underlying mechanisms, thereby providing important information for carbon cycle

science. However, these data are not easily converted into carbon units, making comparisons among studies and inclusion in carbon cycle models difficult.

Several studies have noted regional forest management implications of bark beetle outbreaks. Kurz *et al.* (2008b) described the significant implications of the 1990 baseline used by the UN Framework Convention on Climate Change for forest carbon stocks, a time when Canadian insect outbreaks were minimal. Subsequent insect outbreaks caused managed forests to switch from a carbon sink to a source, with net fluxes approaching 30% of fossil fuel emissions, influencing Canada's decision about forest C management under the Kyoto Protocol. Using simulation modeling, Seidl *et al.* (2008) show that the interaction of European spruce bark beetle (*Ips typographus* L.) outbreak severity and climate change strongly modifies future carbon stocks of central European Norway spruce [*Picea abies* (L.) Karst.] forests.

Knowledge gaps

Our review of published studies indicates substantial gaps in knowledge (Table 6). We have limited understanding of the spatial and temporal characteristics of insect and pathogen outbreaks. Aerial surveys undertaken annually in the United States and Canada provide information about general trends for some major insect species and are rich in spatial, temporal, and attribute information. However, these data sets have limitations associated with extent, subjectivity, and attribute information, have not been collated into a consistent database in Canada, and have large uncertainties (see Aerial surveys and satellite remote sensing below). Even if impact areas were well known, uncertainties exist on how to convert area or number of affected trees to metrics important for carbon cycle studies (e.g., leaf area or carbon pools). This conversion is particularly challenging for growth reducers such as defoliators that may kill trees only after multiple, consecutive years of damage or from which trees often recover. For the many insects and pathogens that do not kill trees, identification of impacts on carbon cycling based on affected area is very difficult because these disturbances often progress slowly, making detection difficult, and we lack much understanding of their effect on trees.

For most species, we lack knowledge of life history traits and drivers that can be incorporated into predictive modeling. For a small number of economically important insect or pathogen species in the United States and Canada, predictive models of a specific climate driver (e.g., winter temperature) have been developed (e.g., Thomson *et al.*, 1984; Wilder, 1999; Hansen *et al.*, 2001; Logan *et al.*, 2003; Tran *et al.*, 2007; Gray,

Table 6 Summary of gaps in knowledge

Topic	Knowledge gap
Disturbance agents	<p>Spatial [area, severity (number of trees attacked within an area or amount of damage to a tree), distribution] and temporal (duration) characteristics of biotic disturbances</p> <p>Knowledge of life history traits and drivers for predictive modeling</p> <p>Predictive capability of invasions by exotic species</p> <p>Interactions with and predisposition to other disturbances including biotic and abiotic factors (particularly fire and drought)</p>
Carbon cycling	<p>Conversion of outbreak area or number of affected trees to carbon variables</p> <p>Impact of outbreaks that do not lead to tree mortality on productivity and carbon cycling</p> <p>Replication of studies</p> <p>Impacts of pathogen outbreaks</p> <p>Responses of carbon pools and fluxes following different types and severities of outbreaks</p> <p>Landscape- to continental-scale impacts, particularly in United States</p> <p>Biotic disturbances in many carbon cycle models</p>

2008; Stone *et al.*, 2008). However, less is known about most pathogens, and biotic disturbance agents in some North American regions, especially Mexico, are little understood even though some may be quite important (Salinas-Moreno *et al.*, 2010). Full integration of forest stand conditions, climate drivers of host condition/susceptibility and insect/pathogen population dynamics, and host/biotic disturbance agent interactions that could allow for more complete simulations has yet to be accomplished for any insect or pathogen. In addition, our capability to predict damaging invasions by insects and pathogens, either through range expansion or introduction of exotic species, is quite limited. Such invasions have the potential to exert large impacts on C stocks and fluxes, yet our ability to estimate when, where, and in which host species invasions will occur is poor.

Interactions with other disturbances are not well quantified. A better understanding is needed of the complex interactions between biotic disturbance agents, such as mountain pine beetle and bluestain fungus (*G. clavigera* or *Ophiostoma clavigerum*) (Six & Wingfield, 2011) or bark beetles and defoliators (Raffa *et al.*, 2008).

