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REVIEW

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

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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).

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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.

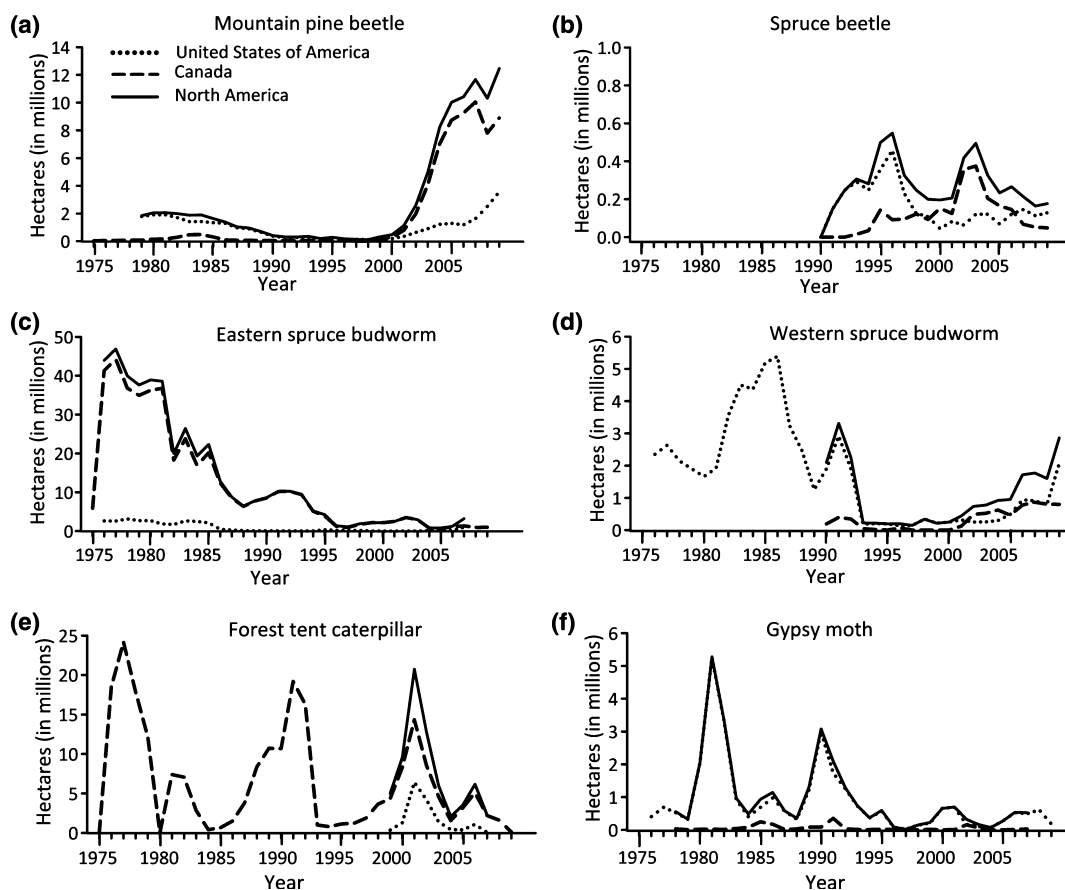


Fig. 1 Annual areas affected by major forest insect species from US (dotted line) and Canadian (dashed line) aerial survey databases and their total (solid line). Example species chosen to illustrate variability among species, through time, and between regions. 'Affected area' includes live and dead 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

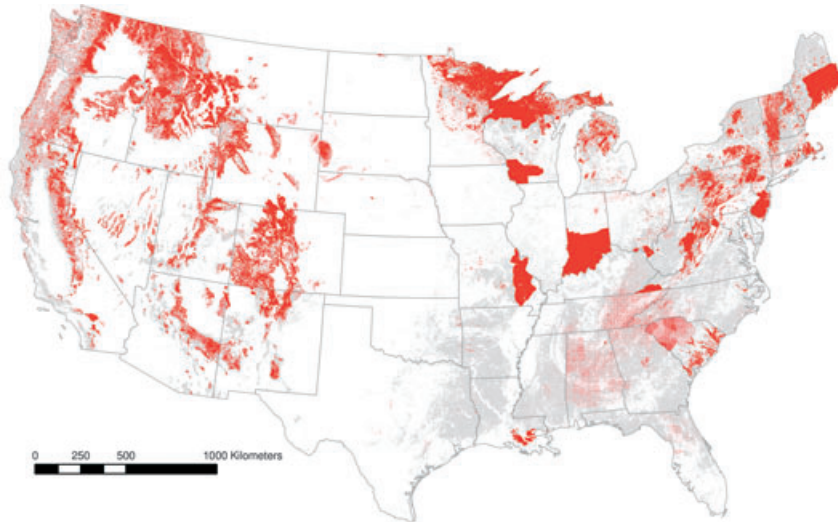


Fig. 2 Locations with insect and disease damage (black) mapped by the USDA Forest Service Aerial Detection Survey, 1997–2010. Affected areas include damaged as well as undamaged trees. Gray indicates forest area (Zhu & Evans, 1994).

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.	Pinaceae and Cupressaceae	Native	<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.)	Numerous spp. identified as potential hosts	Invasive		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

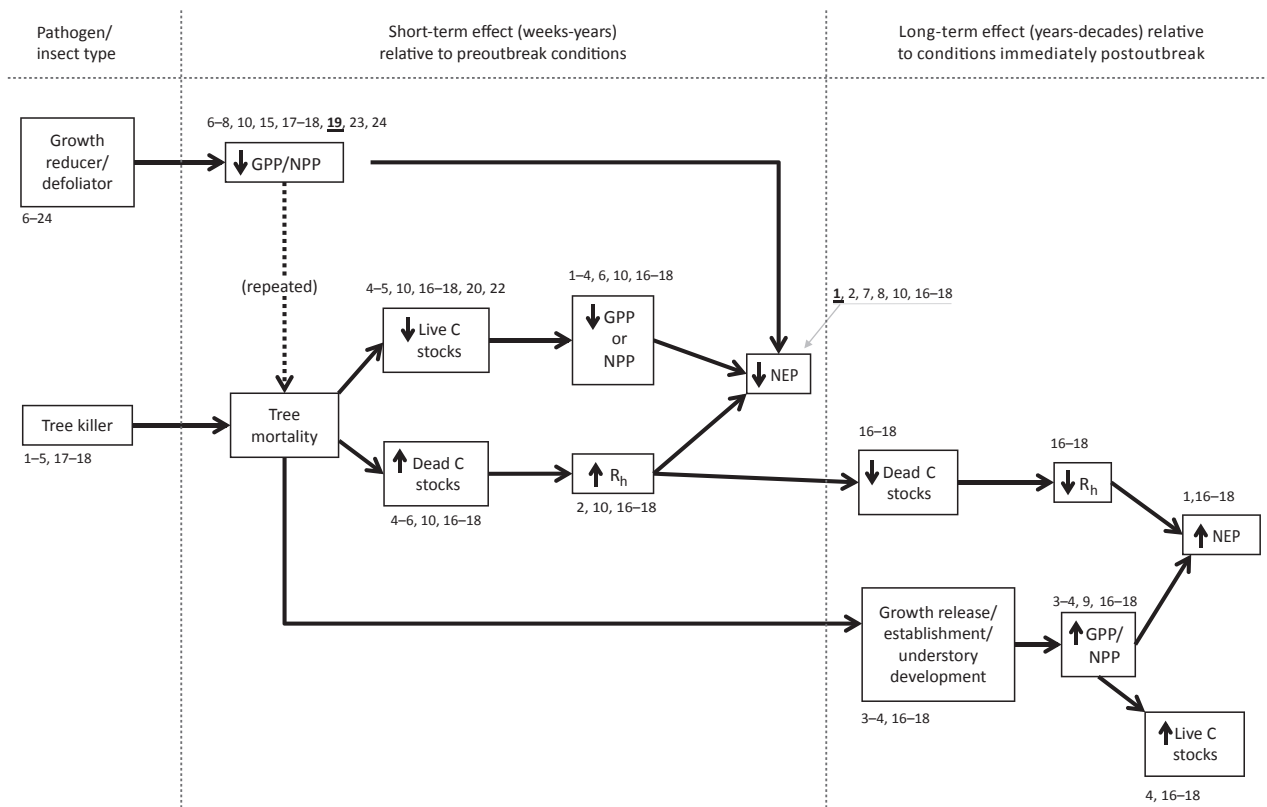


Fig. 3 Conceptual diagram showing impacts of insect and pathogen outbreaks on carbon budgets. Numbers outside of boxes reference studies in Tables 4 and 5 that provide evidence. Studies that provide evidence counter to that indicated in diagram noted in bold underlined text (two cases).