The interactions between drought and heat stress and biotic disturbances as drivers of tree mortality events are poorly understood – there is currently only limited mechanistic knowledge of the physiological processes, thresholds, and linkages involved (McDowell *et al.*, 2008; Adams *et al.*, 2009; Breshears *et al.*, 2009; Bentz *et al.*, 2010; Carnicer *et al.*, 2011; Sturrock *et al.*, 2011). Biotic disturbance and wildfire interactions are also important and require additional study (Fleming *et al.*, 2002; Jenkins *et al.*, 2008). Other feedbacks that have received little attention include how large-scale outbreaks of biotic agents might affect such biophysical processes such as leaf area, forest transpiration/stomatal conductance, and albedo (Hogg *et al.*, 2000; Bonan, 2002; Adams *et al.*, 2010). Modifications to these processes drive changes in surface energy and water budgets (Adams *et al.*, 2011), affecting local and regional weather and climate patterns (including amplification of drought and heat stress).

General conclusions about C cycle processes are subject to large uncertainty as a result of the lack of replicated studies. Few studies of impacts on carbon cycling exist, limiting comparisons among studies. Furthermore, replicating impacts of similar insect/pathogen and host type under similar conditions, particularly amount of defoliation and/or mortality and time since disturbance, is challenging (Fig. 4). For example, whether a bark beetle-infested stand is a net C source or sink depends on the extent of tree mortality, number and size of surviving trees, spatial pattern of mortality, and time since outbreak, among other processes. Attempts to match conditions among published studies currently yield very few meaningful comparisons (Tables 4 and 5). Future comparisons will be facilitated if studies report detailed information about the variables in these tables.

The lack of existing C cycle studies implies several gaps in knowledge. The majority of existing studies concern insect outbreaks; very few studies of pathogen outbreak impacts on the C cycle have been reported. Even so, the insect species studied are primarily mountain pine beetle, hemlock woolly adelgid, gypsy moth, forest tent caterpillar, and eastern spruce budworm. More studies are needed to quantify the changes in carbon pools and fluxes associated with different types and severities of outbreaks. These changes include the direct effects on C stocks and fluxes, such as reductions of GPP, loss of leaf area, and changes in within-plant C allocation patterns. Efforts to assemble and convert published reports of effects of insects and pathogens in units such as volume or basal area to carbon units for comparison among studies are needed, and in some cases, older reports require updating (e.g., Singh, 1993). In addition, little is known about the decomposition

rates of leaves, roots, and fine and coarse woody debris, significant because of the large amount of dead organic matter generated by some biotic disturbances. Snagfall rates influence the rate of dead wood decomposition, yet these rates and drivers are little known. A wide range of snagfall rates following biotic disturbances has been reported, from 50% of killed trees down after 9 years (Mitchell & Preisler, 1998) to 16% down after 25 years (Mielke, 1950); such a broad range has significant implications for carbon cycling (Busse, 1994). Seedling establishment following outbreaks is likewise poorly quantified. The size and number of surviving trees is key to determining how rapidly postoutbreak NPP increases, yet we have little information about how these factors vary within and among outbreaks. Studies of indirect effects and ecosystem feedbacks leading to influences on C cycling, such as changes in microclimate, albedo, and species composition, are needed, as are studies that link changes in carbon cycling to subsequent climate change. Finally, a better understanding of the role of wood decay organisms that do not cause widespread disturbances will lead to a more complete understanding of effects on carbon cycling.

Some information on landscape- to continental-scale impacts on carbon budgets exists, particularly for insects in Canada (Table 4). However, effects of many major, large-scale insect and pathogen outbreaks in the United States have not been studied. In addition to North America, extensive forest dieoff events on other continents have been reported, due in part to biotic disturbance (Allen *et al.*, 2010), suggesting major modifications to carbon stocks and fluxes in these other regions that have yet to be quantified.

Biotic disturbances are missing from most carbon cycle models, and therefore effects of historical and future outbreaks have been evaluated in relatively few instances. To avoid double counting, models that explicitly represent biotic disturbances need to be parameterized with observations that do not include these disturbances (e.g., growth models based on inventory databases). The development of fully integrated predictive models of outbreaks, as discussed above, will expand the capacity of carbon cycling models to assess future impacts. Key challenges remain in conceptualizing the level of complexity needed to accurately constrain carbon cycle impacts from insect and pathogen outbreaks.