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				Simulation modeling	Regional	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										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) Manter <i>et al.</i> (2003)
Foliar	Swiss needle cast, <i>Phaeocryptopus gaeumanni</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			
23											
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)
24											

*See Table 3 for explanation of abbreviations.

†Study identifier used in Fig. 3.

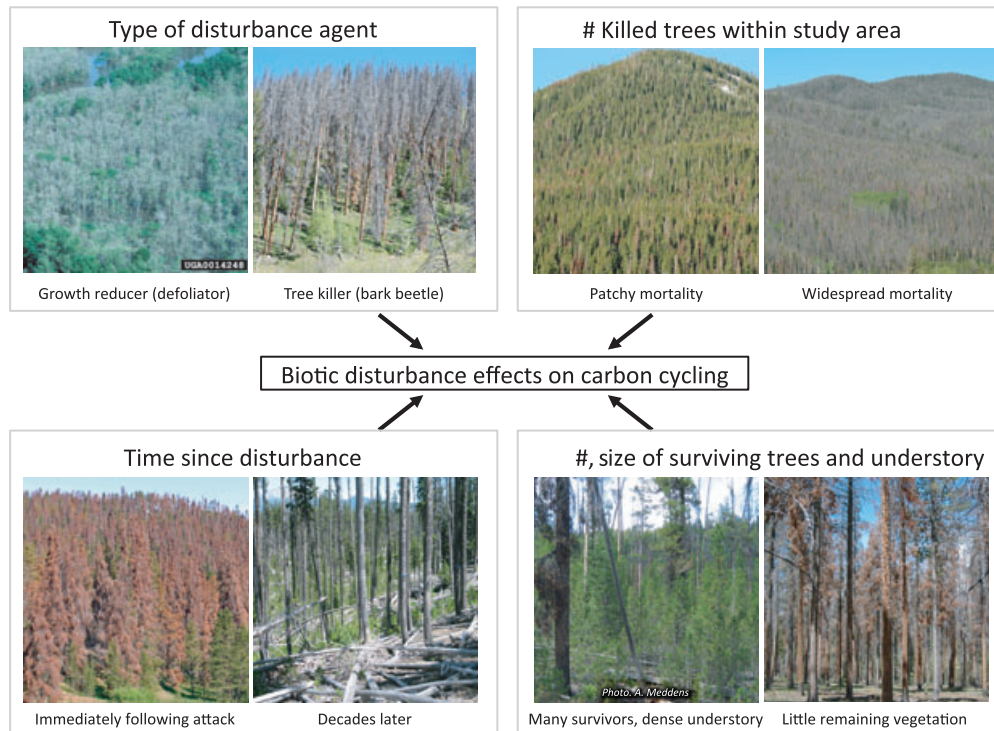


Fig. 4 Processes that influence how biotic disturbances affect carbon cycling. Examples of mountain pine beetle and forest tent caterpillar (upper left) outbreaks illustrate the range of conditions for each process. Photos by J. Hicke except where noted (G. J. Lenhard, Louisiana State University, Bugwood.org,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

Adams HD, Guardiola-Claramonte M, Barron-Gafford GA, Villegas JC, Breshers DD, Zou CB, Huxman TE (2009) Temperature sensitivity of drought-induced tree

- mortality portends increased regional die-off under global-change-type drought. *Proceedings of the National Academy of Sciences of the United States of America*, **106**, 7063–7066.
- Adams HD, Macalady AK, Breshers DD, Allen CD, Stephenson NL, Saleska SR, McDowell NG (2010) Climate-induced tree mortality: earth system consequences. *EOS, Transactions of the American Geophysical Union*, **91**, 153.
- Adams HD, Luce CH, Breshers DD *et al.* (2011) Ecohydrological consequences of drought- and infestation-triggered tree die-off: insights and hypotheses. *Ecophysiology*, in press.
- Agrios GN (2005) *Plant Pathology*. Elsevier Academic Press, USA.
- Ahern FJ (1988) The effects of bark beetle stress on the foliar spectral reflectance of lodgepole pine. *International Journal of Remote Sensing*, **9**, 1451–1468.
- Albani M, Moorcroft PR, Ellison AM, Orwig DA, Foster DR (2010) Predicting the impact of hemlock woolly adelgid on carbon dynamics of eastern United States forests. *Canadian Journal of Forest Research*, **40**, 119–133.
- Allard V, Ourcival JM, Rambal S, Joffre R, Rocheteau A (2008) Seasonal and annual variation of carbon exchange in an evergreen Mediterranean forest in southern France. *Global Change Biology*, **14**, 714–725.
- Allen CD, Macalady AK, Chenchouni H, Bachelet D, McDowell N, Venetier M, Cobb N (2010) A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management*, **259**, 660–684.
- Amiro BD, Barr AG, Barr JG, Black TA, Bracho R, Brown M, Xiao J (2010) Ecosystem carbon dioxide fluxes after disturbance in forests of North America. *Journal of Geophysical Research*, **115**, G00K02, doi: 10.1029/2010JG001390.
- Anagnostakis SL (1987) Chestnut blight: the classical problem of an introduced pathogen. *Mycologia*, **79**, 23–37.
- Anderson RL, McClure JP, Cost ND, Uhler RJ (1986) Estimating fusiform rust losses in five southeast states. *Southern Journal of Applied Forestry*, **10**, 237–240.
- Aukema JE, McCullough DG, Holle BV, Liebhold AM, Britton K, Frankel SJ (2010) Historical accumulation of nonindigenous forest pests in the continental United States. *BioScience*, **60**, 886–897.
- Axelson JN, Alfaro RJ, Hawkes BC (2009) Influence of fire and mountain pine beetle on the dynamics of lodgepole pine stands in British Columbia, Canada. *Forest Ecology and Management*, **257**, 1874–1882.
- Ayres MP, Lombardero MJ (2000) Assessing the consequences of global change for forest disturbance from herbivores and pathogens. *The Science of the Total Environment*, **262**, 263–286.
- Bentz BJ, Logan JA, Amman GD (1991) Temperature-dependent development of mountain pine beetle and simulation of its phenology. *Canadian Entomologist*, **123**, 1083–1094.
- Bentz BJ, Logan JA, Vandygriff JC (2001) Latitudinal variation in *Dendroctonus ponderosae* (Coleoptera: Scolytidae) development time and adult size. *Canadian Entomologist*, **133**, 375–387.
- Bentz B, Logan J, MacMahon J, Allen CD, Ayres M, Berg E, Wood D (2009) *Bark Beetle Outbreaks in Western North America: Causes and Consequences*. University of Utah Press, Salt Lake City, UT.
- Bentz BJ, Régnière J, Fettig CJ, Hansen EM, Hayes JL, Hicke JA, Seybold SJ (2010) Climate change and bark beetles of the western United States and Canada: direct and indirect effects. *BioScience*, **60**, 602–613.
- Berg EE, Henry JD, Fastie CL, De Volder AD, Matsuoka SM (2006) Spruce beetle outbreaks on the Kenai Peninsula, Alaska, and Kluane National Park and Reserve, Yukon Territory: relationship to summer temperatures and regional differences in disturbance regimes. *Forest Ecology and Management*, **227**, 219–232.
- Beukema SJ, Greenough JA, Robinson DCE, Kurz WA, Smith EL, Eav BB (1997) The Westwide Pine Beetle Model: a spatially-explicit contagion model. In: *Proceedings of the Forest Vegetation Simulator Conference. Gen. Tech. Rep. INT-GTR-373* (eds Teck R, Moer M, Adams J), pp. 126–130. U.S. Department of Agriculture, Forest Service, Intermountain Research Station, Fort Collins, CO.
- de Beurs KM, Townsend PA (2008) Estimating the effect of gypsy moth defoliation using MODIS. *Remote Sensing of Environment*, **112**, 3983–3990.
- Bleiker K, Six DL (2007) Dietary benefits of fungal associates to an eruptive herbivore: potential implications of multiple associates on host population dynamics. *Environmental Entomology*, **36**, 1384–1396.
- Bonan G (2002) *Ecological Climatology*. Cambridge University Press, Cambridge, UK.
- Bonan GB (2008) Forests and climate change: forcings, feedbacks, and the climate benefits of forests. *Science*, **320**, 1444–1449.
- Brandt JP, Hiratsuka Y, Pluth DJ (2004) Extreme cold temperatures and survival of overwintering and germinated *Arceuthobium americanum* seeds. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere*, **34**, 174–183.

- Breshears DD, Cobb NS, Rich PM, Price KP, Allen CD, Balice RG, Meyer CW (2005) Regional vegetation die-off in response to global-change-type drought. *Proceedings of the National Academy of Sciences of the United States of America*, **102**, 15144–15148.
- Breshears DD, Myers OB, Meyer CW, Barnes FJ, Zou CB, Allen CD, Pockman WT (2009) Tree die-off in response to global change-type drought: mortality insights from a decade of plant water potential measurements. *Frontiers in Ecology and the Environment*, **7**, 185–189.
- Brown M, Black TA, Nestic Z, Foord VN, Spittlehouse DL, Fredeen AL, Trofyomov JA (2010) Impact of mountain pine beetle on the net ecosystem production of lodgepole pine stands in British Columbia. *Agricultural and Forest Meteorology*, **150**, 254–264.
- Busby PE, Canham CD (2011) An exotic insect and pathogen disease complex reduces aboveground tree biomass in temperate forests of eastern North America. *Canadian Journal of Forest Research*, **41**, 401–411.
- Busse MD (1994) Downed bole-wood decomposition in lodgepole pine forests of Central Oregon. *Soil Science Society of America Journal*, **58**, 221–227.
- Cairns DM, Lafon CW, Waldron JD, Tchakerian M, Coulson RN, Klepzig KD, Xi W (2008) Simulating the reciprocal interaction of forest landscape structure and southern pine beetle herbivory using LANDIS. *Landscape Ecology*, **23**, 403–415.
- Canadell JG, Raupach MR (2008) Managing forests for climate change mitigation. *Science*, **320**, 1456–1457.
- Canadell JG, Le Quere C, Raupach MR, Field CB, Buitenhuis ET, Ciais P, Marland G (2007) Contributions to accelerating atmospheric CO₂ growth from economic activity, carbon intensity, and efficiency of natural sinks. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 18866–18870.
- Candau JN, Fleming RA, Hopkin A (1998) Spatiotemporal patterns of large-scale defoliation caused by the spruce budworm in Ontario since 1941. *Canadian Journal of Forest Research*, **28**, 1733–1741.
- Candau JN, Abt V, Keatley L (2002) *Bioclimatic analysis of declining aspen stands in northeastern Ontario*. Forest Research Report No. 154, Ontario Forest Research Institute, Ontario.
- Carnicer J, Coll M, Ninyerola M, Pons X, Sanchez G, Penuelas J (2011) Widespread crown condition decline, food web disruption, and amplified tree mortality with increased climate change-type drought. *Proceedings of the National Academy of Sciences of the United States of America*, **108**, 1474–1478.
- Carroll AL, Meades JP (1996) The eastern hemlock looper decision support system. In: *The Eastern Hemlock Looper, *Lambdina fuscicollis* (Guen.) (Lepidoptera: Geometridae) in Newfoundland, 1983–1995* (ed. Hudak J). Canadian Forest Service, Newfoundland Forest Research Center, St. John's, NF.
- Carroll AL, Taylor SW, Régnière J, Safranyik L (2004) Effects of climate change on range expansion by the mountain pine beetle in British Columbia. In: *Mountain Pine Beetle Symposium: Challenges and Solutions* (eds Shore T, Brooks JE, Stone JE), pp. 223–232. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Kelowna, BC.
- CCSP (2007) *The First State of the Carbon Cycle Report (SOCCR): The North American Carbon Budget and Implications for the Global Carbon Cycle*. A Report by the U.S. Climate Change Science Program and the Subcommittee on Global Change Research, National Oceanic and Atmospheric Administration, National Climatic Data Center, Asheville, NC.
- Chapin FS, Woodwell GM, Randerson JT, Rastetter EB, Lovett GM, Baldocchi DD, Schulze ED (2006) Reconciling carbon-cycle concepts, terminology, and methods. *Ecosystems*, **9**, 1041–1050.
- Chapin FS, Randerson JT, McGuire AD, Foley JA, Field CB (2008) Changing feedbacks in the climate-biosphere system. *Frontiers in Ecology and the Environment*, **6**, 313–320.
- Churchill GB, John HH, Duncan DP, Hodson AC (1964) Long-term effects of defoliation of aspen by the forest tent caterpillar. *Ecology*, **45**, 630–636.
- Ciais P, Reichstein M, Viovy N, Granier A, Ogee J, Allard V, Valentini R (2005) Europe-wide reduction in primary productivity caused by the heat and drought in 2003. *Nature*, **437**, 529–533.
- Ciesla WM (2000) *Remote sensing in forest health protection*. FHTET 00-03, United States Department Of Agriculture Forest Service, Forest Health Technology Enterprise Team, Fort Collins, CO and Remote Sensing Applications Center, Salt Lake City, UT.
- Clark KL, Skowronski N, Hom J (2010) Invasive insects impact forest carbon dynamics. *Global Change Biology*, **16**, 88–101.
- Collins BJ, Rhoades CC, Hubbard RM, Battaglia MA (2011) Tree regeneration and future stand development after bark beetle infestation and harvesting in Colorado lodgepole pine stands. *Forest Ecology and Management*, **261**, 2168–2175.
- Cook BD, Bolstad PV, Martin JG, Heinsch FA, Davis KJ, Wang WG, Teclaw RM (2008) Using light-use and production efficiency models to predict photosynthesis and net carbon exchange during forest canopy disturbance. *Ecosystems*, **11**, 26–44.
- Coops NC, Johnson M, Wulder MA, White JC (2006) Assessment of QuickBird high spatial resolution imagery to detect red attack damage due to mountain pine beetle infestation. *Remote Sensing of Environment*, **103**, 67–80.
- Coops NC, Wulder MA, Iwanicka D (2009) Large area monitoring with a MODIS-based Disturbance Index (DI) sensitive to annual and seasonal variations. *Remote Sensing of Environment*, **113**, 1250–1261.
- Coyle D, Mattson W, Raffa K (2008) Invasive root feeding insects in natural forest ecosystems of North America. In: *Root Feeders: An Ecosystem Perspective* (eds Johnson S, Murray P), pp. 146–162. CABI, Oxfordshire.
- Cruickshank M (2000) Volume loss of Douglas-fir infected with *Armillaria ostoyae*. In: *From Science to Management and Back: A Science Forum for Southern Interior Ecosystems of British Columbia* (eds Hollstedt C, Sutherland K, Innes T), pp. 127–129. Southern Interior Forest Extension and Research Partnership, Kamloops, BC.
- Cruickshank M, Morrison DJ, Lalumière A (2009) The interaction between competition in interior Douglas-fir plantations and disease caused by *Armillaria ostoyae* in British Columbia. *Forest Ecology and Management*, **257**, 443–452.
- Cruickshank MG, Morrison DJ, Lalumière A (2011) Site, plot, and individual tree yield reduction of interior Douglas-fir associated with non-lethal infection by *Armillaria* root disease in southern British Columbia. *Forest Ecology and Management*, **261**, 297–307.
- Dale VH, Joyce LA, McNulty S, Neilson RP, Ayres MP, Flannigan MD, Wotton BM (2001) Climate change and forest disturbances. *BioScience*, **51**, 723–734.
- Denning AS, Oren R, McGuire D *et al.* (2005) *Science Implementation Strategy for the North American Carbon Program. Report of the NACP Implementation Strategy Group of the U.S. Carbon Cycle Interagency Working Group*. U.S. Carbon Cycle Science Program, Washington, DC.
- Desprez-Loustau ML, Marcais B, Nageleisen LM, Piou D, Vannini A (2006) Interactive effects of drought and pathogens in forest trees. *Annals of Forest Science*, **63**, 597–612.
- Dietze MC, Moorcroft PR (2011) Tree mortality in the eastern and central United States: patterns and drivers. *Global Change Biology*, doi: 10.1111/j.1365-2486.2011.02477.x.
- Drummond DB (1982) *Timber loss estimates for the coniferous forests in the U.S. due to dwarf mistletoes*. Rep. MAG-83-2. U.S. Department of Agriculture, Forest Service, Forest Pest Management, Methods Application Group, Fort Collins, CO.
- Durall DM, Jones MD, Lewis KJ (2005) Effects of forest management on fungal communities. In: *The Fungal Community, its Organization and Role in Ecosystems* (eds Dighton J, White JF, Oudermans P), pp. 833–856. CRC Press, London.
- Dymond CC, Neilson ET, Stinson G, Porter K, MacLean DA, Gray DR, Kurz WA (2010) Future spruce budworm outbreak may create a carbon source in eastern Canadian forests. *Ecosystems*, **13**, 917–931.
- Elkinton JS, Liebhold AM (1990) Population dynamics of gypsy moth in North America. *Annual Review of Entomology*, **35**, 571–596.
- Farrar JL (1995) *Trees in Canada*. Fitzhenry & Whiteside Ltd. and Canadian Forest Service, Ottawa.
- Fellin DG, Dewey JE (1982) *Western Spruce Budworm*. Forest Insect & Disease Leaflet 53. USDA Forest Service, Washington, DC.
- Filip GM, Colbert JJ, Shaw Iii CG, Hessburg PF, Hosman KP (1993) Influence of dwarf mistletoe and western spruce budworm on growth and mortality of Douglas-Fir in unmanaged stands. *Forest Science*, **39**, 465–477.
- Fischer MJ, Waring KM, Hofstetter RW, Kolb TE (2010) Ponderosa pine characteristics associated with attack by the roundheaded pine beetle. *Forest Science*, **56**, 473–483.
- Fleming RA (2000) Climate change and insect disturbance regimes in Canada's boreal forests. *World Resources Review*, **12**, 520–555.
- Fleming RA, Candau JN, McAlpine RS (2002) Landscape-scale analysis of interactions between insect defoliation and forest fire in Central Canada. *Climatic Change*, **55**, 251–272.
- Forrester JA, McGee GG, Mitchell MJ (2003) Effects of beech bark disease on above-ground biomass and species composition in a mature northern hardwood forest, 1985 to 2000. *Journal of the Torrey Botanical Society*, **130**, 70–78.
- Franklin SE, Raske AG (1994) Satellite remote sensing of spruce budworm forest defoliation in western Newfoundland. *Canadian Journal of Remote Sensing*, **20**, 37–48.
- Franklin SE, Wulder MA, Skakun RS, Carroll AL (2003) Mountain pine beetle red-attack forest damage classification using stratified Landsat TM data in British Columbia, Canada. *Photogrammetric Engineering and Remote Sensing*, **69**, 283–288.