Available tools

Field observations

Field observations form a critical set of tools for evaluating impacts. Advantages include providing precise,

accurate, and complete information at fine spatial scales of tree physiology, insect and pathogen identities and population levels, and carbon cycle responses, which are essential for mechanistic understanding. At larger scales, some networks such as the USDA Forest Service Forest Inventory and Analysis (FIA) program can be used for assessing mortality and impacts to C cycling following outbreaks (Thompson, 2009a,b; Busby & Canham, 2011). Dendrochronological methods are useful for assessing forest impacts over longer time periods (e.g., Swetnam & Lynch, 1993; Axelson *et al.*, 2009). Methods and tools available for understanding processes associated with C cycle impacts using field observations are well established.

Several notable challenges exist when using field observations. Major biotic disturbances are relatively uncommon in time and space (e.g., USDA Forest Service, 2010), and we currently lack the capability to generate accurate short-term predictions of locations of these disturbances at local spatial scales. In the case of insects, this capability can be improved by deploying pheromones and host volatiles that attract target species into systematically arranged traps (e.g., Grant, 1991). Establishing a control for comparison of effects may be also a challenge, whether in time (forecasting an outbreak to obtain preoutbreak measurements) or space (finding similar stands and environmental conditions). Developing chronosequences of time since disturbance that substitute space for time requires identification of similar stands with similar levels of impact across decades (Amiro *et al.*, 2010). However, selecting older stands becomes more difficult as the biotic disturbance evidence (e.g., affected trees or indicators of insect or pathogen attack) fades with time. Ground surveys are costly and require personnel in the field timed when outbreaks are most visually obvious, and thus are both limited in scope and constrained by logistical considerations. For measuring carbon cycling with eddy covariance towers, mountainous terrain induces advective air flows within and above the canopy that may pose significant challenges for interpreting results (Yi *et al.*, 2008; Sun *et al.*, 2010). In addition, quantifying the effects of variation in outbreak severity that may occur within the spatially variable footprint of a given tower is important but difficult.

Aerial surveys and satellite remote sensing

Aerial surveys record observations about forest disturbances that include spatial location, areal extent, severity, and host. The resulting databases extend back many years, and are produced by trained observers delineating damaged areas from aircraft (Ciesla, 2000; McConnell *et al.*, 2000). In the United States, regional

data from the annual Aerial Detection Survey program are available from 1997 to the present, with regional subsets available further back in time (e.g., USDA Forest Service, 2009a). In Canada, the Forest Insect and Disease Survey of the Canadian Forest Service conducted annual surveys (Hall *et al.*, 1998) until 1996, following which they became the responsibility of provincial and territorial governments.

Integrating, interpreting, and comparing aerial surveys can be problematic because of their subjective nature, differences in damage classification systems across jurisdictions, and variation in spatial accuracy and resolution (Harris & Dawson, 1979; McConnell *et al.*, 2000; de Beurs & Townsend, 2008). In some instances, aerial surveys provided accurate estimates of damage compared with ground-based observations (MacLean & MacKinnon, 1996; Johnson & Ross, 2008; Taylor & MacLean, 2008). However, spatial and temporal extents of surveys are limited. In Canada, aerial surveys are largely confined to managed forests, and in the United States, surveys were historically limited to timber-producing tree species and did not include national parks or wilderness areas. Damage polygons include live trees, so this 'affected area' overestimates the amounts of tree mortality. Approaches to address this problem include deflation factors to convert the affected area to net area of tree mortality (Kurz & Apps, 1999) as well as combining aerial survey information with remotely sensed imagery to identify the specific area in which the disturbance has taken place (Rogan *et al.*, 2006). The patchy, discontinuous nature of disease caused by many native pathogens means that aerial surveys are generally ineffective for identifying outbreaks of most pathogens. For example, Morrison *et al.* (2000) found belowground incidence of *Armillaria* root disease to be significantly higher than indicated by aboveground symptoms only. Similar problems arise with root-feeding insects and suboutbreak levels of defoliators and bark beetles.

Satellite remote sensing also provides a means of mapping and monitoring damage caused by insect and pathogen outbreaks, including defoliating insects (e.g., Nelson, 1983; Williams & Nelson, 1986; Leckie & Ostaff, 1988; Franklin & Raske, 1994; Hall *et al.*, 2006), bark beetles (Franklin *et al.*, 2003; Wulder *et al.*, 2006), and pathogens (e.g., Leckie *et al.*, 2004; Pu *et al.*, 2008; Hatala *et al.*, 2010). Reasonably accurate damage maps have been obtained by classifying single images (e.g., Ahern, 1988; Radeloff *et al.*, 1999) as well as by assessing interannual spectral changes using multi-temporal data sets (e.g., Hall *et al.*, 2006; Goodwin *et al.*, 2008; Vogelmann *et al.*, 2009).