- Fraser RH, Latifovic R (2005) Mapping insect-induced tree defoliation and mortality using coarse spatial resolution satellite imagery. *International Journal of Remote Sensing*, **26**, 193–200.
- Frost CJ, Hunter MD (2004) Insect canopy herbivory and frass deposition affect soil nutrient dynamics and export in oak mesocosms. *Ecology*, **85**, 3335–3347.
- Geils BW, Cibrian-Tovar J, Moody B (eds) (2002) *Mistletoes of North American Conifers*, Gen. Tech. Rep. RMRS-GTR-98. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ogden, UT.
- Gill LS (1954) *Dwarf Mistletoe of Ponderosa Pine in the Southwest*. Paper 14. Rocky Mountain Forest and Range Experiment Station, U.S. Department of Agriculture, Forest Service, Denver, CO.
- Goheen EM, Hansen E, Kanaskie A, Osterbauer N, Parke J, Pscheidt J, Chastagner G (2006) *Sudden oak death and Phytophthora ramorum, a guide for forest managers, Christmas tree growers, and forest-tree nursery operators in Oregon and Washington*. EM 8877, Oregon State University Extension Service, Corvallis, OR.
- Goodale CL, Apps MJ, Birdsey RA, Field CB, Heath LS, Houghton RA, Shvidenko AZ (2002) Forest carbon sinks in the Northern Hemisphere. *Ecological Applications*, **12**, 891–899.
- Goodwin NR, Coops NC, Wulder MA, Gillanders S, Schroeder TA, Nelson T (2008) Estimation of insect infestation dynamics using a temporal sequence of Landsat data. *Remote Sensing of Environment*, **112**, 3680–3689.
- Govender M, Chetty K, Naiken V, Bulcock H (2008) A comparison of satellite hyperspectral and multispectral remote sensing imagery for improved classification and mapping of vegetation. *Water SA*, **34**, 147–154.
- Grant GG (1991) Development and use of pheromones for monitoring lepidopteran forest defoliators in North America. *Forest Ecology and Management*, **39**, 153–162.
- Gray D (2008) The relationship between climate and outbreak characteristics of the spruce budworm in eastern Canada. *Climatic Change*, **87**, 361–383.
- Griffin JM, Lovett GM, Arthur MA, Weathers KC (2003) The distribution and severity of beech bark disease in the Catskill Mountains, NY. *Canadian Journal of Forest Research*, **33**, 1754–1760.
- Gross HL (1992) Impact analysis for a jack pine budworm infestation in Ontario. *Canadian Journal of Forest Research*, **22**, 818–831.
- Hadley JL, Kuzeja PS, Daley MJ, Phillips NG, Mulcahy T, Singh S (2008) Water use and carbon exchange of red oak- and eastern hemlock-dominated forests in the northeastern USA: implications for ecosystem-level effects of hemlock woolly adelgid. *Tree Physiology*, **28**, 615–627.
- Hall PJ, Bowers WW, Hirvonen H (1998) *Forest Insect and Disease Conditions in Canada*, Natural Resources Canada, Canadian Forest Service, Ottawa.
- Hall RJ, Skakun RS, Arsenault EJ (2006) Remotely sensed data in the mapping of insect defoliation. In: *Understanding Forest Disturbance and Spatial Pattern: Remote Sensing and GIS Approaches* (eds Wulder MA, Franklin SE), pp. 85–111. CRC Press, Taylor and Francis, Boca Raton.
- Hancock JE, Arthur MA, Weathers KC, Lovett GM (2008) Carbon cycling along a gradient of beech bark disease impact in the Catskill Mountains, New York. *Canadian Journal of Forest Research*, **38**, 1267–1274.
- Hansen EM, Goheen EM (2000) *Phellinus weirii* and other native root pathogens as determinants of forest structure and process in western North America. *Annual Review of Phytopathology*, **38**, 515–539.
- Hansen EM, Stone JK, Capitano BR *et al.* (2000) Incidence and impact of Swiss needle cast in forest plantations of Douglas-fir in coastal Oregon. *Plant Disease*, **84**, 773–778.
- Hansen ME, Bentz BJ, Turner DL (2001) Temperature-based model for predicting univoltine brood proportions in spruce beetle (Coleoptera: Scolytidae). *Canadian Entomologist*, **133**, 827–841.
- Harausz E, Pimentel D (2002) North American forest losses due to insects and plant pathogens. In: *Encyclopedia of Pest Management* (ed. Pimentel D), pp. 539–542. Marcel Dekker, Inc., Ithaca, NY.
- Harmon ME, Franklin JF, Swanson FJ, Sollins P, Gregory SV, Lattin JD, Cummins KW (1986) Ecology of coarse woody debris in temperate ecosystems. *Advances in Ecological Research*, **15**, 133–302.
- Harris JWE, Dawson AF (1979) *Evaluation of aerial forest pest damage survey techniques in British Columbia*. BC-X-198., Environment Canada, Canadian Forestry Service, Pacific Forest Research Centre, Victoria, BC.
- Hatala JA, Crabtree RL, Halligan KQ, Moorcroft PR (2010) Landscape-scale patterns of forest pest and pathogen damage in the Greater Yellowstone Ecosystem. *Remote Sensing of Environment*, **114**, 375–384.
- Hatala JA, Dietze MC, Crabtree RL, Kendall K, Six D, Moorcroft PR (2011) An ecosystem-scale model for the spread of a host-specific forest pathogen in the Greater Yellowstone Ecosystem. *Ecological Applications*, **21**, 1138–1153.
- Hawksworth FG, Wiens D (1970) Biology and taxonomy of the dwarf mistletoes. *Annual Review of Phytopathology*, **8**, 187–208.
- Hebertson EG, Jenkins MJ (2008) Climate factors associate with historical spruce beetle (Coleoptera: Curculionidae) outbreaks in Utah and Colorado. *Environmental Entomology*, **37**, 281–292.
- Heliasz M, Johansson T, Lindroth A, Mölder M, Mastepanov M, Friberg T, Christensen TR (2011) Quantification of C uptake in subarctic birch forest after setback by an extreme insect outbreak. *Geophysical Research Letters*, **38**, L01704, doi: 10.1029/2010GL044733.
- Hennigar CR, MacLean DA (2010) Spruce budworm and management effects on forest and wood product carbon for an intensively managed forest. *Canadian Journal of Forest Research*, **40**, 1736–1750.
- Hicke JA, Logan JA (2009) Mapping whitebark pine mortality caused by a mountain pine beetle outbreak with high spatial resolution satellite imagery. *International Journal of Remote Sensing*, **30**, 4427–4441.
- Hicke JA, Asner GP, Randerson JT, Tucker C, Los S, Birdsey R, Field C (2002) Trends in North American net primary productivity derived from satellite observations, 1982–1998. *Global Biogeochemical Cycles*, **16**, doi: 10.1029/2001GB001550.
- Hicke JA, Asner GP, Kasiske ES, French NHF, Randerson JT, Collatz GJ, Field CB (2003) Postfire response of North American boreal forest net primary productivity analyzed with satellite observations. *Global Change Biology*, **9**, 1145–1157.
- Hicke JA, Logan JA, Powell J, Ojima DS (2006) Changing temperatures influence suitability for modeled mountain pine beetle (*Dendroctonus ponderosae*) outbreaks in the western United States. *Journal of Geophysical Research-Biogeosciences*, **111**, G02019, doi: 10.1029/2005JG000101.
- Hogg EH (1999) Simulation of inter-annual responses of trembling aspen stands to climatic variation and insect defoliation in western Canada. *Ecological Modelling*, **114**, 175–193.
- Hogg EH (2001) Modeling Aspen Responses to Climatic Warming and Insect Defoliation in Western Canada. In: *Sustaining aspen in western landscapes. Proceedings RMRS-P-18* (eds Shepperd WD, Binkley D, Bartos DL, Stohlgren TJ, Eskew LG), pp. 325–338. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, CO.
- Hogg EH, Price DT, Black TA (2000) Postulated feedbacks of deciduous forest phenology on seasonal climate patterns in the western Canadian interior. *Journal of Climate*, **13**, 4229–4243.
- Hogg EH, Brandt JP, Kochtubajda B (2002) Growth and dieback of aspen forests in northwestern Alberta, Canada, in relation to climate and insects. *Canadian Journal of Forest Research*, **32**, 823–832.
- Hogg EH, Brandt JP, Michaelian M (2008) Impacts of a regional drought on the productivity, dieback and biomass of western Canadian aspen forests. *Canadian Journal of Forest Research*, **38**, 1373–1384.
- Houghton RA, Skole DL (1990) Carbon. In: *The Earth as Transformed by Human Action* (eds Turner BL, Clark WC, Kates RW, Richards JF, Mathews JT, Meyer WB), pp. 393–408. Cambridge University Press, Cambridge.
- Houston DR (1994) Major new tree disease epidemics: Beech bark disease. *Annual Review of Phytopathology*, **32**, 75–87.
- IPCC (2007) *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, UK and New York.
- Iqbal J, MacLean DA, Kershaw JA Jr (2011) Impacts of hemlock looper defoliation on growth and survival of balsam fir, black spruce and white birch in Newfoundland, Canada. *Forest Ecology and Management*, **261**, 1106–1114.
- Jenkins JC, Aber JD, Canham CD (1999) Hemlock woolly adelgid impacts on community structure and N cycling rates in eastern hemlock forests. *Canadian Journal of Forest Research*, **29**, 630–645.
- Jenkins MJ, Hebertson E, Page W, Jorgensen CA (2008) Bark beetles, fuels, fires and implications for forest management in the Intermountain West. *Forest Ecology and Management*, **254**, 16–34.
- Johnson EW, Ross J (2008) Quantifying error in aerial survey data. *Australian Forestry*, **71**, 216–222.
- Jung T (2009) Beech decline in Central Europe driven by the interaction between Phytophthora infections and climatic extremes. *Forest Pathology*, **39**, 73–94.
- Kashian DM, Romme WH, Tinker DB, Turner MG, Ryan MG (2006) Carbon storage on landscapes with stand-replacing fires. *BioScience*, **56**, 598–606.
- Kirschbaum MUF, Keith H, Leuning R, Cleugh HA, Jacobsen KL, van Gorsel E, Raison RJ (2007) Modelling net ecosystem carbon and water exchange of a temperate *Eucalyptus delegatensis* forest using multiple constraints. *Agricultural and Forest Meteorology*, **145**, 48–68.
- Kizilinski ML, Orwig DA, Cobb RC, Foster DR (2002) Direct and indirect ecosystem consequences of an invasive pest on forests dominated by eastern hemlock. *Journal of Biogeography*, **29**, 1489–1503.

- Kleczkowski A, Gilligan CA, Bailey DJ (1997) Scaling and spatial dynamics in plant-pathogen systems: from individuals to populations. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **264**, 979–984.
- Klepzig KD, Raffa KF, Smalley EB (1991) Association of insect-fungal complexes with Red Pine Decline in Wisconsin. *Forest Science*, **37**, 1119–1139.
- Klepzig KD, Kruger EL, Smalley EB, Raffa KF (1995) Effects of biotic and abiotic stress on the induced accumulation of terpenes and phenolics in red pines inoculated with a bark beetle vectored fungus. *Journal of Chemical Ecology*, **21**, 601–626.
- Kliejunas JT, Geils B, Glaeser JM, Goheen EM, Hennon P, Mee-Sook K, Frankel SJ (2009) *Review of Literature on Climate Change and Forest Diseases of Western North America, General Technical Report, PSW-GTR-225*. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, CA.
- Krist FJ, Sapio FJ, Tkacz BM (2007) *Mapping Risk from Forest Insects and Diseases*. FHTE 2007-06. Forest Health Technology Enterprise Team, USDA Forest Service, Washington, DC.
- Kurz WA, Apps MJ (1999) A 70-year retrospective analysis of carbon fluxes in the Canadian forest sector. *Ecological Applications*, **9**, 526–547.
- Kurz WA, Dymond CC, Stinson G, Rampley GJ, Neilson ET, Carroll AL, Safranyik L (2008a) Mountain pine beetle and forest carbon feedback to climate change. *Nature*, **452**, 987–990.
- Kurz WA, Stinson G, Rampley GJ, Dymond CC, Neilson ET (2008b) Risk of natural disturbances makes future contribution of Canada's forests to the global carbon cycle highly uncertain. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 1551–1555.
- Kurz WA, Dymond CC, White TM, Stinson G, Shaw CH, Rampley GJ, Apps MJ (2009) CBM-CFS3: a model of carbon-dynamics in forestry and land-use change implementing IPCC standards. *Ecological Modelling*, **220**, 480–504.
- Le Quere C, Raupach MR, Canadell JG, Marland G, Bopp L, Ciais P, Woodward FI (2009) Trends in the sources and sinks of carbon dioxide. *Nature Geoscience*, **2**, 831–836.
- Leckie DG, Ostaf DP (1988) Classification of airborne multispectral scanner data for mapping current defoliation caused by the spruce budworm. *Forest Science*, **34**, 259–275.
- Leckie DG, Jay C, Gougeon FA, Sturrock RN, Paradine D (2004) Detection and assessment of trees with *Phellinus weirii* (laminated root rot) using high resolution multi-spectral imagery. *International Journal of Remote Sensing*, **25**, 793–818.
- Littke WR, Browning JE (1989) *Heterobasidion* (Fomes) *annosum* incidence in pre-commercially thinned coastal Washington western hemlock stands. In: *Proceedings of the Symposium on Research and Management of Annosus Root Disease (Heterobasidion annosum) in Western North America* (eds Orosina WJ, Scharpf RF). Pacific Southwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture, Monterey, CA.
- Litvak M, Miller S, Wofsy SC, Goulden M (2003) Effect of stand age on whole ecosystem CO₂ exchange in the Canadian boreal forest. *Journal of Geophysical Research*, **108**, doi: 10.1029/2001JD000854.
- Logan JA, Powell JA (2001) Ghost forests, global warming and the mountain pine beetle (Coleoptera: Scolytidae). *American Entomologist*, **47**, 160–173.
- Logan JA, White P, Bentz BJ, Powell JA (1998) Model analysis of spatial patterns in mountain pine beetle outbreaks. *Theoretical Population Biology*, **53**, 236–255.
- Logan J, Régnière J, Powell JA (2003) Assessing the impacts of global warming on forest pest dynamics. *Frontiers in Ecology and the Environment*, **1**, 130–137.
- Lombardero MJ, Ayres MP, Ayres BD (2006) Effects of fire and mechanical wounding on *Pinus resinosa* resin defenses, beetle attacks, and pathogens. *Forest Ecology and Management*, **225**, 349–358.
- Loo J (2009) Ecological impacts of non-indigenous invasive fungi as forest pathogens. *Biological Invasions*, **11**, 81–96.
- Loomis RC, Tucker S, Hofacker TH (1985) *Insect and Disease Conditions in the United States 1979–1983*. U. S. Department of Agriculture, Washington, DC.
- Lovett GM, Canham CD, Arthur MA, Weathers KC, Fitzhugh RD (2006) Forest ecosystem responses to exotic pests and pathogens in eastern North America. *BioScience*, **56**, 395–405.
- Lovett GM, Arthur MA, Weathers KC, Griffin JM (2010) Long-term changes in forest carbon and nitrogen cycling caused by an introduced pest/pathogen complex. *Ecosystems*, **13**, 1188–1200.
- Luque J, Cohen M, Save R, Biel C, Alvarez IF (1999) Effects of three fungal pathogens on water relations, chlorophyll fluorescence and growth of *Quercus suber* L. *Annals of Forest Science*, **56**, 19–26.
- MacLean DA, Ebert P (1999) The impact of hemlock looper (*Lambdina fiscellaria* fiscellaria (Guen.)) on balsam fir and spruce in New Brunswick, Canada. *Forest Ecology and Management*, **120**, 77–87.
- MacLean DA, MacKinnon WE (1996) Accuracy of aerial sketch-mapping estimates of spruce budworm defoliation in New Brunswick. *Canadian Journal of Forest Research*, **26**, 2099–2108.
- MacLean DA, Erdle TA, MacKinnon WE, Porter KB, Beaton KP, Cormier G, Budd M (2001) The spruce budworm decision support system: forest protection planning to sustain long-term wood supply. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere*, **31**, 1742–1757.
- Magarey RD, Fowler GA, Borchert DM, Sutton TB, Colunga-Garcia M, Simpson JA (2007) NAPPFAST: an internet system for the weather-based mapping of plant pathogens. *Plant Disease*, **91**, 336–345.
- Mainwaring DB, Maguire DA, Kanaskie J, Brandt J (2005) Growth responses to commercial thinning in Douglas-fir stands with varying intensity of Swiss needle cast. *Canadian Journal of Forest Research*, **35**, 2394–2402.
- Man R, Rice JA (2010) Response of aspen stands to forest tent caterpillar defoliation and subsequent overstory mortality in northwestern Ontario, Canada. *Forest Ecology and Management*, **26**, 1853–1860.
- Manion PD, Lachance D (1992) *Forest Decline Concepts*. APS Press, St. Paul, MN.
- Manter DK, Bond BJ, Kavanagh KL, Stone JK, Filip GM (2003) Modelling the impacts of the foliar pathogen, *Phaeocryptopus gaumnianii*, on Douglas-fir physiology: net canopy carbon assimilation, needle abscission and growth. *Ecological Modelling*, **164**, 211–226.
- Manter DK, Reeser PW, Stone JK (2005) A climate-based model for predicting geographic variation in Swiss needle cast severity in the Oregon Coast Range. *Phytopathology*, **95**, 1256–1265.
- Marosy M, Parmeter JR (1989) The incidence and impact of *Heterobasidion annosum* on pine and incense-cedar in California forests. In: *Proceedings of the Symposium on Research and Management of Annosus Root Disease (Heterobasidion annosum) in Western North America* (eds Orosina WJ, Scharpf RF). Pacific Southwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture, Monterey, CA.
- Mayfield AE, Allen DC, Briggs RD (2005) Radial growth impact of pine false webworm defoliation on eastern white pine. *Canadian Journal of Forest Research*, **35**, 1071–1086.
- McConnell TJ, Johnson EW, Burns B (2000) *A guide to conducting aerial sketchmapping surveys*. FHTE 00-01. U.S. Department of Agriculture, Forest Service, Fort Collins, CO.
- McDowell N, Pockman WT, Allen CD, Breshears DD, Cobb N, Kolb T, Yezpe EA (2008) Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? *New Phytologist*, **178**, 719–739.
- Meinzer FC, Woodruff DR, Shaw DC (2004) Integrated responses of hydraulic architecture, water and carbon relations of western hemlock to dwarf mistletoe infection. *Plant, Cell and Environment*, **27**, 937–946.
- le Mellec A, Michalzik B (2008) Impact of a pine lappet (*Dendrolimus pini*) mass outbreak on C and N fluxes to the forest floor and soil microbial properties in a Scots pine forest in Germany. *Canadian Journal of Forest Research*, **38**, 1829–1841.
- le Mellec A, Habermann M, Michalzik B (2009) Canopy herbivory altering C to N ratios and soil input patterns of different organic matter fractions in a Scots pine forest. *Plant and Soil*, **325**, 255–262.
- Michaelian M, Hogg EH, Hall RJ, Arsenault E (2011) Massive mortality of aspen following severe drought along the southern edge of the Canadian boreal forest. *Global Change Biology*, **17**, 2084–2094.
- Mielke JL (1950) Rate of deterioration of beetle-killed Engelmann spruce. *Journal of Forestry*, **48**, 882–888.
- Mitchell RG, Preisler HK (1998) Fall rate of lodgepole pine killed by mountain pine beetle in central Oregon. *Western Journal of Applied Forestry*, **13**, 23–26.
- Moorcroft PR, Pacala SW, Lewis MA (2006) Potential role of natural enemies during tree range expansions following climate change. *Journal of Theoretical Biology*, **241**, 601–616.
- Morehouse K, Johns T, Kaye J, Kaye A (2008) Carbon and nitrogen cycling immediately following bark beetle outbreaks in southwestern ponderosa pine forests. *Forest Ecology and Management*, **255**, 2698–2708.
- Morrison DJ, Mallet KI (1996) Silvicultural management of *Armillaria* root disease in western Canadian forests. *Canadian Journal of Forest Research*, **18**, 194–199.
- Morrison DJ, Fellow KW, Norris DJ, Nemeck AFL (2000) Visible versus actual incidence of *Armillaria* root disease in juvenile coniferous stands in the southern interior of British Columbia. *Canadian Journal of Forest Research*, **30**, 405–414.
- Natural Resources Canada (2009a) *Forest Pest Management Forum: Proceedings of the Forest Pest Management Forum*. Canadian Forest Service, Gatineau, QC.
- Natural Resources Canada (2009b) *Statistical data – Canada's forests*. Available at <http://canadaforests.nrcan.gc.ca/statsprofile/forest/ca> (accessed 11 August 2011).