Several key characteristics determine the usefulness of satellite imagery for quantifying outbreaks. Spatial

resolution is important: relatively smaller outbreaks can be detected using high spatial resolution sensors (2–4 m such as IKONOS or QuickBird) (Coops *et al.*, 2006; Hicke & Logan, 2009), whereas medium-resolution (ca. 30 m, such as Landsat) (Hall *et al.*, 2006; Wulder *et al.*, 2006; Vogelmann *et al.*, 2009) and coarse-resolution (250–1000 m, such as Moderate Resolution Imaging Spectroradiometer) (Fraser & Latifovic, 2005; de Beurs & Townsend, 2008; Coops *et al.*, 2009) imagery are useful for mapping relatively larger outbreaks because such imagery increases the spatial extent (although at the expense of spatial resolution) and decreases the cost. Temporal resolution is also a key characteristic. High temporal frequency imagery is less important for tree mortality events but is needed for capturing short-lived defoliation events. The location of spectral bands is important, although most sensors provide imagery in visible and near-infrared wavelengths useful for mapping tree mortality. Hyperspectral remote sensing appears to be a promising technology for the detection of pathogens because it can detect plant stress far in advance of actual defoliation (Govender *et al.*, 2008) as well as quantify fine-scale patchy damage patterns (Pu *et al.*, 2008; Hatala *et al.*, 2010) and detect root disease (Leckie *et al.*, 2004).

Compared with aerial survey information, satellite imagery can provide more extensive mapping using objective, repeatable methods. Although remote sensing has demonstrated promise in mapping biotic disturbances, operational methods are relatively few. Aerial surveys provide a greater likelihood of guaranteeing data acquisition, and some information (type of disturbance agent, host species) in aerial survey databases is not yet widely available from satellite imagery. Remote sensing, however, provides more spatially precise and consistent detection and mapping of disturbances. Future investigations could explore integrating aerial surveys with satellite remote sensing to take advantage of the strengths of each.

Simulation models

Predicting when and where outbreaks of forest insects and pathogens will occur is needed for assessing future C budgets, particularly because such disturbances are significantly affected by climate. Models of forest insects and pathogens have been developed from a number of different perspectives and with different goals. 'Hazard rating' models estimate the susceptibility of a stand to attack based on vegetation composition and structure (age, stem density, etc.) (Krist *et al.*, 2007), and may include simple representations of climate and populations (Shore & Safranyik, 1992). Climate suitability models assess whether conditions

are conducive to outbreaks based on temperature and/or drought. Such models can be based on empirical analysis (e.g., Carroll *et al.*, 2004), climate envelop models (e.g., Magarey *et al.*, 2007), or processes measured in the laboratory (e.g., Bentz *et al.*, 1991). Neither hazard rating nor climate suitability models predict individual outbreaks, but can be used to assess conditions that could potentially lead to outbreaks. Decision support systems or landscape models for different biotic disturbance agents exist and could be incorporated into predictions of C cycle impacts (e.g., Carroll & Meades, 1996; MacLean *et al.*, 2001; Sturtevant *et al.*, 2004; Shore *et al.*, 2006).

Models of population dynamics, which are often based on spatial extensions of traditional epidemiological models, simulate the course of an epidemic, and may include biotic interactions between host, insect/pathogen, and natural enemies. These models may include such processes as insect outbreak initiation, dispersal, and collapse (e.g., Beukema *et al.*, 1997; Logan *et al.*, 1998; Sturtevant *et al.*, 2004; Cairns *et al.*, 2008). Models of pathogens have been used to simulate pathogen transmission (Kleczkowski *et al.*, 1997), assess the role of pathogens in facilitating plant migration through enemy release (Moorcroft *et al.*, 2006), and simulate disease population dynamics and associated uncertainties (Hatala *et al.*, 2011).