- Neary DG, Ryan KC, DeBano LF (2005) *Wildland fire in ecosystems: effects of fire on soils and water*. Gen. Tech. Rep. RMRS-GTR-42, Vol 4. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ogden, UT.
- Nelson RF (1983) Detecting forest canopy change due to insect activity using Landsat MSS. *Photogrammetric Engineering and Remote Sensing*, **49**, 1303–1314.
- Neuenschwander LF, Byler JW, Harvey AE, McDonald GI, Ortiz DS, Osborne HL, Zack A (1999) *White pine in the American West: a vanishing species—Can we save it?* Gen. Tech. Rep. RMRS-GTR-35. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ogden, UT.
- Nuckolls AE, Wurzbarger N, Ford CR, Hendrick RL, Vose JM, Kloepfel BD (2009) Hemlock declines rapidly with hemlock woolly adelgid infestation: Impacts on the carbon cycle of southern Appalachian forests. *Ecosystems*, **12**, 179–190.
- Odum EP (1969) Strategy of ecosystem development. *Science*, **164**, 262–270.
- Papaik MJ, Canham CD, Latty EF, Woods KD (2005) Effects of an introduced pathogen on resistance to natural disturbance: beech bark disease and windthrow. *Canadian Journal of Forest Research*, **35**, 1832–1843.
- Parker TJ, Clancy KM, Mathiasen RL (2006) Interactions among fire, insects and pathogens in coniferous forests of the interior western United States and Canada. *Agricultural and Forest Entomology*, **8**, 167–189.
- Peltzer DA, Allen RB, Lovett GM, Whitehead D, Wardle DA (2010) Effects of biological invasions on forest carbon sequestration. *Global Change Biology*, **16**, 732–746.
- Peifer EM, Hicke JA, Meddens AJH (2011) Observations and modeling of above-ground tree carbon stocks and fluxes following a bark beetle outbreak in the western United States. *Global Change Biology*, **17**, 339–350.
- Poland TM, McCullough DG (2006) Emerald ash borer: invasion of the urban forest and the threat to North America's ash resource. *Journal of Forestry*, **104**, 118–124.
- Powers HR Jr, Schmidt RA, Snow GA (1981) Current status and management of fusiform rust on southern pines. *Annual Review of Phytopathology*, **19**, 353–371.
- Pu R, Kelly M, Anderson GL, Gong P (2008) Using CASI hyperspectral imagery to detect mortality and vegetation stress associated with a new hardwood forest disease. *Photogrammetric Engineering and Remote Sensing*, **74**, 65–75.
- Radeloff VC, Mladenoff DJ, Boyce MS (1999) Detecting jack pine budworm defoliation using spectral mixture analysis: separating effects from determinants. *Remote Sensing of Environment*, **69**, 156–169.
- Raffa KF, Aukema BH, Bentz BJ, Carroll AL, Hicke JA, Turner MG, Romme WH (2008) Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. *BioScience*, **58**, 501–517.
- Raffa KF, Berryman AA (1987) Interacting selective pressures in conifer-bark beetle systems: a basis for reciprocal adaptations? *American Naturalist*, **129**, 234–262.
- Régnière J, Bentz B (2007) Modeling cold tolerance in the mountain pine beetle, *Dendroctonus ponderosae*. *Journal of Insect Physiology*, **53**, 559–572.
- Régnière J, Nealis V, Porter K (2009) Climate suitability and management of the gypsy moth invasion into Canada. *Biological Invasions*, **11**, 135–148.
- Roe AL, Amman GD (1970) *The mountain pine beetle in lodgepole pine forests*. Research Paper INT-71. USDA Forest Service, Intermountain Forest and Range Experiment Station, Ogden, UT.
- Rogan J, Miller J, Wulder MA, Franklin SE (2006) Integrating GIS and remotely sensed data for mapping forest disturbance and change. In: *Understanding Forest Disturbance and Spatial Pattern: Remote Sensing and GIS Approaches* (eds Wulder MA, Franklin SE), pp. 133–171. Taylor & Francis (CRC Press), Boca Raton, FL.
- Romme WH, Clement J, Hicke J, Kulakowski D, MacDonald LH, Schoennagel TL, Veblen TT (2006) *Recent Forest Insect Outbreaks and Fire Risk in Colorado Forests: A Brief Synthesis of Relevant Research*. Colorado Forest Restoration Institute, Colorado State University, Fort Collins, CO.
- Romme WH, Knight DH, Yavitt JB (1986) Mountain pine beetle outbreaks in the Rocky Mountains: regulators of primary productivity. *American Naturalist*, **127**, 484–494.
- Salinas-Moreno Y, Ager A, Vargas CF, Hayes JL, Zuniga G (2010) Determining the vulnerability of Mexican pine forests to bark beetles of the genus *Dendroctonus* Erichson (Coleoptera: Curculionidae: Scolytinae). *Forest Ecology and Management*, **260**, 52–61.
- Schäfer KVR, Clark KL, Skowronski N, Hamerlynck EP (2010) Impact of insect defoliation on forest carbon balance as assessed with a canopy assimilation model. *Global Change Biology*, **16**, 546–560.
- Schimel DS, House JJ, Hibbard KA, Bousquet P, Ciais P, Peylin P, Wirth C (2001) Recent patterns and mechanisms of carbon exchange by terrestrial ecosystems. *Nature*, **414**, 169–172.
- Schmidt RA, Holley RC, Klapproth MC, Miller T (1986) Temporal and spatial patterns of fusiform rust epidemics in young plantations of susceptible and resistant slash and loblolly pines. *Plant Disease*, **70**, 661–666.
- Schmitz RF, Gibson KE (1996) *Douglas-fir Beetle*. Forest Insect & Disease Leaflet 5. USDA Forest Service, Washington, DC.
- Seidl R, Rammer W, Jager D, Lexer MJ (2008) Impact of bark beetle (*Ips typographus* L.) disturbance on timber production and carbon sequestration in different management strategies under climate change. *Forest Ecology and Management*, **256**, 209–220.
- Shore TL, Riel BC, Safranyik L, Fall A (2006) Decision support systems. In: *The Mountain Pine Beetle: A Synthesis of Biology, Management, and Impacts on Lodgepole Pine* (eds Safranyik L, Wilson WR), pp. 193–230. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, BC.
- Shore TL, Safranyik L (1992) *Susceptibility and risk rating systems for the mountain pine beetle in lodgepole pine stands*. BC-X-336. Forestry Canada, Pacific and Yukon Region, Pacific Forestry Centre, Victoria, BC.
- Simard M, Powell EN, Griffin JM, Raffa KF, Turner MG (2008) *Annotated Bibliography for Forest Managers on Fire-Bark Beetle Interactions*.
- Sinclair WA, Lyon HH, Johnson WT (2005) *Diseases of Trees and Shrubs*. Cornell University Press, Ithaca, NY.
- Singh P (1993) Research and management strategies for major tree diseases in Canada: synthesis .1. *Forestry Chronicle*, **69**, 151–162.
- Six DL, Wingfield MJ (2011) The role of phytopathogenicity in bark beetle-fungus symbioses: A challenge to the classic paradigm. *Annual Review of Entomology*, **56**, 255–272.
- Stinson G, Kurz WA, Smyth CE, Neilson ET, Dymond CC, Metsaranta JM, Blain D (2011) An inventory-based analysis of Canada's managed forest carbon dynamics, 1990 to 2008. *Global Change Biology*, **17**, 2227–2244.
- Stone JK, Coop LB, Manter DK (2008) Predicting effects of climate change on Swiss needle cast disease severity in Pacific Northwest forests. *Canadian Journal of Plant Pathology-Revue Canadienne De Phytopathologie*, **30**, 169–176.
- Sturrock RN, Frankel SJ, Brown AV, Hennon PE, Kliejunas JT, Lewis KJ, Woods AJ (2011) Climate change and forest diseases. *Plant Pathology*, **60**, 133–149.
- Sturtevant BR, Gustafson EJ, Li W, He HS (2004) Modeling biological disturbances in LANDIS: a module description and demonstration using spruce budworm. *Ecological Modelling*, **180**, 153–174.
- Sun J, Oncley SP, Burns SP, Stephens BB, Lenschow DH, Campos T, Coons T (2010) A multiscale and multidisciplinary investigation of ecosystem-atmosphere CO₂ exchange over the Rocky Mountains of Colorado. *Bulletin of the American Meteorological Society*, **91**, 209–230.
- Swetnam TW, Lynch AM (1993) Multicentury, regional-scale patterns of western spruce budworm outbreaks. *Ecological Monographs*, **63**, 399–424.
- Tauber MJ, Tauber CA, Masaki S (1986) *Seasonal Adaptations of Insects*. Oxford University Press, New York.
- Taylor SL, MacLean DA (2008) Validation of spruce budworm outbreak history developed from aerial sketch mapping of defoliation in New Brunswick. *Northern Journal of Applied Forestry*, **25**, 139–145.
- Thompson MT (2009a) Analysis of conifer mortality in Colorado using Forest Inventory and Analysis's annual forest inventory. *Western Journal of Applied Forestry*, **24**, 193–197.
- Thompson MT (2009b) Mountain pine beetle infestations and sudden aspen decline in Colorado: can the Forest Inventory and Analysis annual inventory system address the issues? In: *Forest Inventory and Analysis (FIA) Symposium 2008* (eds McWilliams W, Moisen G, Czaplowski R). U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Park City, UT.
- Thomson AJ, Shepherd RF, Harris JWE, Silversides RH (1984) Relating weather to outbreaks of western spruce budworm, *Choristoneura occidentalis* (Lepidoptera, Tortricidae), in British Columbia. *Canadian Entomologist*, **116**, 375–381.
- Tkacz BM, Hansen EM (1982) Damage by laminated root rot in two succeeding stands of Douglas-fir. *Journal of Forestry*, **80**, 788–791.
- Tran JK, Ylloja T, Billings RF, Regniere J, Ayres MP (2007) Impact of minimum winter temperatures on the population dynamics of *Dendroctonus frontalis*. *Ecological Applications*, **17**, 882–899.
- Turetsky MR, Kane ES, Harden JW, Ottmar RD, Manies KL, Hoy E, Kasischke ES (2011) Recent acceleration of biomass burning and carbon losses in Alaskan forests and peatlands. *Nature Geoscience*, **4**, 27–31.
- USDA Forest Service (2000) *Forest Insect and Disease Conditions in the United States 1999*. USDA Forest Service, Forest Health Protection, Washington, DC.
- USDA Forest Service (2002) *Major Forest Insect and Disease Conditions in the United States 2000*. USDA Forest Service, Forest Health Protection, Washington, DC.
- USDA Forest Service (2003a) *Forest Insect and Disease Conditions in the Rocky Mountain Region, 2002*. USDA Forest Service, Forest Health Protection, Washington, DC.
- USDA Forest Service (2003b) *Forest Insect and Disease Conditions in the United States 2001*. USDA Forest Service, Forest Health Protection, Washington, DC.