Models of carbon cycling often include wildfire and harvest disturbances, but few include biotic disturbance agents. Exceptions include studies of the role of defoliation (Cook *et al.*, 2008; Kurz *et al.*, 2009), aspen decline (Hogg, 1999, 2001), and insect-caused tree mortality (Kurz *et al.*, 2009; Albani *et al.*, 2010; Pfeifer *et al.*, 2011). In general, C cycle models are positioned to include biotic disturbances because they include the main processes needed to simulate impacts (photosynthesis, allocation, decomposition), though challenges remain. Responses of historical carbon stocks and fluxes can be ascertaining by prescribing the location and year of outbreak using remote sensing databases. Methods to assess future impacts of these disturbances range from simpler representations [scenarios that combine information on current outbreaks and expert opinion as in Kurz *et al.* (2008a)] to more complex modeling of outbreak dynamics (e.g., Albani *et al.*, 2010). In addition to prescribing or predicting the number of trees attacked (through an outbreak submodel, for instance), correct simulation requires understanding how to model responses of the carbon cycle to insect or pathogen outbreaks in terms of tree growth reduction and mortality. Impacts to subsequent ecosystem processes such as decomposition, snagfall rate, regeneration, and surviving stand composition also suggest their importance for accurate simulations of C cycling.

Summary and conclusions

Numerous insect and pathogen species impact forests of the United States and Canada. A few species are particularly important to carbon cycling at regional to continent scales because they cause significant damage across large areas of forest during major outbreaks. However, life histories of only a few significant species are understood well enough to provide a basis for predictive modeling of their impacts on the forest carbon cycle.

Biotic disturbances affect several aspects of carbon cycling. Tree productivity is reduced by growth reductions such as defoliation, root herbivory, or disease. After multiple years of growth reductions, or attack by aggressive bark beetles or pathogens, tree mortality occurs, leading to decreases in primary productivity and creating dead organic matter that subsequently decomposes over long time periods. As a result of decreasing C uptake by live biomass and increases in C loss through decomposition of dead biomass, NEP is often reduced substantially and may result in a forest switching from a C sink to a source. NPP following tree mortality events can recover within a decade or so, whereas changes in decomposition continue for decades to centuries. Following an outbreak, NEP may recover to nearly zero within a few years of a major outbreak or may be strongly negative (a substantial source) for decades. At broader scales, impacts on C stocks and fluxes can be significant when large areas experience substantial tree mortality. When the total number of affected trees within a study region is small, however, the effect on carbon cycling may be greatly reduced.

There are relatively few studies of biotic disturbance impacts on carbon cycling, and these cover only a limited subset of study conditions, implying many uncertainties for generalizing responses. Important factors affecting possible biotic agent impacts include the number of affected trees, type of disturbance agent (growth reducer or tree killer), and duration of attack. In addition, time since outbreak is a major influence on carbon stocks and fluxes, and different studies have focused on different periods. Future studies of biotic disturbance effects on forest carbon cycling should include key information that permits comparisons across studies, including spatial and temporal extent of damage, outbreak severity (degree of damage and number of trees affected within study region), time since disturbance, and postoutbreak stand structure.

Additional research is needed in several key areas. Tracking forest carbon responses for years to decades following disturbances will aid in quantifying recovery rates. Knowledge of the influences of a variety of biotic disturbance agents, both insects and pathogens, and

across a range of spatial and temporal scales, is needed. Technologies and methods that result in more spatially precise and accurate monitoring and mapping will lead to improved assessment of impacts. Increased understanding of how climate affects insects and pathogens, interactions with other disturbances, construction and testing of predictive models of outbreaks, and inclusion of these models into carbon cycle models will allow for simulation of future impacts to C cycling given future climate change.

Insects and diseases are strongly influenced by climate and weather, and future warming will likely increase the severity and extent of outbreaks. Alterations in future forest composition and structure and therefore carbon sequestration have implications for atmospheric CO₂ concentrations and thus future climate. Projections that include biotic disturbances to forests together with feedbacks to future climate have yet to be produced, however.

It is clear that insect and pathogen outbreaks are important disturbances of forests in the United States and Canada, and major changes may be expected under projected future changes in climate. Their capacity to reduce productivity and kill trees, often across extensive areas, means that they have large influences on the North American carbon budget, as supported by the studies discussed here. However, numerous uncertainties and knowledge gaps currently constrain our ability to estimate or predict many effects of biotic agents on forest carbon cycling. Further research is needed across a range of disturbance types and spatial and temporal scales to provide more reliable assessments of the effects of insect and pathogen outbreaks on the continental carbon cycle.

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