- USDA Forest Service (2004) *Forest Insect and Disease Conditions in the United States, 2003*. USDA Forest Service, Forest Health Protection, Washington, DC.
- USDA Forest Service (2005) *Forest Insect and Disease Conditions in the United States 2004*. USDA Forest Service, Forest Health Protection, Washington, DC.
- USDA Forest Service (2006) *Forest Insect and Disease Conditions in the United States, 2005*. USDA Forest Service, Forest Health Protection, Washington, DC.
- USDA Forest Service (2007) *Forest Insect and Disease Conditions in the United States 2006*. USDA Forest Service, Forest Health Protection, Washington, DC.
- USDA Forest Service (2009a) *Major Forest Insect and Disease Conditions in the United States 2007*. USDA Forest Service, Forest Health Protection, Washington, DC.
- USDA Forest Service (2009b) *Major Forest Insect and Disease Conditions in the United States: 2008 Update*. FS-933. USDA Forest Service, Forest Health Protection, Washington, DC.
- USDA Forest Service (2010) *Major Forest Insect and Disease Conditions in the United States: 2009 Update*. FS-952. USDA Forest Service, Forest Health Protection, Washington, DC.
- van Mantgem PJ, Stephenson NL, Byrne JC, Daniels LD, Franklin JF, Fule PZ, Veblen TT (2009) Widespread increase of tree mortality rates in the western United States. *Science*, **323**, 521–524.
- Venette RC, Cohen SD (2006) Potential climatic suitability for establishment of *Phytophthora ramorum* within the contiguous United States. *Forest Ecology and Management*, **231**, 18–26.
- Vogelmann JE, Tolk B, Zhu ZL (2009) Monitoring forest changes in the southwestern United States using multitemporal Landsat data. *Remote Sensing of Environment*, **113**, 1739–1748.
- Volney WJA (1994) *Jack pine budworm*. Forest Leaflet 32. Natural Resources Canada, Canadian Forest Service, Northwest Region, Northern Forestry Centre, Edmonton, AB.
- Volney WJA, Fleming RA (2000) Climate change and impacts of boreal forest insects. *Agriculture Ecosystems & Environment*, **82**, 283–294.
- Wallin KF, Raffa KF (2001) Effects of folivory on subcortical plant defenses: can defense theories predict interguild processes? *Ecology*, **82**, 1387–1400.
- Watt MS, Kriticos DJ, Alcaraz S, Brown AV, Leriche A (2008) The hosts and potential geographic range of *Dothistroma* needle blight. *Forest Ecology and Management*, **257**, 1505–1519.
- Wilder JW (1999) A predictive model for gypsy moth population dynamics with model validation. *Ecological Modelling*, **116**, 165–181.
- Williams DL, Nelson RF (1986) Use of remotely sensed data for assessing forest stand conditions in the eastern United States. *IEEE Transactions on Geoscience and Remote Sensing*, **24**, 130–138.
- Woods A, Coates KD, Hamann AH (2005) Is an unprecedented *Dothistroma* needle blight epidemic related to climate change? *BioScience*, **55**, 761–769.
- Worrall JJ, Egeland L, Eager T, Mask RA, Johnson EW, Kemp PA, Shepperd WD (2008) Rapid mortality of *Populus tremuloides* in southwestern Colorado, USA. *Forest Ecology and Management*, **255**, 686–696.
- Worrall JJ, Marchetti SB, Egeland L, Mask RA, Eager T, Howell B (2010) Effects and etiology of sudden aspen decline in southwestern Colorado, USA. *Forest Ecology and Management*, **260**, 638–648.
- Wulder MA, Dymond CC, White JC, Leckie DG, Carroll AL (2006) Surveying mountain pine beetle damage of forests: a review of remote sensing opportunities. *Forest Ecology and Management*, **221**, 27–41.
- Wygant ND (1940) *Effects of Low Temperature on the Black Hills Beetle (Dendroctonus ponderosae Hopkins)*. PhD dissertation, State College of New York, Syracuse, NY.
- Yi C, Anderson DE, Turnipseed AA, Burns SP, Sparks JP, Stannard DI, Monson RK (2008) The contribution of advective fluxes to net ecosystem exchange in a high-elevation, subalpine forest. *Ecological Applications*, **18**, 1379–1390.
- Zhu Z, Evans DL (1994) U.S. forest types and predicted percent forest cover from AVHRR data. *Photogrammetric Engineering and Remote Sensing*, **60**, 525–531.